

Plan de rapport final d'un projet de recherche financé dans le cadre du plan Écophyto II+

ESPRES : Evaluation du Service de Pollinisation dans des territoires en REduction d'utilisation de pesticides et interaction avec le Service de régulation des ravageurs



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Plan Ecophyto II+ – Volet 2 de l'Appel à projets national
2020 – 2021 »

***Synthèse pour les décideurs [Alice Michelot-Antalik,
Thibault Gandara, Antoine Gardarin et Emmanuelle
Porcher]***

Date de la version du rapport : 12/11/2025

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Action pilotée par les Ministères chargés de la Transition écologique, de la Biodiversité, de la Forêt, de la Mer et de la Pêche (MTEBFMP), de l'Agriculture et de la Souveraineté Alimentaire (MASA), du Travail, de la Santé, des Solidarités et des Familles (MTSSF), et de l'Education nationale, de l'Enseignement supérieur et de la Recherche (MENESR) avec l'appui financier de l'Office Français pour la Biodiversité (OFB), par les crédits issus de la redevance pour pollutions diffuses attribués au plan Écophyto II+.

Table des matières

SYNTHÈSE.....	4
Contexte général et enjeux scientifiques et techniques.....	5
Objectifs généraux du projet	5
Quelques éléments de méthodologie (et difficultés éventuelles rencontrées).....	5
Résultats obtenus	8
Implications pratiques, recommandations, réalisations pratiques, valorisation	11
Réalisations pratiques et valorisation	14
Partenariats mis en place, projetés, envisagés.....	14
Pour en savoir plus (quelques références)	15
Liste des opérations de valorisations issues du contrat (articles de valorisation, participation à des colloques, enseignement et formation, communication, expertises...).....	16
Résumés	18
RAPPORT SCIENTIFIQUE.....	21
1. Contexte général et enjeux scientifiques et techniques.....	22
2. Objectifs et questions de recherche	22
3. Matériels et méthodes.....	23
4. Résultats	27
5. Discussion	32
6. Limites et perspectives	33

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SYNTHÈSE



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Contexte général et enjeux scientifiques et techniques

La pollinisation est un service crucial pour l'agriculture dont dépend la majorité des cultures et l'un des plus vulnérables aux pesticides. Elle reste peu étudiée à l'échelle territoriale en raison de la difficulté de mise en œuvre des méthodes de mesure existantes sur de grandes étendues spatiales. C'est pourtant un service de premier plan pour penser la réduction, voire la sortie complète, de l'usage des pesticides. En effet, pour les cultures dépendantes des pollinisateurs, d'éventuelles pertes de rendement associées à un moindre usage de pesticides pourraient être compensées par des communautés de pollinisateurs plus abondantes et efficaces que dans les espaces agricoles soumis à forte pression phytosanitaire. Pour tester cette prédiction, il faut donc être capable (1) de mesurer l'efficacité de la pollinisation des cultures sur de grandes étendues spatiales, (2) de caractériser la relation entre pollinisation et usage des pesticides, et (3) de comprendre la relation entre la pollinisation et d'autres régulations biologiques, notamment la régulation biologique des ravageurs, pour laquelle les espèces impliquées peuvent utiliser en partie les mêmes ressources que les pollinisateurs. Afin d'accompagner la transition vers des systèmes de culture économes en pesticides, notre projet propose de tester la pertinence, à l'échelle des territoires, d'indicateurs simples à mettre en œuvre, mais développés pour le moment seulement à l'échelle nationale. Il met également en évidence le rôle des déterminants environnementaux dont l'usage des pesticides influence la fourniture de services écosystémiques que sont la pollinisation et la régulation des ravageurs.

Dans cette perspective, notre projet s'inscrit pleinement dans les objectifs du plan Écophyto II+, qui vise à réduire la consommation de produits phytopharmaceutiques et les risques associés à leur usage pour la santé humaine et l'environnement. En mettant en évidence les déterminants de la pollinisation et de la régulation des ravageurs dans les paysages de grandes cultures, il contribue à identifier des leviers écologiques permettant de diminuer la dépendance aux intrants chimiques. Les indicateurs développés pourront ainsi servir à évaluer les bénéfices d'une réduction de l'usage des pesticides, tant en termes de maintien des rendements que de préservation de la biodiversité, et à appuyer la transition vers des systèmes de culture plus résilients et économes en produits phytopharmaceutiques.

Objectifs généraux du projet

Notre projet a pour principaux objectifs de :

- 1- comparer plusieurs indicateurs de pollinisation à l'échelle d'un paysage agricole ;
- 2- analyser l'effet des pesticides et de la composition paysagère sur les pollinisateurs et la pollinisation en paysage de grandes cultures ;
- 3- comparer les services de pollinisation et de régulation des ravageurs à l'aide d'expérimentations réalisées sur des parcelles de colza.

Quelques éléments de méthodologie (et difficultés éventuelles rencontrées)

L'objectif 1 de l'étude se focalise sur la comparaison d'indicateurs de pollinisation à l'échelle d'un paysage agricole, à savoir un indicateur de "pollinisation réalisée" fondé sur les rendements des cultures, et un indicateur de "pollinisation potentielle" basé sur l'occupation du sol. Pour cet objectif, et également pour aborder l'objectif 2 liant pollinisation et déterminants agricoles et paysagers, nous avons étudié le territoire de

Fénay (Côte d'Or) qui se compose de 140 parcelles de grandes cultures contiguës (950 ha au total) gérées par 23 agriculteurs dans la plaine de Dijon, en partenariat avec l'UMR Agroécologie à Dijon. Entre 2007 et 2019, un total de 79 espèces dont 26 cultures maraîchères ont été cultivées. Les agriculteurs ont été interrogés chaque année de 2007 à 2019 pour établir un enregistrement complet des pratiques agricoles, incluant des informations détaillées sur l'usage des pesticides et le rendement de chaque parcelle. L'indice de pollinisation réalisée que nous avons calculé utilise les données de rendement des cultures et la dépendance des cultures aux pollinisateurs, c'est un indicateur direct du service de pollinisation. Sa philosophie générale est simple : elle repose sur l'hypothèse que, toutes choses égales par ailleurs, dans un site avec un déficit de pollinisation, le rendement des cultures dépendantes des pollinisateurs devrait être inférieur, en moyenne, au rendement des cultures non-dépendantes des pollinisateurs. L'indicateur de pollinisation réalisée est alors calculé comme la pente de la régression linéaire entre les rendements des cultures -préalablement standardisés- et la dépendance des cultures aux pollinisateurs, dans un site d'intérêt (un département, une parcelle agricole...). Pour l'indicateur de pollinisation potentielle nous avons sélectionné le modèle InVEST (Sharp et al., 2018). Ce modèle est une mesure indirecte basée sur les ressources végétales sauvages et cultivées pour les pollinisateurs et sur la connaissance des sites de nidification pour les pollinisateurs. L'indicateur de pollinisation potentielle estime l'abondance des pollinisateurs selon les modes d'occupation des sols plus ou moins favorables aux pollinisateurs. Une comparaison entre l'indicateur de pollinisation réalisée et l'indicateur de pollinisation potentielle a été réalisée, explorant différentes résolutions spatiales d'analyse. Des analyses statistiques ont permis de quantifier les corrélations entre les deux indicateurs et d'évaluer l'effet de l'usage des pesticides (estimés par l'indice de fréquence de traitement) sur l'indicateur de pollinisation réalisée.

Sur le territoire de grandes cultures du bassin parisien (dispositif Scarabée), nous n'avons pas pu aborder l'objectif 1 de comparaison des indicateurs, car nous n'avons pas pu calculer l'indicateur de pollinisation réalisée du fait de données de rendements non disponibles en nombre suffisant. Nous nous sommes donc concentrés sur les déterminants environnementaux (pratiques et paysage) de la pollinisation (objectif 2), ainsi que sur sa relation avec le service de régulation (objectif 3). Le réseau d'agriculteurs « Scarabée » est réparti entre l'Eure-et-Loir (28), l'Essonne (91) et les Yvelines (78). Il est suivi par l'UMR Agronomie depuis 2018. L'utilisation de produits phytosanitaires est contrastée selon les parcelles ce qui permet d'étudier l'effet de leur réduction sur les services de régulation. Le travail avec les agriculteurs de ce réseau offre des échanges facilités et des données déjà disponibles concernant les itinéraires techniques. Au total, 41 parcelles de colza ont été sélectionnées dans quatre types de paysages distincts (**fig. 1**), en fonction de deux gradients indépendants : (1) la proportion d'éléments semi-naturels présents dans un rayon de 1000 mètres autour de chaque parcelle, et (2) le niveau d'utilisation de pesticides dans les parcelles, déterminé à partir d'entretiens menés avec les agriculteurs. Ces gradients ont été choisis en raison de leur influence reconnue sur les dynamiques des populations de pollinisateurs et d'auxiliaires des cultures.

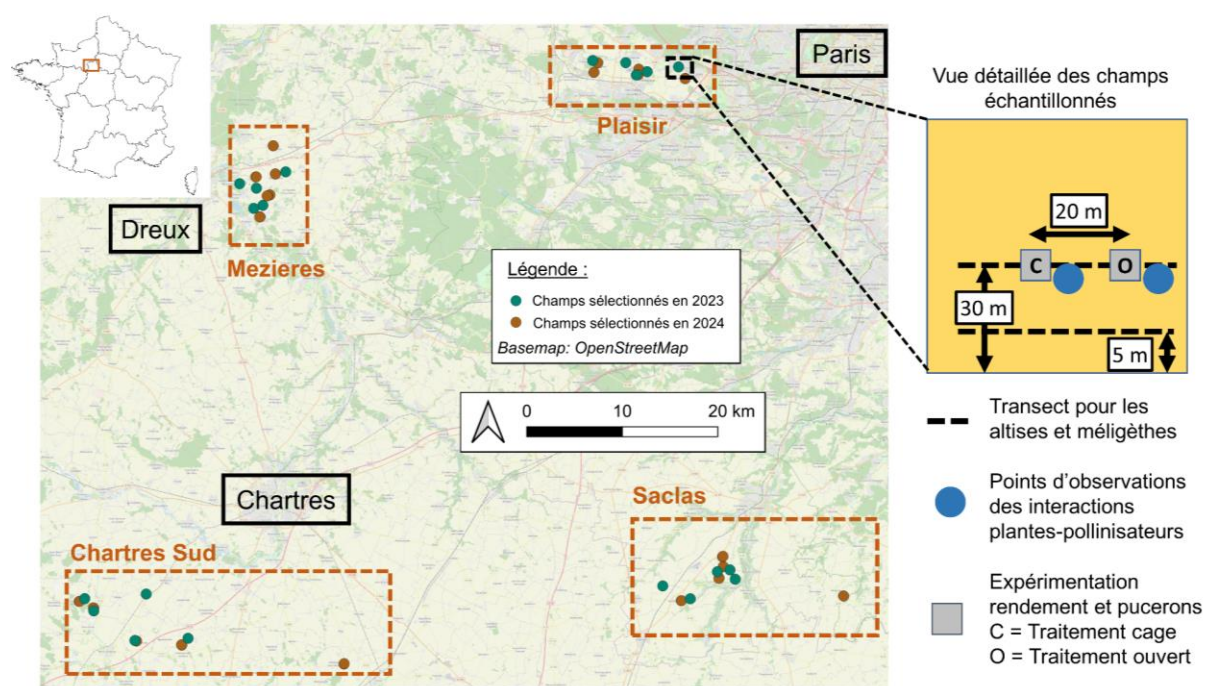


Figure 1. Localisation des parcelles de colza suivies sur Scarabée et vue détaillée du dispositif expérimental mis en place en 2023 sur chaque parcelle ; adapté de Gandara, 2025.

Sur 20 parcelles de colza en 2023, nous avons installé un dispositif d'exclusion des insectes pour comparer le rendement avec et sans pollinisateurs. Nous avons observé les groupes de pollinisateurs visitant les fleurs de colza mais également les fleurs des bordures herbacées de parcelles céréalières dans un rayon de 500 m et 1000 m autour des parcelles de colza durant les mois d'avril et mai (méthode non létale). Nous avons disposé des plants de fraisiers à 500 et 1000 m de chaque parcelle de colza afin de mesurer le service de pollinisation par le poids des fraises au mois de mai. En effet, les fraisiers sont appelés plantes phytomètres car ils dépendent de la pollinisation des insectes pour produire des graines et des fruits. En installant des fraisiers avec des filets pour exclure les insectes et d'autres sans filets, nous pouvons ainsi mesurer le différentiel de pollinisation avec ou sans pollinisateurs. En 2024, nous avons refait des observations de pollinisateurs avec la même méthode autour de 21 nouvelles parcelles de colza prises dans les mêmes paysages agricoles et nous avons réinstallé des fraisiers en plus grand nombre sur deux paysages parmi les quatre étudiés. Des analyses statistiques nous ont ensuite permis de déterminer les effets des pesticides et de la composition paysagère (déterminants environnementaux) sur les communautés de pollinisateurs visitant les colzas, les bandes enherbées et les fraisiers. Des comparaisons ont été réalisées entre nos différentes mesures de la pollinisation et nous avons identifié leurs déterminants environnementaux via des modèles statistiques.

En parallèle du suivi de pollinisateurs, pour réaliser une comparaison avec le service de régulation biologique (objectif 3), nous avons mesuré en avril 2023 et 2024 le taux de parasitisme des méligèthes et des altises sur les mêmes parcelles de colza que pour l'objectif 2. Nous avons également quantifié les pucerons présents dans les cages d'exclusion et hors des cages d'exclusion du colza en 2023 pour avoir une estimation

de leur régulation par les ennemis naturels car il n'y a pas de régulation dans les cages. Ces mesures nous ont permis de voir si le service de pollinisation et de régulation des ravageurs étaient corrélés entre eux et d'analyser leurs déterminants environnementaux respectifs par des modèles statistiques.

Résultats obtenus

1. Comparaison d'indicateurs de pollinisation sur le territoire de Fénay

Grâce aux données pluriannuelles de rendement collectées sur chaque parcelle du territoire de Fénay, nous avons pu calculer l'indicateur de pollinisation réalisée. Les deux indicateurs de pollinisation (réalisée et potentielle) déclinés spatialement avec la méthode des fenêtres glissantes sur le territoire de Fénay sont représentés sur la **figure 2**. Ils présentent le même gradient est-ouest. Ainsi, à l'échelle du paysage, l'indice de pollinisation réalisée est positivement corrélé à l'indice de pollinisation potentielle, révélant le rôle positif des éléments semi-naturels (pris en compte dans l'indicateur de pollinisation potentielle) pour la pollinisation des cultures. De plus, ses variations temporelles sont fortement corrélées à celles observées aux échelles régionale ou nationale. Les corrélations entre ces deux indices ne sont toutefois pas complètes, révélant des déterminants de la pollinisation réalisée au-delà des seules ressources prises en compte dans le calcul de l'indicateur de pollinisation potentielle. À l'échelle de la parcelle, l'indicateur de pollinisation réalisée est négativement corrélé à l'utilisation de pesticides. Ces résultats suggèrent que cet indicateur basé sur le rendement reflète avec précision la variation des services de pollinisation à travers les paysages, en intégrant les effets de la composition du paysage, ainsi que les effets plus locaux de l'usage des pesticides. Cet indice pourrait constituer un outil inédit pour mettre en œuvre une évaluation de la pollinisation, depuis les parcelles individuelles jusqu'à une échelle plus large comme celle d'un territoire ou d'une région agricole, et aider les acteurs à concevoir des paysages favorables à la biodiversité assurant efficacement la fourniture de services écosystémiques.

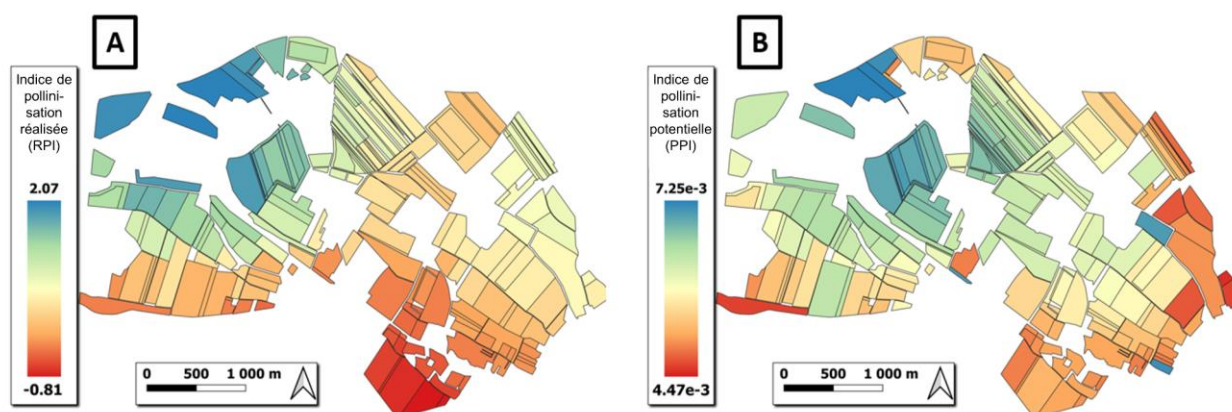


Figure 2. Comparaison de l'indice de pollinisation réalisé calculé (A) et de l'indice de pollinisation potentielle (B) sur des parcelles du territoire agricole de Fénay ; adapté de Gandara et al., (2025).

2. Effet des pesticides et de la composition paysagère sur les pollinisateurs et la pollinisation

Dans le réseau de parcelles d'agriculteurs Scarabée, le nombre de visites de tous les groupes de pollinisateurs dans les parcelles de colza, sur les fleurs des bords de champ et sur les fraisiers augmente avec la proportion d'éléments semi-naturels dans le paysage environnant (**fig. 3A**). Il augmente également avec la présence de colza cultivé l'année précédente autour de chaque site d'observation (**fig. 3B**). Le nombre de visites de pollinisateurs sur les parcelles de colza diminue avec l'utilisation des pesticides (**fig. 3C**).

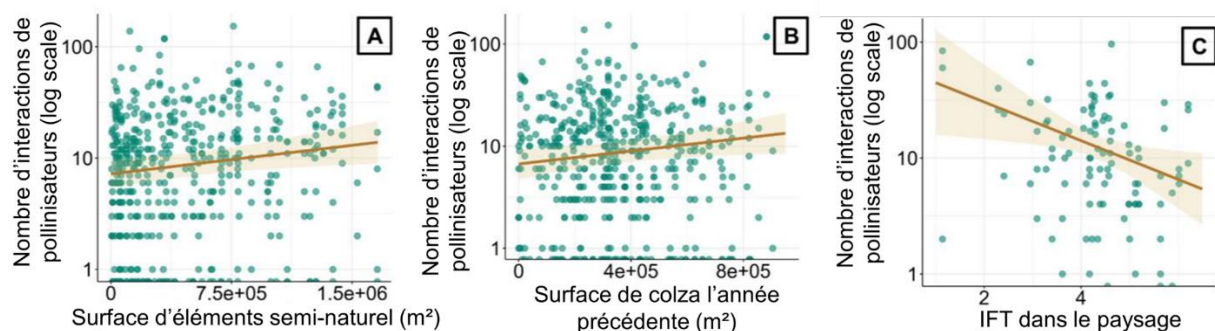


Figure 3. Effets modélisés des relations significatives entre le nombre de visites de pollinisateurs et les variables environnementales. Les figures A et B présentent les résultats pour l'ensemble des communautés de pollinisateurs et la figure C pour la communauté de pollinisateurs du colza. Les valeurs observées sont les points verts ; adapté de Gandara, 2025.

Avec les dispositifs d'exclusion, nous observons que la visite des insectes améliore significativement la production (masse et nombre de graines de colza, poids des fraises) (**fig. 4A et B**) et diminue la longueur des colonies de pucerons (**fig. 4C**). Nos modèles statistiques mettent également en évidence un effet négatif de l'utilisation des pesticides et un effet positif de la proportion en éléments semi-naturels et en colza dans le paysage environnant sur la masse des graines par pied de colza dans les dispositifs ouverts. Les déterminants environnementaux n'ont en revanche pas d'effet sur la masse ou la déformation des fraises.

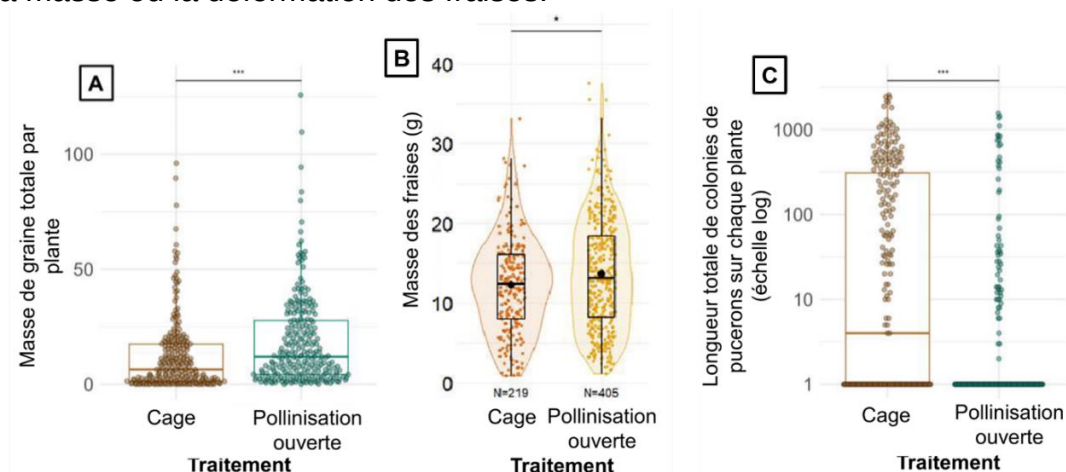


Figure 4. Effets du traitement de pollinisation (cage ou ouverte) sur la masse totale de graines par pied de colza, la masse des fraises et la longueur des colonies de pucerons par pied de colza. Les différences entre les traitements sont significatives : *** $p < 0.001$; * $p < 0.05$; adapté de Gandara, 2025.

3. Comparaison des services de pollinisation et de régulation des ravageurs sur colza et relation avec des variables locales et paysagères

Les différents services de régulation étudiés sont positivement corrélés, indiquant que les milieux favorables aux pollinisateurs peuvent aussi soutenir les ennemis naturels des ravageurs (**fig. 5**). En particulier, des relations positives significatives sont observées entre le nombre d'interactions plantes-pollinisateurs et la régulation des pucerons, des altises et des méligèthes.

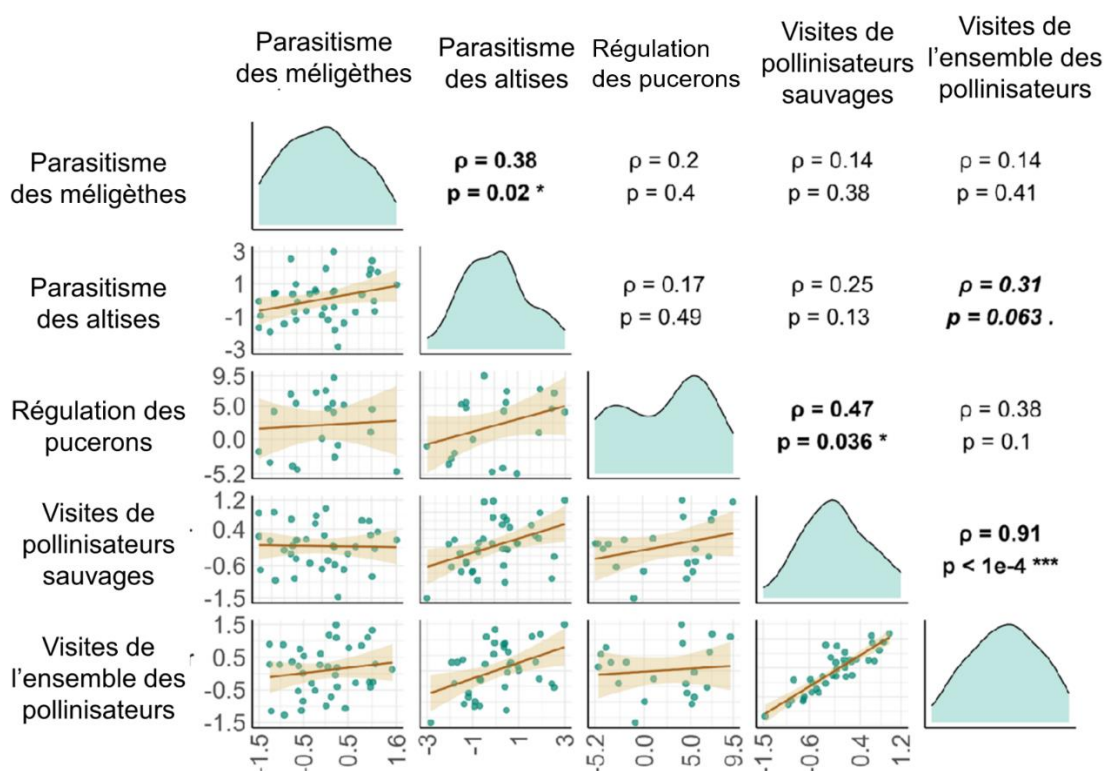


Figure 5. Corrélations par paires entre les indicateurs de services écosystémiques au niveau de la parcelle, corrigées des variables de contrôle. Les corrélations de Spearman par paires (ρ), pondérées par l'erreur standard de chaque estimation de service, sont présentées dans la partie supérieure du graphique. La partie inférieure montre les régressions linéaires non pondérées pour visualiser les tendances générales. Chaque point représente une parcelle, et les courbes dans la diagonale illustrent les histogrammes de densité pour chaque indicateur de service ; adapté de Gandara, 2025.

L'usage des pesticides (IFT) à la parcelle réduit le nombre de visites des pollinisateurs sauvages et le parasitisme des altises (**fig. 6A et C**), tandis que la surface d'éléments boisés et herbacés dans le paysage environnant augmente le nombre de visites de pollinisateurs sauvages et diminue le parasitisme des méligèthes (**fig. 6B et E**). Le parasitisme des altises est favorisé par la surface en colza de l'année précédente dans le paysage environnant (**fig. 6D**).

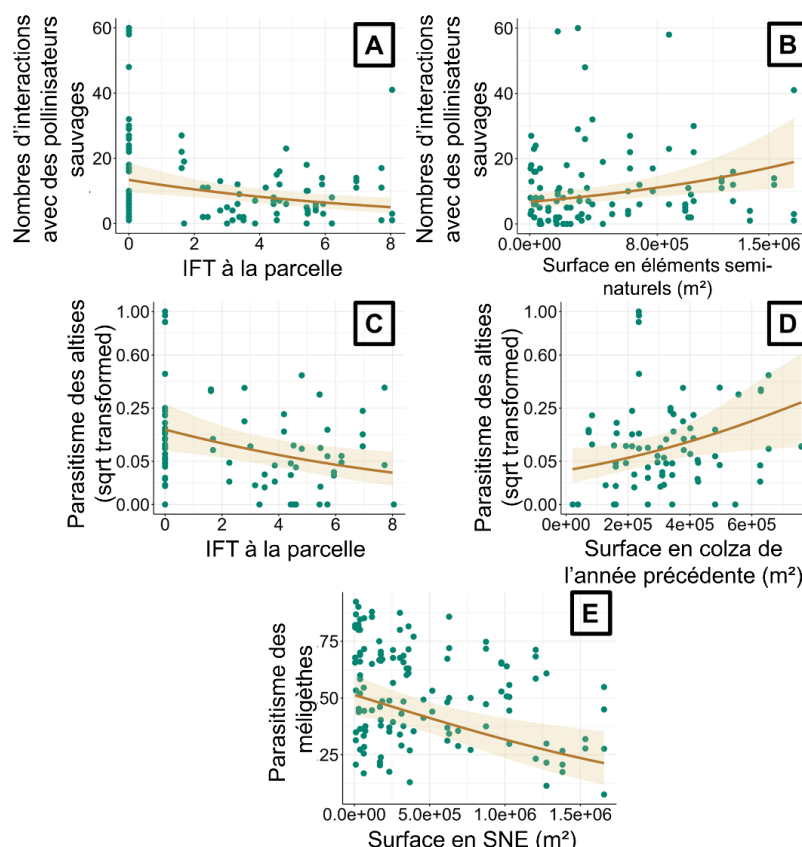


Figure 6. Effets prédits des modèles illustrant l'influence des variables paysagères et de l'indice de fréquence de traitement sur les services écosystémiques. Les valeurs observées sont représentées par les points verts ; adapté de Gandara, 2025.

Implications pratiques, recommandations, réalisations pratiques, valorisation

Implications pratiques

Le projet ESPRES a permis de valider la preuve de concept de l'utilisation d'un nouvel indice de pollinisation basé sur les rendements : celui-ci semble apporter une information à la fois cohérente avec l'autre indicateur déjà utilisé (indicateur de pollinisation potentielle), mais aussi plus riche en information car corrélé à des pratiques agricoles dans les parcelles, en plus des effets du paysage. Son application à l'échelle des territoires, pour des grandes cultures, semble donc réaliste. Cet indice permettra par la suite de proposer des recommandations d'aménagement et de pratiques à l'échelle du territoire. Le déploiement de l'indice dans d'autres territoires permettrait d'identifier aussi bien des systèmes de culture, des pratiques, ou des paysages permettant de maintenir, voire d'augmenter les rendements des cultures dépendantes des pollinisateurs dans un contexte zéro Phyto. Ce déploiement se heurte cependant à la disponibilité de données de rendement des cultures à des résolutions spatiales fines. Nous avons pour cela soumis un article dans Innovations Agronomiques pour faire connaître l'indicateur et lancer un appel pour identifier les sources de telles données.

Le projet a mis en évidence le rôle essentiel des éléments semi-naturels dans les paysages de grande culture pour favoriser le nombre de visites de pollinisateurs et le

rendement du colza et des fraisiers. Il a également mis en relief l'effet négatif de l'utilisation des pesticides, mesurée par l'IFT, sur les pollinisateurs, la pollinisation et le taux de régulation des altises. En pratique, ces résultats soulignent la nécessité de diminuer l'usage des pesticides et de mettre en place des aménagements agro-écologiques dans les paysages de grande culture. Concernant la réduction des pesticides, la diversification végétale de la parcelle au paysage semble être une voie prometteuse pour promouvoir les services de régulation (Tibi et al., 2022). Cependant, il est indispensable que cette transition soit intégrée à l'échelle des territoires et discutée avec les acteurs des systèmes agricoles afin de déverrouiller les freins au changement de pratiques. En parallèle du projet ESPRES, la thèse de Thibault Gandara s'inscrit dans le projet BE-CREATIVE (Built pEstiCide-free agRoecosystEms At Terrlitory leVEI, PPR "Cultiver et protéger autrement) qui vise à co-concevoir avec les acteurs des territoires aux pratiques innovantes avec moins de pesticides. Ces projets alliant sciences agronomiques, écologiques et diagnostics socio-territoriaux sont essentiels pour faciliter le changement de pratiques. Les indicateurs de pollinisation que nous avons développés permettent d'évaluer les pratiques mises en place dans les territoires pour savoir si elles sont favorables à l'établissement de la diversité des pollinisateurs. Les aménagements agroécologiques peuvent consister à intégrer des zones dédiées à la conservation de la biodiversité dans les paysages de grandes cultures en maintenant la connectivité des habitats afin d'assurer la durabilité des services de pollinisation et régulation des ravageurs.

Enfin, une question importante pour la multifonctionnalité des agroécosystèmes est de savoir si les contextes écologiques qui favorisent la pollinisation favorisent également la régulation des ravageurs, générant ainsi des synergies entre ces deux services. Nos résultats apportent un soutien partiel à l'existence de telles complémentarités : la pollinisation et la régulation des ravageurs sont positivement corrélées, bien que ces relations n'aient pas toujours été significatives et que leur intensité varie selon les paysages et l'intensité d'utilisation des pesticides. Ces synergies potentielles proviennent probablement du fait que les deux services sont rendus par des communautés d'insectes différentes mais qui réagissent de manière similaire aux facteurs écologiques - étant favorisées par la disponibilité de ressources florales à l'intérieur et autour des parcelles, et contraintes par l'usage de pesticides et la simplification des habitats. Dans l'ensemble, ces résultats soulignent que, bien qu'il existe des opportunités de promouvoir simultanément ces deux services, leur gestion conjointe nécessite une compréhension fine des compromis écologiques et des synergies à travers les paysages agricoles (Bartual et al., 2019) ainsi que des pratiques agricoles qui y sont associées.

Recommandations

- Déployer l'indice de pollinisation réalisé à différentes échelles spatiales et temporelles.

L'indice développé offre un outil pertinent pour évaluer la qualité des services de pollinisation à l'échelle territoriale mais également à l'échelle nationale. Son application à d'autres contextes agricoles permettra d'identifier les systèmes, pratiques et paysages favorables à la pollinisation, notamment dans des démarches de réduction des pesticides.

- Réduire l'usage des pesticides et favoriser la diversification végétale.

La diminution de l'IFT est essentielle pour restaurer les populations de pollinisateurs et d'auxiliaires de culture comme nous l'avons démontré. Les aménagements agroécologiques qui favorisent la diversité et la complémentarité des ressources florales et des sites de nidification comme les haies, les bandes fleuries, les jachères fleuries et la diminution des herbicides constituent une voie prometteuse pour renforcer les services de pollinisation et de régulation des ravageurs.

- Augmenter les analyses conjointes des services de pollinisation et de la régulation des ravageurs. Nous avons mis en évidence des synergies possibles entre ces deux services mais celles-ci sont dépendantes des contextes paysagers et des pratiques agricoles. Afin de consolider les bases scientifiques d'une gestion durable des agroécosystèmes, nous recommandons d'évaluer conjointement la pollinisation et la régulation des ravageurs dans une diversité de paysages agricoles, et d'expérimenter l'effet d'aménagements agroécologiques sur ces services clés.

Limites ou généralisations éventuelles des résultats

Dans notre travail, nous avons examiné les pratiques agricoles à travers le prisme de l'utilisation des pesticides, en reconnaissant que, conjointement avec la perte d'habitats, elles constituent les principaux moteurs du déclin de la biodiversité dans les paysages agricoles. Au-delà de l'usage des pesticides mesuré par l'indice de fréquence de traitement, les travaux futurs pourraient tirer profit de mesures plus fines, telles que des indicateurs de la toxicité des pesticides, car tous les produits n'ont pas les mêmes effets. Relier la toxicité de substances actives spécifiques, de mélanges et d'éventuels effets « cocktail » à leur utilisation sur le terrain permettrait une évaluation plus détaillée de l'impact de certains produits sur la biodiversité (Cairo et al., 2024). Une plus grande disponibilité des données concernant les doses d'application des pesticides renforcerait également la capacité à examiner ces effets en profondeur. Par ailleurs, ces effets peuvent aussi être confondus avec ceux d'autres pratiques associées. Par exemple, le travail du sol est bien connu pour avoir un fort impact sur les populations d'insectes bénéfiques, notamment les pollinisateurs, tandis que la fertilisation azotée peut influencer les pollinisateurs de manière indirecte, à travers ses effets sur les communautés végétales des champs et de leurs bordures.

Notre projet met en évidence les difficultés d'avoir une estimation des services de pollinisation à l'échelle du paysage. Nous avons ainsi identifié les limites méthodologiques des différentes approches de mesures sur le terrain. Les observations non létales de groupes de pollinisateurs ont l'avantage d'être relativement accessibles mais temporellement limitées pour avoir une quantification optimum de l'activité des pollinisateurs. L'utilisation de plantes phytomètres comme le fraisier s'est avérée difficile à mettre en place et montre des résultats contrastés sur la quantification de la pollinisation réalisée (masse des fraises et déformation). Les mesures par exclusion de pollinisateurs sur colza sont également chronophages à mettre en place sur un grand nombre de parcelles et les pieds de colza ont été en partie colonisés par les pucerons.

Une limite importante de notre étude réside dans la manière dont nous avons évalué la régulation des ravageurs. Nos mesures se sont limitées aux taux de parasitisme, sans quantifier les populations de ravageurs elles-mêmes dans les parcelles. Un cadre plus large, intégrant à la fois les pollinisateurs, les ravageurs des cultures et leurs ennemis naturels, permettrait une compréhension plus complète des paramètres

ESPRES : Evaluation du Service de Pollinisation dans des territoires en REduction d'utilisation de pesticides et interaction avec le Service de régulation des ravageurs

environnementaux et des mécanismes qui régissent la dynamique de multiples services écosystémiques simultanément, mais cela nécessiterait davantage de travail de terrain. Une telle approche semble particulièrement pertinente dans le contexte actuel d'augmentation de la résistance des ravageurs aux insecticides, d'autant plus que nos résultats mettent en évidence des impacts négatifs des pesticides sur les organismes non cibles.

Ces relations entre pollinisation et régulation des ravageurs peuvent être fortement dépendantes du contexte, ce qui limite leur généralisation, car la plupart des études, y compris la nôtre, sont menées dans des contextes spécifiques de culture et de paysage, ici dans des systèmes de monoculture intensive, où les effets locaux peuvent être fortement modulés par la composition et la configuration du paysage environnant. Cependant, la bonne corrélation entre les variations temporelles de l'indicateur de pollinisation à l'échelle d'un territoire et à l'échelle nationale suggère des potentialités de généralisation.

Réalisations pratiques et valorisation

- Gandara, T., Gardarin, A., Desaegher, J., Petit, S., Porcher, E., Michelot-Antalik, A., 2025. A crop yield-based pollination index reveals the impacts of land cover and pesticide use on realized pollination at a landscape scale. *Agriculture Ecosystems and Environment* 392, 109747. <https://doi.org/10.1016/j.agee.2025.109747>

- Manuscrit de thèse de Thibault Gandara rédigé le 13 octobre 2025 et incluant 4 chapitres sous forme d'articles scientifiques (dont un publié) : Évaluation du service de pollinisation en grandes cultures : spatialisation, déterminismes environnementaux et relation avec le service de régulation des ravageurs. *Museum National d'Histoire Naturelle*. 258 pages.

- Sirami C., Porcher E., Gandara T., Agnoux S., 2024. Agriculture et pollinisateurs : vers une nouvelle alliance ? Pour la Science <https://www.pourlascience.fr/sd/ecologie/agriculture-et-pollinisateurs-vers-une-nouvelle-alliance-26651.php>

- Porcher, E., Accatino, F., Desaegher, J., Fontaine, C., Gandara, T., Gardarin, A., Martin, G., Michelot-Antalik, A., 2025. Une méthode accessible pour évaluer la pollinisation animale des cultures, déployable de la parcelle à la France entière. *Innovations Agronomiques* (soumis).

Partenariats mis en place, projetés, envisagés

Nous avons collaboré avec différents partenaires tout au long du projet qui sont cités ci-après : Institut d'écologie et des sciences de l'environnement de Paris, Chambre d'Agriculture d'Eure-et-Loir, UMR Agroécologie Dijon, Unité de Recherche Abeilles et Environnement Avignon, DYNAFOR Toulouse.

Nous avons déposé une demande de financement à l'Observatoire National de la Biodiversité (coordonnée par Emmanuelle Porcher et Antoine Gardarin) pour valoriser notre indicateur de pollinisation réalisée. « Développement d'un indicateur de pollinisation animale dans les agroécosystèmes : perspectives temporelles et spatiales ».

ESPRES : Evaluation du Service de Pollinisation dans des territoires en REduction d'utilisation de pesticides et interaction avec le Service de régulation des ravageurs

Nous envisageons pour le déploiement de l'indicateur de pollinisation réalisée des partenariats avec les coopératives agricoles.

Pour en savoir plus (quelques références)

- Bartual, A.M., Sutter, L., Bocci, G., Moonen, A.-C., Cresswell, J., Entling, M., Giffard, B., Jacot, K., Jeanneret, P., Holland, J., Pfister, S., Pintér, O., Veromann, E., Winkler, K., Albrecht, M., 2019. The potential of different semi-natural habitats to sustain pollinators and natural enemies in European agricultural landscapes. *Agriculture, Ecosystems & Environment* 279, 43–52. <https://doi.org/10.1016/j.agee.2019.04.009>
- Cairo, M., Monnet, A.-C., Robin, S., Porcher, E., Fontaine, C., 2024. Identifying pesticide mixtures at country-wide scale. *Peer Community Journal* 4. <https://doi.org/10.24072/pcjournal.472>
- Gandara, T., 2025. Évaluation du service de pollinisation en grandes cultures : spatialisation, déterminismes environnementaux et relation avec le service de régulation des ravageurs. *Museum National d'Histoire Naturelle, Paris*, 258 p.
- Gandara, T., Gardarin, A., Desaegher, J., Petit, S., Porcher, E., Michelot-Antalik, A., 2025. A crop yield-based pollination index reveals the impacts of land cover and pesticide use on realized pollination at a landscape scale. *Agriculture, Ecosystems & Environment* 392, 109747. <https://doi.org/10.1016/j.agee.2025.109747>
- Sharp, R., Tallis, H.T., Ricketts, T., Guerry, A.D., Wood, S.A., Chaplin-Kramer, R., Nelson, E., Ennaanay, D., Wolny, S., Olwero, N., 2018. Invest 3.6. 0 user's guide. collaborative publication by the natural capital project, The Nature Conservancy, and the World Wildlife Fund. Stanford University, the University of Minnesota Stanford University
- Tibi, A., Martinet, V., Vialatte, A., Alignier, A., Angeon, V., Bohan, D., Bougherara, D., Cordeau, S., Courtois, P., Deguine, J.-P., Enjalbert, J., Fabre, F., Fréville, H., Grateau, R., Grimonprez, B., Gross, N., Hannachi, M., Launay, M., Lelievre, V., Lemarié, S., Martel, G., Navarrete, M., Plantegenest, M., Ravigné, V., Rusch, A., Suffert, F., Thoyer, S.S., 2022. Protéger les cultures en augmentant la diversité végétale des espaces agricoles. Synthèse de l'expertise scientifique collective (report). INRAE. <https://doi.org/10.17180/awsn-rf06>

Liste des opérations de valorisations issues du contrat (articles de valorisation, participation à des colloques, enseignement et formation, communication, expertises...)

PUBLICATIONS SCIENTIFIQUES	
Publications scientifiques parues	Gandara, T., Gardarin, A., Desaegher, J., Petit, S., Porcher, E., Michelot-Antalik, A., 2025. A crop yield-based pollination index reveals the impacts of land cover and pesticide use on realized pollination at a landscape scale. <i>Agriculture, Ecosystems & Environment</i> 392, 109747. https://doi.org/10.1016/j.agee.2025.109747
Publications scientifiques à paraître	
Publications scientifiques prévues	Gandara T., Michelot-Antalik A., Duarte S., Gardarin A, Porcher E. From pollinators to yield: comparing pollination measurements reveal benefits of landscape diversification and negative impact of pesticides. En préparation. Gandara T.*, Blareau E.*, Lachaise M.*, Michelot-Antalik A., Porcher E., Collard B., Gardarin A., Requier F., Dajoz I. Are strawberries reliable phytometers for studying pollination across agricultural, suburban and urban landscapes? Sera soumis à Basic and Applied Ecology en novembre-décembre 2025. *Contribution égale. Gandara T, Michelot-Antalik A., Lacoïn J., Blondeau L., Morisseau A., Le Floch D., Porcher E., Gardarin A. Pollination and conservation biological control are positively correlated but driven by contrasting landscape composition and agricultural practices. Sera soumis en novembre-décembre 2025 à Agriculture Ecosystems and Environment.
COLLOQUES	
Participations passées à des colloques	T. Gandara Novembre 2022 Metz SFE² GfÖ EEF International Conference on Ecological Sciences "Ecology and Evolution: New perspectives and societal challenges" Evaluation and comparison of pollination service indicators at agricultural landscape level T. Gandara Octobre 2023 Bordeaux 5ème réunion annuelle du GDR Pollineco Évaluation de l'abondance et la diversité de pollinisateurs en milieu agricole en fonction des pratiques et du paysage. T. Gandara Octobre 2024 Lyon SFE² International Congress in Ecology and Evolution Poster: Evaluation/Assessment of pollination services across farmed landscapes reveal negative impacts of pesticide use and habitat loss on pollination T. Gandara Octobre 2024 Dijon 6ème réunion annuelle du RT

	Pollineco New approaches to assess pollination services across farmed landscapes reveal negative impacts of pesticide use and habitat loss on pollination E. Porcher Octobre 2025 Montpellier 17e rencontres Ecology & Behaviour Plant-pollinator interactions in a changing world E. Porcher Novembre 2025 Grenoble EcoTum How do plants respond to global changes? E. Porcher Juin 2025 3e rencontres “Les indicateurs de biodiversité dans le cadre de l'action publique” Un nouvel indicateur de pollinisation fondé sur les données de rendement des cultures, déployable de la parcelle à la France entière
THÈSES	
Thèses passées	
Thèses en cours	Thèse avec soutenance prévue le 9/12/2025
ARTICLES DE VALORISATION/ VULGARISATION	
Articles de valorisation parus	Clélia Sirami, Emmanuelle Porcher, Thibault Gandara, Solène Agnoux, 2024. Agriculture et pollinisateurs : vers une nouvelle alliance ? Pour la Science https://www.pourlascience.fr/sd/ecologie/agriculture-et-pollinisateurs-vers-une-nouvelle-alliance-26651.php
Articles de valorisation à paraître	Emmanuelle Porcher, Francesco Accatino, James Desaegher, Colin Fontaine, Thibault Gandara, Antoine Gardarin, Gabrielle Martin, Alice Michelot-Antalik. Une méthode accessible pour évaluer la pollinisation animale des cultures, déployable de la parcelle à la France entière. Innovations Agronomiques.
AUTRES ACTIONS VERS LES MÉDIAS	
Actions vers les médias (interviews...) effectuées	La Corneille 3e Assises nationales des insectes pollinisateurs : “Quels indicateurs pour évaluer l'état des pollinisateurs et le service de pollinisation ?”
ENSEIGNEMENT/ FORMATION	
Enseignements/formations dispensés	Mission doctorale complète avec 32h/an consacrées à la vulgarisation auprès de scolaires sur la biodiversité et sa conservation

Résumés

☐ Résumé court

ESPRES a testé différentes méthodes pour évaluer la pollinisation et la régulation des ravageurs à l'échelle territoriale en lien avec l'utilisation des pesticides et le paysage. Nous montrons que la diversité paysagère favorise la pollinisation, tandis que les pesticides la limitent. La pollinisation et la régulation des ravageurs sont corrélés positivement, suggérant des synergies possibles. Ces résultats guident la mise en place d'aménagements agroécologiques pour des systèmes favorisant les régulations.

☐ Résumé long

- Contexte général et enjeux scientifiques et techniques

La pollinisation, essentielle à la majorité des cultures, est fortement menacée par l'usage des pesticides. Ce projet développe et teste à l'échelle territoriale des indicateurs simples pour évaluer la pollinisation et la régulation naturelle des ravageurs. Il analyse leurs liens avec les pratiques agricoles et les déterminants environnementaux, notamment l'usage des pesticides. Les résultats permettront d'identifier des leviers écologiques pour réduire la dépendance aux intrants chimiques. Ce travail s'inscrit dans les objectifs du plan Écophyto II+ et soutient la transition vers des systèmes agricoles plus résilients et durables.

- Objectifs

- 1- comparer plusieurs indicateurs de pollinisation à l'échelle d'un paysage agricole ;
- 2- analyser l'effet des pesticides et de la composition paysagère sur la pollinisation en paysage de grandes cultures ;
- 3- comparer les services de pollinisation et de régulation des ravageurs sur des parcelles de colza.

- Méthodologie

L'étude compare deux indicateurs de pollinisation à l'échelle du paysage : un indicateur de pollinisation réalisée basé sur les rendements, et un indicateur de pollinisation potentielle fondé sur l'occupation des sols. Ces indicateurs ont été testés sur un territoire de grandes cultures en Côte-d'Or à partir de données agricoles détaillées afin d'évaluer leurs liens avec l'usage des pesticides.

Sur le dispositif Scarabée, dans le bassin parisien, des observations de pollinisateurs et des mesures de pollinisation sur colza et fraisiers ont été menés le long de gradients de composition paysagère et d'intensité d'usage des pesticides. Les données recueillies ont permis d'analyser les effets du paysage et des pratiques sur la pollinisation et la régulation des ravageurs, mesurée par le parasitisme des altises et des méligèthes et la régulation des pucerons. Des analyses statistiques ont permis de relier les services de pollinisation et de régulation à leurs déterminants environnementaux.

- Principaux résultats obtenus

Les analyses menées sur le territoire agricole de Fénay montrent que les deux indicateurs développés – de pollinisation réalisée (basé sur les rendements) et potentielle (fondé sur l'occupation des sols) – présentent des variations spatiales communes à l'échelle territoriale, soulignant le rôle clé des éléments semi-naturels dans la pollinisation des cultures. L'indicateur de pollinisation réalisée, sensible à l'usage des pesticides, s'avère un outil robuste et opérationnel pour évaluer le service de pollinisation à différentes échelles.

Dans le réseau de parcelles « Scarabée », les observations confirment que la composition paysagère et la présence de colza l'année précédente favorisent l'abondance des pollinisateurs et la pollinisation, tandis que l'usage de pesticides la réduit significativement. Les dispositifs expérimentaux montrent que la pollinisation par les insectes améliore les rendements du colza et des fraisiers et que les insectes contribuent indirectement à la régulation des pucerons.

Enfin, une corrélation positive est observée entre les services de pollinisation et de régulation des ravageurs : les paysages favorables aux pollinisateurs peuvent aussi soutenir les ennemis naturels des ravageurs même si ces relations dépendent des contextes environnementaux. Ces résultats démontrent qu'une agriculture moins dépendante des pesticides et des aménagements agroécologiques (haies, bandes fleuries, jachères...) permettraient de renforcer simultanément les régulations biologiques, les rendements agricoles et la biodiversité des paysages de grandes cultures.

- Sorties opérationnelles pour décideurs, applications éventuelles

Le projet ESPRES a validé un nouvel indicateur de pollinisation basé sur les rendements, cohérent avec les modèles existants mais plus sensible aux pratiques agricoles. Cet outil, déployable à l'échelle territoriale, permettra d'évaluer et orienter les aménagements et pratiques favorables à la pollinisation et à la durabilité des cultures.

Les résultats montrent que les éléments semi-naturels renforcent les rendements et la visite des pollinisateurs, tandis que les pesticides les réduisent, de même que la régulation naturelle des ravageurs. Ces constats appellent à diversifier les paysages agricoles et à développer des aménagements agroécologiques connectés pour soutenir la biodiversité.

L'approche met en évidence des synergies partielles entre pollinisation et régulation biologique, suggérant qu'une gestion intégrée des habitats peut optimiser plusieurs services écosystémiques à la fois.

Ces outils et connaissances sont mobilisables pour appuyer les politiques territoriales de réduction des pesticides, accompagner la co-conception de systèmes agricoles sans intrants chimiques, et suivre l'efficacité des transitions agroécologiques à différentes échelles.

- Recommandations

- Déployer l'indice de pollinisation réalisé à différentes échelles spatiales et temporelles.
- Réduire l'usage des pesticides et favoriser la diversification végétale.

ESPRES : Evaluation du Service de Pollinisation dans des territoires en REduction d'utilisation de pesticides et interaction avec le Service de régulation des ravageurs

- Augmenter les analyses conjointes des services de pollinisation et de la régulation des ravageurs.

☐ Mots-clés

Pollinisation, pesticides, indicateurs, rendements, régulation des ravageurs, territoire

ESPRES : Evaluation du Service de Pollinisation dans des territoires en REduction d'utilisation de pesticides et interaction avec le Service de régulation des ravageurs

RAPPORT SCIENTIFIQUE



ESPRES : Evaluation du Service de Pollinisation dans des territoires en REduction d'utilisation de pesticides et interaction avec le Service de régulation des ravageurs

Plan Ecophyto II+ – Volet 2 de l'Appel à projets national
2020 – 2021 »

***Synthèse pour les décideurs [Alice Michelot-Antalik,
Thibault Gandara, Antoine Gardarin et Emmanuelle
Porcher]***

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Action pilotée par les Ministères chargés de la Transition écologique, de la Biodiversité, de la Forêt, de la Mer et de la Pêche (MTEBFMP), de l'Agriculture et de la Souveraineté Alimentaire (MASA), du Travail, de la Santé, des Solidarités et des Familles (MTSSF), et de l'Education nationale, de l'Enseignement supérieur et de la Recherche (MENESR) avec l'appui financier de l'Office Français pour la Biodiversité (OFB), par les crédits issus de la redevance pour pollutions diffuses attribués au plan Écophyto II+

Préambule : Ce rapport est une synthèse du manuscrit de thèse de Thibault Gandara rédigé en octobre 2025 lors du projet ESPRES (258 pages). Nous avons sélectionné deux questions de recherche pour les trois objectifs présentés.

1. Contexte général et enjeux scientifiques et techniques

La vulnérabilité de la plupart des espèces sauvages, et des services qu'elles rendent dans les agroécosystèmes, aux systèmes de culture intensifs en intrants rend nécessaire la création de territoires agricoles reposant sur des régulations biologiques accrues permettant une utilisation réduite, voire nulle, des pesticides. Ces territoires doivent s'appuyer sur une connaissance et une gestion optimisée de la biodiversité à différentes échelles (Duru et al., 2015; Therond et al., 2017) afin de concevoir des agroécosystèmes répondant aux attentes des agriculteurs et de la société en termes de multifonctionnalité. Parmi les services contribuant à la production agricole, ceux de fertilité du sol et les services liés aux cycles des éléments sont de loin les plus étudiés (Tamburini et al., 2020). À l'inverse, le service de régulation des ravageurs, et plus encore celui de pollinisation, ont été beaucoup moins considérés. Optimiser le service de pollinisation (transfert de pollen des étamines vers les stigmates des fleurs par des animaux) pourrait être une voie envisageable pour maintenir les rendements agricoles dans des territoires économes en pesticides. D'une part, 60 à 80 % des espèces de plantes cultivées dépendent, au moins en partie, des pollinisateurs pour la production de graines et de fruits, ce qui représente 35 % de la production alimentaire mondiale (Klein et al., 2007). D'autre part, en milieu tempéré, les animaux qui pollinisent sont principalement des insectes, ce qui fait de la pollinisation des cultures un des services les plus vulnérables à l'exposition aux pesticides. Un déclin global des insectes est observé depuis plusieurs décennies notamment en milieu agricole, du fait de la fragmentation des habitats et de l'exposition aux pesticides (Potts et al., 2010) et quelques études suggèrent que pour les espèces dépendantes des pollinisateurs, la réduction des traitements phytosanitaires ne s'accompagne pas nécessairement d'une baisse de rendement, grâce à un effet positif sur les communautés de pollinisateurs (Catarino et al., 2019). Les insectes sont également impliqués dans la régulation des ravageurs des cultures, mais peu de travaux ont évalué la fourniture des deux services simultanément.

Les études caractérisant les effets d'une réduction des pesticides sur le service de pollinisation restent très localisées, en particulier parce que la mesure du service de pollinisation demande beaucoup de moyens et n'est souvent menée qu'à l'échelle de quelques parcelles. Un enjeu essentiel est ainsi d'évaluer le service de pollinisation à l'échelle des territoires, ce qui n'a jamais été fait à notre connaissance, et de caractériser les relations avec le service de régulation des ravageurs dans des systèmes de culture en réduction de pesticides.

2. Objectifs et questions de recherche

Notre premier objectif est de comparer des indicateurs de pollinisation à l'échelle d'un territoire. Pour cela nous avons étudié le territoire de grandes cultures de Fénay au sud de Dijon. Les questions de recherche sont les suivantes :

- L'indice de pollinisation réalisée (RPI) est-il corrélé à l'indice de pollinisation potentielle (PPI) ?
- Le RPI varie-t-il en fonction de l'usage des pesticides ?

Notre deuxième objectif est d'analyser l'effet des pesticides (IFT) et de la composition paysagère sur les pollinisateurs et la pollinisation en paysage de grandes cultures.

ESPRES : Evaluation du Service de Pollinisation dans des territoires en REduction d'utilisation de pesticides et interaction avec le Service de régulation des ravageurs

Pour cela, nous avons réalisé des mesures sur le dispositif Scarabées au sud-ouest de Paris. Les questions de recherche sont les suivantes :

- Comment les pollinisateurs réagissent à la composition du paysage et aux pesticides ?

- Quels sont les effets de la composition du paysage et des pesticides sur nos différents estimateurs de la pollinisation ?

Notre troisième objectif vise à comparer les services de pollinisation et de régulation des ravageurs avec des mesures effectuées sur des parcelles de colza du dispositif Scarabée. Les questions de recherche sont les suivantes :

- Les services de pollinisation et de régulation des ravageurs sont-ils corrélés ?

- Quels sont les effets des variables paysagères et des pesticides sur les deux services ?

3. Matériels et méthodes

3.1. Site d'étude de Fénay et calcul des indicateurs de pollinisation

Pour le territoire de Fénay (Côte d'Or) qui se compose de 140 parcelles de grandes cultures contiguës (950 ha au total) gérées par 23 agriculteurs dans la plaine de Dijon, en partenariat avec l'UMR Agroécologie à Dijon, une comparaison de l'indicateur de pollinisation réalisée (RPI) basé sur les rendements des cultures et de l'indicateur de pollinisation potentielle basé sur les modes d'occupation des sols (PPI) a été effectuée. Les agriculteurs ont été interrogés chaque année de 2007 à 2019 pour établir un enregistrement complet des pratiques agricoles, incluant des informations détaillées sur l'usage des pesticides et le rendement de chaque parcelle. Les rendements annuels des cultures ont été collectés pour l'ensemble de la zone, et 14 espèces de cultures ont été sélectionnées, correspondant à des plantes récoltées pour leurs fruits et/ou leurs graines.

L'indice de pollinisation réalisée utilise les données de rendement des cultures et la dépendance des cultures aux pollinisateurs : c'est un indicateur direct du service de pollinisation. Sa philosophie générale est simple : elle repose sur l'hypothèse que, toutes choses égales par ailleurs, dans un site avec un déficit de pollinisation, le rendement des cultures dépendantes des pollinisateurs devrait être inférieur, en moyenne, au rendement des cultures non-dépendantes des pollinisateurs. L'indicateur de pollinisation réalisée est alors calculé comme la pente de la régression linéaire entre les rendements des cultures - préalablement standardisés- et la dépendance des cultures aux pollinisateurs, dans un site d'intérêt (un département, une parcelle agricole...). Une adaptation de cet indicateur, initialement développé à l'échelle nationale (Martin et al., 2019), vers l'échelle du territoire, a été réalisée en explorant différentes résolutions spatiales, couvrant une gamme allant d'une échelle de la mosaïque de parcelles et lissée soit sur des fenêtres glissantes à une échelle plus fine, soit de groupements de parcelles, soit de la parcelle elle-même (Gandara et al., 2025).

Pour l'indicateur de pollinisation potentielle qui nous sert de référence sur le territoire, nous avons sélectionné le modèle INVEST (Sharp et al., 2018). Ce modèle est une mesure indirecte basée sur les ressources florales pour les pollinisateurs et sur la connaissance de leurs sites de nidification. Les deux indicateurs de pollinisation ont été spatialisés avec différentes méthodes d'agrégation (fenêtres glissantes et clusters) et plusieurs résolutions spatiales.

3.2. Choix des parcelles dans le réseau agricole Scarabée

Le réseau d'agriculteurs « Scarabée » est réparti entre l'Eure-et-Loir (28), l'Essonne (91) et les Yvelines (78) dans des plaines de grandes cultures. Il est suivi par l'UMR Agronomie depuis 2018. Au total, 41 parcelles de colza ont été sélectionnées dans quatre types de paysages distincts, en fonction de deux gradients indépendants : (1) la proportion d'éléments semi-naturels présents dans un rayon de 1000 mètres autour de chaque parcelle, et (2) le niveau d'utilisation de pesticides dans les parcelles, déterminé à partir d'entretiens menés avec les agriculteurs. Sur les 41 parcelles étudiées pour les pollinisateurs (20 la première année et 21 la seconde), 39 ont également fait l'objet d'un suivi des mégilèthes (20 en 2023 et 19 en 2024), 37 ont été observées pour les altises (20 en 2023 et 17 en 2024), et 20 parcelles en 2023 ont en outre été suivies pour les colonies de pucerons et les paramètres de rendement du colza.

3.3. Mesures des services de pollinisation

La pollinisation a été évaluée à l'aide de trois approches : l'observation des interactions plantes-pollinisateurs dans les colzas, les bordures de parcelles céréalières autour de la parcelle de colza et sur les fraisiers ; la mesure de la différence de masse des fraises entre pollinisation ouverte et exclusion d'insectes ; et des mesures de composantes de rendement sur le colza entre pollinisation ouverte et exclusion d'insectes.

Observation des interactions plantes-pollinisateurs

Le potentiel de pollinisation a été mesuré entre mars et mai à partir des observations non létales des interactions entre pollinisateurs et colza ou de plantes sauvages dans les bandes enherbées. Dans chaque parcelle de colza, deux quadrats de 2 m × 2 m ont été observés (à 30 m du bord et 20 m d'écart), sous conditions standardisées (ensoleillées, > 12 °C, vent ≤ 20 km/h). Deux sites supplémentaires en bordure de parcelle céréalière, situés à 500 m et 1000 m de chaque parcelle de colza, ont été observés. Chaque session d'observation durait 5 minutes par quadrat, avec trois sessions en 2023 (360 observations) et deux en 2024 (244 observations). Les pollinisateurs ont été classés en 13 morphogroupes et les données de quadrats ont été regroupées par session de 10 minutes. La surface florale totale par quadrat a été estimée à partir du nombre d'unités florales et de la moyenne des aires florales de chaque espèce végétale fleurie estimée sur 20 individus (Michelot-Antalik et al., 2025).

Utilisation des fraisiers comme phytomètres

Pour mesurer la pollinisation après la floraison du colza, des fraisiers (*Fragaria × ananassa*, cv. Charlotte) ont été utilisés comme phytomètres, cultivés en pots. Des traitements ont été appliqués pour comparer l'effet de la pollinisation ouverte, manuelle et l'exclusion des pollinisateurs. En 2023, six fraisiers ont été disposés en bordure de 20 parcelles de colza et dans 20 bandes enherbées situées à 500 m de ces parcelles. Deux plants par site étaient ensachés pour exclure les insectes, tandis que quatre restaient ouverts. Un tiers des fleurs de fraisiers a été pollinisé manuellement dans les deux cas. Au total, 240 fraisiers ont été placés sur le terrain entre le 25 et le 28 avril, avant le début de leur floraison et à la fin de celle du colza. Ils ont été laissés trois semaines après l'apparition des premières fleurs, puis retirés entre le 1er et le 4 juin. En 2024, afin d'améliorer la cohérence des données et de réduire les pertes dues au vandalisme ou à l'herbivorie, 10 fraisiers ont été installés sur deux paysages au lieu

des 4 initiaux (10 parcelles de colza et 10 bandes enherbées), soit 200 fraisiers au total. Trois fraisiers par site étaient ensachés et sept restaient ouverts. Un tiers des fleurs a de nouveau été pollinisé manuellement. Les fraisiers ont été installés entre le 13 et le 17 mai et retirés trois semaines après le début de la floraison, les 13–14 juin. Les observations d'interactions fraisiers-pollinisateurs ont été réalisées pendant 10 minutes sur quatre fraisiers ouverts de la même façon que les observations réalisées sur le colza, et le nombre de fleurs ouvertes a été compté pour estimer la surface florale totale.

Après exposition, les fraisiers ont été transférés vers un site commun pour une maturation homogène. Le poids, la taille et la déformation des fruits ont été mesurés afin d'évaluer la qualité de la pollinisation.

Mesures des composantes du rendement du colza

En 2023, la contribution des insectes au rendement du colza a été mesurée grâce à une expérience en cages appariées menée dans 20 parcelles. Chaque parcelle comportait deux traitements : une cage d'exclusion des pollinisateurs et un témoin ouvert avec filet supérieur uniquement, assurant les mêmes conditions d'ombrage tout en permettant l'accès aux insectes. Les cages ont été installées au début de la floraison, à 30 m du bord de la parcelle, puis retirées un mois plus tard. En juin, tous les pieds de colza sur une surface de 1 m² par traitement ont été récoltés pour mesurer la masse fraîche et sèche, le nombre de siliques pleines, avortées ou éclatées, ainsi que la proportion de pédicelles courts et longs. Cinquante siliques séchées ont servi à estimer le nombre moyen de graines par silique, et les siliques supplémentaires ont permis de déterminer le poids de mille grains. Comme l'année était marquée par une forte présence de pucerons, la longueur des colonies a été mesurée sur chaque tige. Cette mesure sera intégrée comme covariable afin de distinguer l'effet de la pollinisation de celui de la pression parasitaire et également comme une estimation du service de régulation des pucerons.

3.4. Mesures des services de régulation des ravageurs

Le taux de parasitisme de deux ravageurs du colza : l'altise (*Psylliodes chrysocephala*) et la méligèthe (*Brassicogethes aeneus*), a été étudié pour évaluer le service de régulation des ravageurs. Pour les altises, des larves de dernier stade ont été prélevées dans les pétioles à la base des plantes le long de deux transects à 5 et 30 m du bord de la parcelle, correspondant aux points d'observation des pollinisateurs. Quand cela était possible, au moins 100 larves ont été collectées par parcelle. Elles ont été placées dans des boîtes d'élevage incubées à 20–25 °C, puis les adultes émergents ont été comptés après trois semaines. Pour permettre l'émergence des parasitoïdes, les boîtes ont ensuite été placées à 5°C pendant quatre mois (simulation hivernale), puis réincubées à 20-25°C ; les émergences de parasitoïdes ont été relevées quotidiennement. En parallèle, le parasitisme des larves de méligèthes a été évalué fin avril, à la fin de la floraison, sur les mêmes transects. Au moins 100 larves bien développées (> 4 mm) ont été collectées par parcelle et conservées dans de l'éthanol à 70 %. Le parasitisme par *Tersilochus heterocerus* (espèce dominante dans la région) a ensuite été identifié sous loupe binoculaire par la détection d'œufs translucides visibles à travers la cuticule larvaire. Lorsque les grandes larves étaient rares, des larves moyennes (≈ 3 mm) ont été incluses.

Le taux de parasitisme a été calculé comme le rapport entre le nombre de parasitoïdes et le total d'adultes (coléoptères + parasitoïdes).

3.5. Estimation des variables paysagères et de l'utilisation des pesticides

Pour quantifier la composition du paysage, nous avons défini trois zones tampons autour des sites d'observation (500 m, 1000 m et 2000 m). Le pourcentage de couverture en éléments semi-naturels a été obtenu à partir de deux sources complémentaires : BD TOPO® pour les éléments semi-naturels ligneux tels que les forêts, les bois et les haies, tandis que les éléments herbacés, incluant friches et prairies, ont été obtenus à partir du Registre Parcellaire Graphique. Nous avons utilisé la surface totale des éléments semi-naturels, soit la somme de toutes ces surfaces. La couverture en colza de l'année précédente et les autres cultures à floraison massive de l'année précédente ont également été extraites du RPG. La couverture en colza de l'année de prélèvement a été récupérée en 2023 via le RPG, et en 2024 par analyse manuelle des images aériennes du programme Sentinel.

Pour nos trois objectifs, notre évaluation de l'utilisation des pesticides a été réalisée à partir de l'indice de fréquence de traitement (IFT). Il est calculé comme la somme des doses appliquées de chaque substance active sur le cycle de la culture (commençant après la récolte de la culture précédente et se terminant à la récolte de la culture en cours), divisée par la dose maximale autorisée selon la réglementation nationale française et pondérée par la surface relative de la parcelle traitée.

Pour les analyses sur le territoire de Fénay, nous avons utilisé l'IFT à la parcelle de 2007 à 2019 à partir des enquêtes réalisées auprès des agriculteurs. Pour les analyses sur le dispositif Scarabée, l'IFT a été quantifié au niveau des parcelles grâce à des enquêtes auprès des agriculteurs. L'IFT au niveau du paysage a été estimé à l'échelle communale à partir des données fournies par Solagro en calculant une moyenne pondérée par la surface représentée par chaque commune dans les trois zones tampons (500 m, 1000 m et 2000 m) autour de chaque parcelle.

3.6. Analyses statistiques

Pour le premier objectif, les analyses réalisées consistent en l'utilisation de corrélations de Pearson pour évaluer les relations entre les indicateurs, et de modèles linéaires (lm) et d'analyses de variance (ANOVA) pour analyser les relations entre pollinisation et variables environnementales.

Pour le deuxième objectif, nous avons construit des modèles linéaires mixtes afin d'expliquer l'abondance des pollinisateurs en fonction des variables paysagères et de l'IFT. Le modèle intègre plusieurs variables explicatives fixes, notamment la surface florale totale, la vitesse du vent, la température, l'heure d'observation, la proportion d'éléments semi-naturels, l'IFT du paysage, la surface de colza (de l'année en cours et de l'année précédente), l'hétérogénéité des cultures et la présence de cultures fleuries l'année précédente. Un effet aléatoire associé au site d'étude permet de prendre en compte la variabilité non expliquée entre sites.

Nous avons examiné l'influence des variables environnementales sur la contribution des insectes aux composantes du rendement du fraisier et du colza. Les variables explicatives, comprenaient la proportion d'éléments semi-naturels, l'IFT au paysage, la proportion de parcelles de colza durant l'année d'échantillonnage et l'année précédente, l'indice d'hétérogénéité des cultures de l'année précédente, ainsi que la surface de cultures fleuries autres que le colza l'année précédente. Ces variables ont été calculées dans un rayon de 1000 m autour de chaque site.

Pour le troisième objectif, nous avons estimé la valeur globale de chaque service écosystémique pour chaque parcelle, en tenant compte des mesures répétées

effectuées dans des conditions d'observation variables et en contrôlant les covariables pertinentes. À cette fin, chaque indicateur de service a été modélisé à l'aide de modèles linéaires mixtes (ou généralisés), incluant les covariables appropriées et un intercept aléatoire correspondant à l'identité de la parcelle. Nous avons ensuite extrait les effets aléatoires de chaque parcelle ainsi que leurs erreurs standards et des estimateurs BLUP (*Best Linear Unbiased Predictors*). Ces estimations corrigées des services à l'échelle de la parcelle ont ensuite été utilisées pour calculer les corrélations de rang de Spearman entre les différents services étudiés, pondérées par l'inverse de leurs erreurs standards respectives afin de tenir compte des différences de précision. Afin d'identifier l'effet du paysage et de l'IFT sur les services écosystémiques, nous avons ajusté des modèles linéaires mixtes généralisés intégrant l'ensemble des variables environnementales explicatives, la date d'échantillonnage et les conditions météorologiques en effet fixe dans une zone tampon de 1000 m autour du centroïde des parcelles.

4. Résultats

4.1. Comparer des indicateurs de pollinisation à l'échelle d'un territoire

La spatialisation territoriale du RPI et du PPI obtenus par l'approche à fenêtre glissante est globalement cohérente. Le PPI présentait un gradient nord-ouest/sud-est, (**fig. 1A**), avec des valeurs plus élevées sur le versant nord-est du territoire de Fénay. Un gradient similaire, bien que non totalement identique, a été observé pour le RPI projeté sur les parcelles stables (**fig. 1B**). La relation entre le RPI calculé à partir des fenêtres glissantes et le PPI est donc positive et forte ($p < 0.001$, **fig. 2**). Lorsque le RPI a été calculé à la plus fine résolution spatiale, c'est-à-dire à l'intérieur de chacune des 87 parcelles stables, les tendances observées sont similaires à celles obtenues avec les groupes à résolution plus grossière, c'est-à-dire une relation négative entre le RPI et l'utilisation de pesticides (IFT), mais aucune relation avec le PPI.

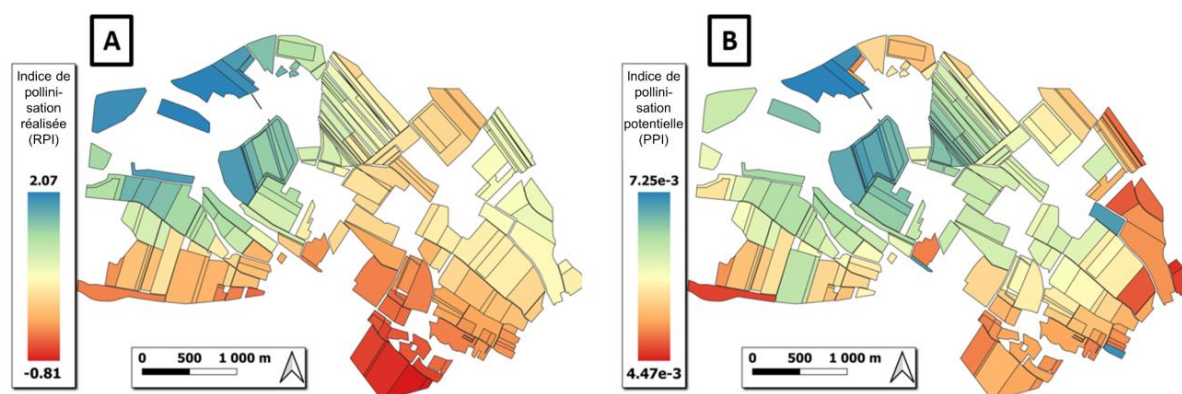


Figure 1. Comparaison spatiale entre l'Indice de Pollinisation Réalisée (RPI) et l'Indice de Pollinisation Potentielle (PPI) projetés sur les parcelles stables sur la période 2007 à 2019 du territoire de Fénay.

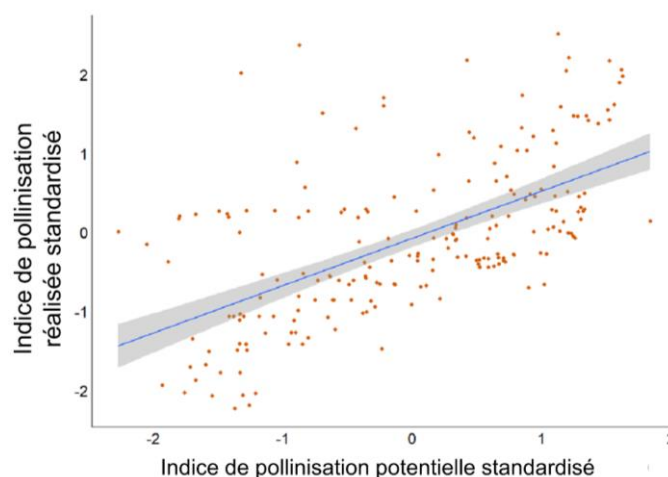


Figure 2. Régression de l'indice de pollinisation réalisé (RPI) normalisé, calculé à l'aide d'une fenêtre glissante de 2000 m × 2000 m et de pixels de sortie de 500 m × 500 m, en fonction de l'indice de pollinisation potentiel (PPI) normalisé.

4.2. Analyser l'effet des pesticides et du paysage sur la pollinisation en grandes cultures

Le nombre total d'interactions plantes–pollinisateurs observé est positivement influencé par la surface en éléments semi-naturels ($p = 0,02$; **fig. 3A**) et par la présence de colza l'année précédente ($p = 0,03$; **fig. 3B**) dans un rayon de 1000 m. Nous avons également observé une relation significative négative entre le nombre d'interactions et l'intensité d'utilisation des pesticides, en particulier pour la communauté de pollinisateurs du colza ($p = 0,01$; **fig. 3C**), ainsi qu'une relation positive avec les éléments semi-naturels pour les communautés de pollinisateurs des fraisières ($p = 0,042$; **fig. 3D**).

Le traitement en pollinisation ouverte a une masse totale de graine par pied de colza plus élevée, une masse des fraises plus élevée et une longueur de colonies de pucerons par pied de colza plus faible que le traitement d'exclusion des insectes ($p < 0.05$; **fig. 4**).

Pour les fraises, seule la pollinisation ouverte a un effet significatif sur la masse des fruits ($p = 0,011$) (**tab. 2**). Chez le colza, le poids de mille grains, le nombre de graines par silique et la masse totale de graines par plante étaient plus élevés sous pollinisation ouverte que dans les cages d'exclusion. Nous avons mis en évidence un effet positif de la proportion d'éléments semi-naturels ($p = 0,003$) et de la présence de parcelles de colza l'année précédente ($p < 0.05$) sur le nombre de graines par silique de colza en pollinisation ouverte. Concernant la masse totale des graines par plant de colza, elle est positivement reliée à la proportion d'éléments semi-naturels ($p < 0.001$) et de colza ($p = 0.021$) et à la proportion de colza de l'année précédente ($p = 0.001$) mais négativement reliée à l'IFT au paysage ($p = 0.034$) en pollinisation ouverte.

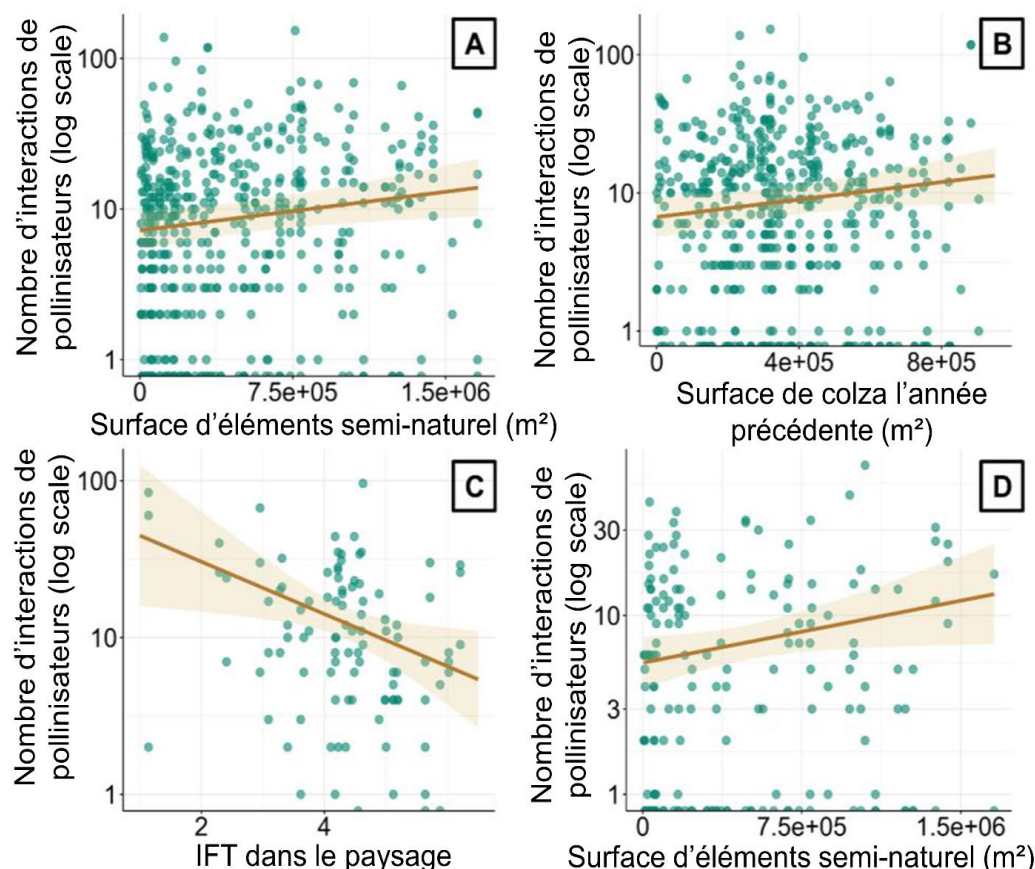


Figure 3. Effets modélisés des relations significatives entre le nombre d'interactions plantes-pollinisateurs et les variables environnementales. Les figures A et B présentent les résultats pour l'ensemble de la communauté de pollinisateurs, la figure C pour la communauté de pollinisateurs du colza, et la figure D pour celle des fraisiers. Les effets marginaux prédits sont en lignes pleines, les intervalles de confiance à 95 % en zones ombrées et les valeurs observées en points verts.

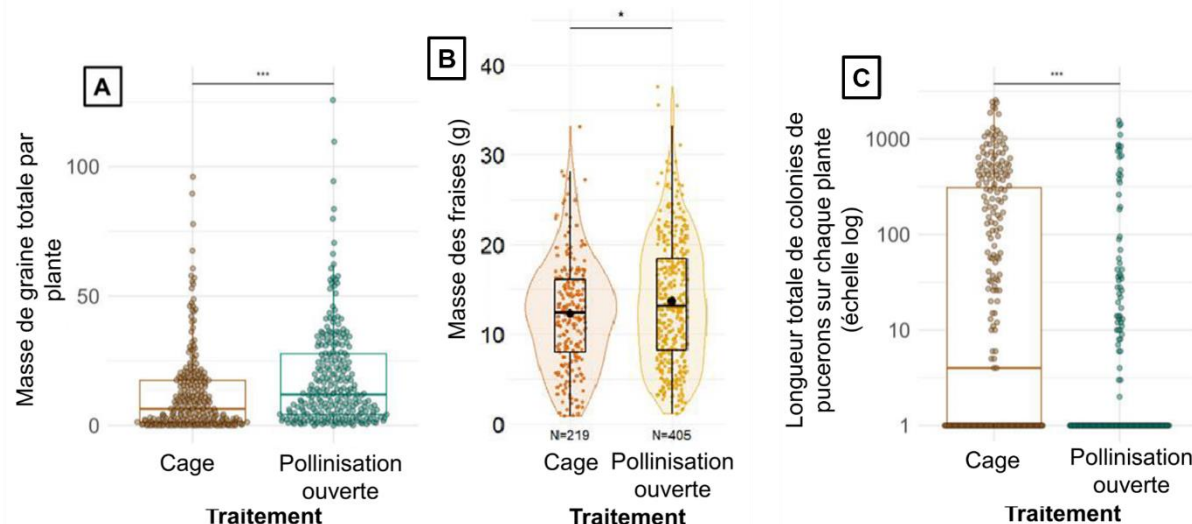


Figure 4. Effets du traitement de pollinisation (cage ou ouverte) sur la masse totale de graines par pied de colza, la masse des fraises et la longueur des colonies de pucerons par pied de colza. Les différences entre les traitements sont significatives : *** $p < 0.001$; * $p < 0.05$; adapté de Gandara, 2025.

Tableau 2. Résultats (estimates) des modèles mixtes réalisés pour estimer les composantes du rendement des fraisiers et du colza selon les variables paysagères et le traitement d'exclusion des insectes (cage fermée ou ouverte).

	Fraises		Colza		
Variables explicatives	Masse	Déformation	Poids de 1000 grains	Graines par silique	Masse totale de graines par plante
Traitement	1.61 *	-0.002	0.41 **	3.03 ***	0.41 ***
Ouvert x Surface éléments semi-naturels	-0.78	0.002	0.13	2.90 ***	0.31 ***
Ouvert x IFT paysager	0.21	-0.008	0.37	-0.97	-0.27 *
Ouvert x Surface en colza N-1	-0.35	-0.016	-0.06	2.50 *	0.27 **
Ouvert x Surface en colza N	-0.38	0.034	-0.20	-0.17	0.23 *
Ouvert x Hétérogénéité en culture N-1	-0.16	-0.020	0.09	-1.89	-0.04
Ouvert x Plantes à fleurs cultivées N-1	0.24	0.018	0.45.	1.64	0.05
R ² du modèle	R ² _c = 0.17 R ² _m = 0.06	R ² _c = 0.37 R ² _m = 0.06	R ² _c = 0.79 R ² _m = 0.40	R ² _c = 0.55 R ² _m = 0.46	R ² _c = 0.75 R ² _m = 0.64

4.3. Comparer les services de pollinisation et de régulation des ravageurs

Les corrélations par paires entre les variables liées aux services écosystémiques : le parasitisme des altises, le parasitisme des méligèthes, la régulation des pucerons, le nombre de visites des pollinisateurs sauvages et de tous les pollinisateurs sont toutes positives (**fig. 5**). Cela suggère que les environnements favorables aux ennemis naturels peuvent également accueillir les pollinisateurs. En particulier, le nombre d'interactions plantes-pollinisateurs est corrélé significativement à la régulation des pucerons ($\rho = 0.47$; $p = 0,036$). Le parasitisme des altises et celui des méligèthes sont significativement corrélés ($\rho = 0.38$; $p = 0,02$).

L'IFT a un effet négatif sur le nombre d'interactions des plantes avec les pollinisateurs sauvages ($\beta = -0.32 \pm 0,01$, $p = 0.0012$) et le taux de parasitisme des altises ($\beta = -0.62 \pm 0,24$, $p = 0.01$) mais aucun effet statistiquement significatif sur le parasitisme des méligèthes ($p = 0.79$) et il est positivement associé à la régulation des pucerons ($\beta = 0.71 \pm 0.29$, $p = 0.014$) (**fig. 6**). À l'échelle du paysage l'IFT dans un rayon de 1 km a un effet négatif sur le nombre d'interactions des pollinisateurs sauvages ($\beta = -0,29 \pm 0,12$, $p = 0.019$) et la régulation des pucerons ($\beta = -1,02 \pm 0,41$, $p = 0.012$).

La surface en éléments boisés et herbacés dans un rayon de 1 km a des effets positifs sur le nombre d'interactions des pollinisateurs sauvages ($\beta = 0.29 \pm 0.10$, $p = 0.0033$) et des effets négatifs sur le parasitisme des méligèthes ($\beta = -0,39 \pm 0.13$, $p = 0.002$).

La surface de colza est positivement associée à la régulation des pucerons ($\beta = 1.91 \pm 0.41$, $p < 0.001$) et la surface de colza de l'année précédente a un effet positif sur le parasitisme des altises ($\beta = 0.57 \pm 0.25$, $p = 0.022$).

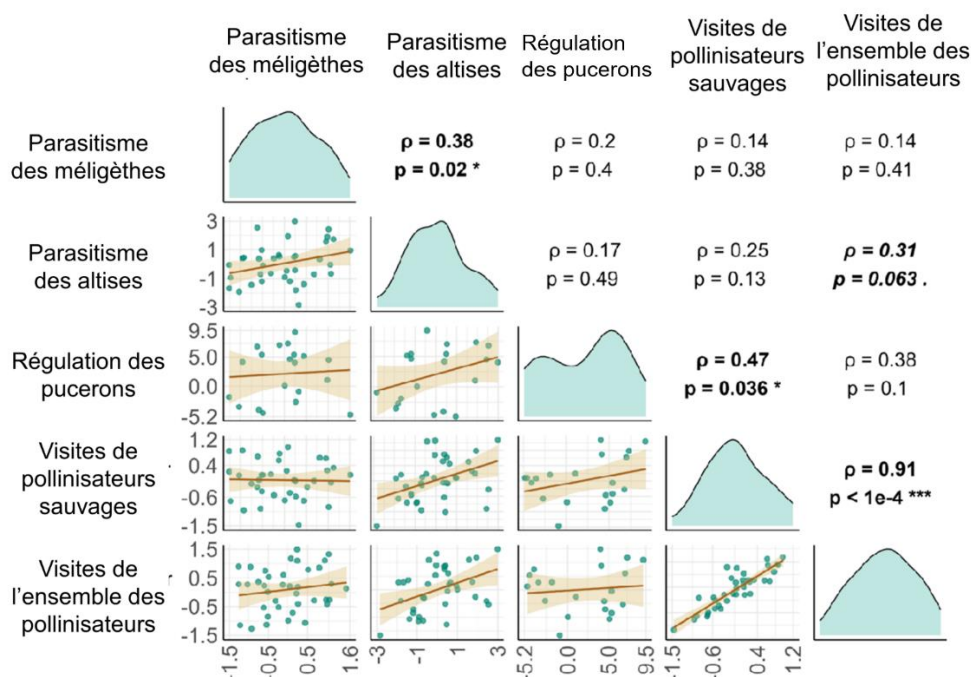


Figure 5. Corrélations par paires entre les indicateurs de services écosystémiques au niveau de la parcelle, corrigées des variables de contrôle. Les corrélations de Spearman par paires (ρ), pondérées par l'erreur standard de chaque estimation de service, sont présentées dans la partie supérieure du graphique. La partie inférieure montre les régressions linéaires non pondérées.

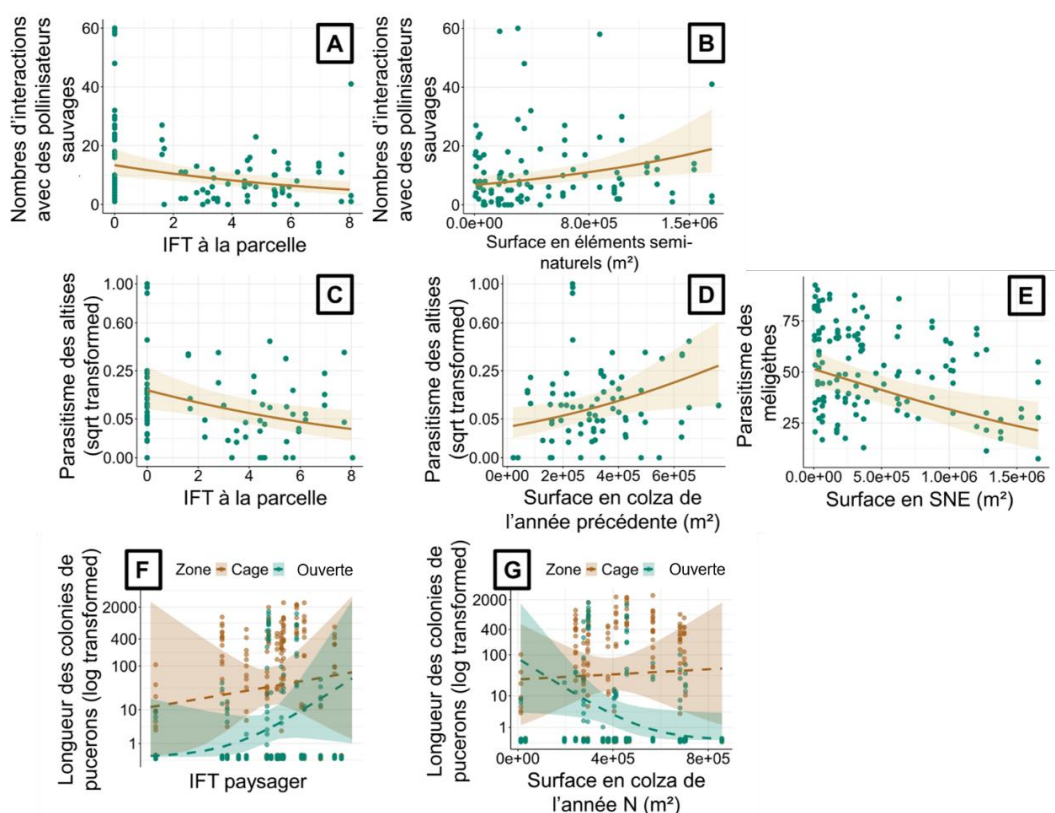


Figure 6. Effets marginaux prédits (lignes pleines) et intervalles de confiance à 95 % (zones ombrées) issus des modèles linéaires mixtes, illustrant l'influence des variables paysagères et de l'indice de fréquence de traitement sur les services écosystémiques. Les valeurs observées sont superposées aux régressions du modèle.

5. Discussion

5.1. Développement de l'indicateur de pollinisation réalisée

Nous avons adapté un indicateur de pollinisation réalisée (RPI) à l'échelle territoriale, corrélé positivement à l'indicateur de pollinisation potentielle (PPI). Cette relation s'explique par des déterminants environnementaux tels que la proportion d'éléments semi-naturels, qui favorisent l'abondance des pollinisateurs et l'efficacité du transfert de pollen (Maurer et al., 2022; Raderschall et al., 2021). Cette corrélation dépend toutefois de la méthode d'agrégation spatiale, discutée dans Gandara et al., (2025).

L'utilisation des pesticides, mesurée par l'IFT, a un effet négatif sur le RPI. Les effets des insecticides et fongicides sur la santé et le comportement des pollinisateurs sont bien établis (Stanley et al., 2015). Les herbicides perturbent également les communautés végétales fournissant les ressources florales indispensables (Godara et al., 2023). Les pesticides apparaissent ainsi comme un facteur majeur du déclin des pollinisateurs dans les paysages agricoles intensifs. Notre étude confirme que ces effets se traduisent par une baisse mesurable de la pollinisation des cultures (Perrot et al., 2024; Stanley et al., 2015).

Le RPI, validé à différentes échelles constitue un outil prometteur pour identifier les zones à déficit de pollinisation et orienter les pratiques agricoles ou l'aménagement du territoire. Facile à calculer à partir des rendements de cultures dépendantes et non dépendantes des pollinisateurs, il intègre les effets des pratiques agricoles. Son déploiement est en cours, avec un article soumis à Innovations Agronomiques pour diffusion.

5.2. Effets des déterminants environnementaux sur les pollinisateurs et effets de la pollinisation sur la production

Les analyses montrent que la composition du paysage influence fortement les communautés de pollinisateurs. Les éléments semi-naturels favorisent leur diversité et leur abondance en offrant des ressources et habitats durables, tout en atténuant les effets négatifs des pratiques intensives, notamment l'usage des pesticides (Neumüller et al., 2020). À l'inverse, les pesticides ont des effets létaux et sublétaux sur les pollinisateurs (Basu et al., 2024) et réduisent les ressources florales par la diminution des plantes adventices (Nicholls and Altieri, 2013), entraînant une baisse des interactions et des services de pollinisation (Brittain et al., 2010).

La présence de cultures à floraison massive, en particulier le colza, l'année précédente, renforce la diversité et l'abondance des pollinisateurs grâce à une floraison précoce et un effet de débordement temporel.

Les traitements en pollinisation ouverte ont significativement amélioré les rendements du colza (nombre et masse de graines) et de la fraise (poids des fruits), confirmant le rôle essentiel des pollinisateurs dans la productivité agricole (Bommarco et al., 2013). Les paysages riches en habitats semi-naturels et peu traités favorisent ainsi la production et renforcent les équilibres écologiques, notamment par une réduction des pucerons.

Par soucis de synthèse, nous ne mentionnons pas dans ce rapport que la mise en relation des indices de pollinisation (différences de rendement entre les traitements en pollinisation ouverte et cage) avec les observations de pollinisateurs, ne montre aucune relation significative. Les limites de l'utilisation des fraisiers comme phytomètres sont discutées dans l'article de Gandara et al. prochainement soumis à Basic and Applied Ecology qui compare l'utilisation des fraisiers dans trois contextes paysagers : agricole, péri-urbain et urbain.

5.3. Complémentarité entre pollinisation et régulation des ravageurs selon les contextes agricoles

L'usage des pesticides à la parcelle apparaît comme un facteur négatif pour la plupart des services écosystémiques étudiés, hormis la régulation des pucerons. L'intensification des traitements réduit fortement l'activité des pollinisateurs sauvages (Guzman et al., 2024) et le parasitisme des altises, confirmant les effets néfastes de l'agriculture intensive sur les régulations biologiques (Li et al., 2024; Ortega-Ramos et al., 2022). À l'échelle du paysage, cette pression chimique affecte aussi la pollinisation et la régulation des pucerons, illustrant son impact sur les pollinisateurs et leurs ennemis naturels comme les syrphes aphidiphages (Brittain et al., 2010; Ricci et al., 2019).

Les éléments semi-naturels exercent un effet positif marqué sur les pollinisateurs sauvages, confirmant leur rôle d'habitats de nidification et de butinage (Eeraerts, 2023; Steffan-Dewenter et al., 2002). En revanche, la réponse des services de régulation est plus variable. La régulation des altises ne montre pas de tendance claire, tandis que celle des méligèthes peut être négativement relié à la proportion d'éléments semi-naturels. Ce résultat est possiblement lié à des prairies pâturées pauvres en ressources florales ou servant de sites d'hivernation aux ravageurs (Sutter et al., 2018).

Enfin, la régulation des altises augmente dans les paysages où le colza a été cultivé l'année précédente, ce qui suggère qu'une continuité interannuelle dans la répartition des cultures peut soutenir les populations d'ennemis naturels. La régulation des pucerons est fortement associée à la proportion de colza de l'année en cours. Ce résultat pourrait traduire un effet de dilution des pucerons sur de grandes surfaces hôtes ou une attraction accrue de leurs ennemis naturels vers ces zones riches en ressources (Gontijo et al., 2013).

6. Limites et perspectives

L'étude présente plusieurs limites méthodologiques et écologiques à considérer. D'une part, les méthodes de mesure de la pollinisation potentielle et réalisée ne convergent pas toujours, probablement en raison de la dépendance modérée des cultures testées (colza et fraisiers) vis-à-vis des pollinisateurs et de la durée limitée des observations, qui ne capture pas toute la variabilité temporelle de leur activité. Ces limites ouvrent des perspectives pour des recherches futures : l'intégration de suivis automatisés des pollinisateurs (capteurs acoustiques, GPS) permettrait d'obtenir des données plus fines et continues. D'autre part, certaines pratiques agricoles, comme le travail du sol ou l'apport en azote, n'ont pas été intégrées dans les analyses, bien qu'elles puissent influencer la dynamique des pollinisateurs et des ennemis naturels.

Notre projet a permis de développer un indicateur prometteur de pollinisation réalisée pour identifier les zones déficitaires et guider la gestion, à court terme par l'adaptation des assolements et à plus long terme par des aménagements favorables aux pollinisateurs. Enfin, les études conjointes de la pollinisation et de la régulation des ravageurs doivent être amplifiées afin de renforcer la complémentarité des régulations biologiques dans les paysages agricoles diversifiés.

Bibliographie citée

- Basu, P., Ngo, H. T., Aizen, M. A., Garibaldi, L. A., Gemmill-Herren, B., Imperatriz-Fonseca, V., Klein, A. M., Potts, S. G., Seymour, C. L., & Vanbergen, A. J. (2024). Pesticide impacts on insect pollinators: Current knowledge and future research challenges. *Science of The Total Environment*, 954, 176656. <https://doi.org/10.1016/j.scitotenv.2024.176656>
- Bommarco, R., Kleijn, D., & Potts, S. G. (2013). Ecological intensification: Harnessing ecosystem services for food security. *Trends in Ecology & Evolution*, 28, 230–238. <https://doi.org/10.1016/j.tree.2012.10.012>
- Brittain, C., Bommarco, R., Vighi, M., Barmaz, S., Settele, J., & Potts, S. G. (2010). The impact of an insecticide on insect flower visitation and pollination in an agricultural landscape. *Agricultural and Forest Entomology*, 12, 259–266. <https://doi.org/10.1111/j.1461-9563.2010.00485.x>
- Catarino, R., Bretagnolle, V., Perrot, T., Vialloux, F., & Gaba, S. (2019). Bee pollination outperforms pesticides for oilseed crop production and profitability. *Proceedings of the Royal Society B: Biological Sciences*, 286, 20191550. <https://doi.org/10.1098/rspb.2019.1550>
- Duru, M., Therond, O., Martin, G., Martin-Clouaire, R., Magne, M.-A., Justes, E., Journet, E.-P., Aubertot, J.-N., Savary, S., Bergez, J.-E., & Sarthou, J.-P. (2015). How to implement biodiversity-based agriculture to enhance ecosystem services: A review. *Agronomy for Sustainable Development*, 35, 1259–1281. <https://doi.org/10.1007/s13593-015-0306-1>
- Eeraerts, M. (2023). A minimum of 15% semi-natural habitat facilitates adequate wild pollinator visitation to a pollinator-dependent crop. *Biological Conservation*, 278, 109887. <https://doi.org/10.1016/j.biocon.2022.109887>
- Gandara, T. (2025). *Évaluation du service de pollinisation en grandes cultures : spatialisation, déterminismes environnementaux et relation avec le service de régulation des ravageurs* [Doctoral dissertation, Muséum national d'Histoire naturelle]. Paris.
- Gandara, T., Gardarin, A., Desaegeher, J., Petit, S., Porcher, E., & Michelot-Antalik, A. (2025). A crop yield-based pollination index reveals the impacts of land cover and pesticide use on realized pollination at a landscape scale. *Agriculture, Ecosystems & Environment*, 392, 109747. <https://doi.org/10.1016/j.agee.2025.109747>
- Godara, N., Williamson, R. C., Koo, D., & Askew, S. D. (2023). Effect of herbicides on pollinator foraging behavior and flower morphology in white clover (*Trifolium repens* L.)-infested turfgrass. *Weed Technology*, 37, 221–225. <https://doi.org/10.1017/wet.2023.33>
- Gontijo, L. M., Beers, E. H., & Snyder, W. E. (2013). Flowers promote aphid suppression in apple orchards. *Biological Control*, 66, 8–15. <https://doi.org/10.1016/j.biocontrol.2013.03.007>
- Guzman, L. M., Elle, E., Morandin, L. A., Cobb, N. S., Chesshire, P. R., McCabe, L. M., Hughes, A., Orr, M., & M'Gonigle, L. K. (2024). Impact of pesticide use on wild bee distributions across the United States. *Nature Sustainability*, 7, 1324–1334. <https://doi.org/10.1038/s41893-024-01413-8>
- Klein, A.-M., Vaissière, B. E., Cane, J. H., Steffan-Dewenter, I., Cunningham, S. A., Kremen, C., & Tscharntke, T. (2007). Importance of pollinators in changing landscapes for world crops. *Proceedings of the Royal Society B: Biological Sciences*, 274, 303–313. <https://doi.org/10.1098/rspb.2006.3721>
- Li, Z., Costamagna, A. C., Beran, F., & You, M. (2024). Biology, ecology, and management of flea beetles in *Brassica* crops. *Annual Review of Entomology*, 69, 199–217. <https://doi.org/10.1146/annurev-ento-033023-015753>

Martin, G., Fontaine, C., Accatino, F., & Porcher, E. (2019). New indices for rapid assessment of pollination services based on crop yield data: France as a case study. *Ecological Indicators*, 101, 355–363. <https://doi.org/10.1016/j.ecolind.2019.01.022>

Maurer, C., Sutter, L., Martínez-Núñez, C., Pellissier, L., & Albrecht, M. (2022). Different types of semi-natural habitat are required to sustain diverse wild bee communities across agricultural landscapes. *Journal of Applied Ecology*, 59, 2604–2615. <https://doi.org/10.1111/1365-2664.14260>

Michelot-Antalik, A., Langlois, A., de Bello, F., Desaegher, J., Genty, L., Goulnik, J., Grosjean, J., Jacquemart, A.-L., Kergunteuil, A., Junker, R. R., Jeannerod, L., Odoux, J.-F., Proffit, M., Schatz, B., Vanderplanck, M., E-Vojtkó, A., & Baude, M. (2025). Handbook of protocols for standardized measurements of floral traits for pollinators in temperate communities. *Methods in Ecology and Evolution*, 16, 988–1001. <https://doi.org/10.1111/2041-210X.70031>

Neumüller, U., Burger, H., Krausch, S., Blüthgen, N., & Ayasse, M. (2020). Interactions of local habitat type, landscape composition and flower availability moderate wild bee communities. *Landscape Ecology*, 35, 2209–2224. <https://doi.org/10.1007/s10980-020-01096-4>

Nicholls, C. I., & Altieri, M. A. (2013). Plant biodiversity enhances bees and other insect pollinators in agroecosystems: A review. *Agronomy for Sustainable Development*, 33, 257–274. <https://doi.org/10.1007/s13593-012-0092-y>

Ortega-Ramos, P. A., Coston, D. J., Seimandi-Corda, G., Mauchline, A. L., & Cook, S. M. (2022). Integrated pest management strategies for cabbage stem flea beetle (*Psylliodes chrysocephala*) in oilseed rape. *GCB Bioenergy*, 14, 267–286. <https://doi.org/10.1111/gcbb.12918>

Perrot, T., Bretagnolle, V., Acar, N., Febvret, V., Matejcek, A., Grégoire, S., & Gaba, S. (2024). Bees improve oil quality of oilseed rape. *Basic and Applied Ecology*, 76, 41–49. <https://doi.org/10.1016/j.baae.2024.02.002>

Potts, S. G., Biesmeijer, J. C., Kremen, C., Neumann, P., Schweiger, O., & Kunin, W. E. (2010). Global pollinator declines: Trends, impacts and drivers. *Trends in Ecology & Evolution*, 25, 345–353. <https://doi.org/10.1016/j.tree.2010.01.007>

Raderschall, C. A., Bommarco, R., Lindström, S. A. M., & Lundin, O. (2021). Landscape crop diversity and semi-natural habitat affect crop pollinators, pollination benefit and yield. *Agriculture, Ecosystems & Environment*, 306, 107189. <https://doi.org/10.1016/j.agee.2020.107189>

Ricci, B., Lavigne, C., Alignier, A., Aviron, S., Biju-Duval, L., Bouvier, J. C., Choisis, J.-P., Franck, P., Joannon, A., Ladet, S., Mezerette, F., Plantegenest, M., Savary, G., Thomas, C., Vialatte, A., & Petit, S. (2019). Local pesticide use intensity conditions landscape effects on biological pest control. *Proceedings of the Royal Society B: Biological Sciences*, 286, 20182898. <https://doi.org/10.1098/rspb.2018.2898>

Sharp, R., Tallis, H. T., Ricketts, T., Guerry, A. D., Wood, S. A., Chaplin-Kramer, R., Nelson, E., Ennaanay, D., Wolny, S., & Olwero, N. (2018). *InVEST 3.6.0 user's guide*. The Natural Capital Project, Stanford University, The Nature Conservancy, and World Wildlife Fund.

Stanley, D. A., Garratt, M. P. D., Wickens, J. B., Wickens, V. J., Potts, S. G., & Raine, N. E. (2015). Neonicotinoid pesticide exposure impairs crop pollination services provided by bumblebees. *Nature*, 528, 548–550. <https://doi.org/10.1038/nature16167>

Steffan-Dewenter, I., Münzenberg, U., Bürger, C., Thies, C., & Tscharntke, T. (2002). Scale-dependent effects of landscape context on three pollinator guilds. *Ecology*, 83, 1421–1432. [https://doi.org/10.1890/0012-9658\(2002\)083\[1421:SDEOLC\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2002)083[1421:SDEOLC]2.0.CO;2)

Sutter, L., Amato, M., Jeanneret, P., & Albrecht, M. (2018). Overwintering of pollen beetles and their predators in oilseed rape and semi-natural habitats. *Agriculture, Ecosystems & Environment*, 265, 275–281. <https://doi.org/10.1016/j.agee.2018.06.030>

ESPRES : Evaluation du Service de Pollinisation dans des territoires en REduction d'utilisation de pesticides et interaction avec le Service de régulation des ravageurs

Tamburini, G., Bommarco, R., Wanger, T. C., Kremen, C., van der Heijden, M. G. A., Liebman, M., & Hallin, S. (2020). Agricultural diversification promotes multiple ecosystem services without compromising yield. *Science Advances*, 6, eaba1715. <https://doi.org/10.1126/sciadv.aba1715>

Therond, O., Duru, M., Roger-Estrade, J., & Richard, G. (2017). A new analytical framework of farming system and agriculture model diversities: A review. *Agronomy for Sustainable Development*, 37, 21. <https://doi.org/10.1007/s13593-017-0429-7>

Annexe : textes des publications

Deux publications complètes numérotées 1 et 2 dans la liste ci-dessous sont fournies en annexe.

☐ Publications scientifiques parues

- Une publication scientifique est parue dans Agriculture Ecosystems and Environment en 2025. Son texte est le chapitre 3 du manuscrit de la thèse de Thibault Gandara qui est fourni ci-après (258 pages).

☐ Publications scientifiques à paraître

L'ensemble de ces publications sont confidentielles et non diffusables en attendant leur parution.

1- Le manuscrit de thèse de Thibault Gandara est en cours d'évaluation par son jury de thèse et a été finalisé en octobre 2025.

2- L'article ci-après a été soumis à Innovations Agronomiques en septembre 2025.

☐ Publications scientifiques prévues

L'ensemble de ces publications sont confidentielles et non diffusables. Elles seront soumises prochainement dans des revues scientifiques.

Trois publications scientifiques sont prévues prochainement et elles constituent respectivement les chapitres 2, 3 et 5 du manuscrit de thèse de Thibault Gandara.



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THESE

Pour obtenir le grade de

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Spécialité : Sciences écologiques et agronomiques

Présentée et soutenue publiquement par

Thibault Gandara

Le 09/12/2025 sous réserve d'autorisation par les rapporteurs

**Évaluation du service de pollinisation en grandes cultures :
spatialisation, déterminismes environnementaux et relation
avec le service de régulation des ravageurs**

Sous la direction de : **Emmanuelle Porcher, Professeure au Muséum National
d'Histoire Naturelle, Alice Michelot-Antalik, Professeure à l'université de
Lorraine et Antoine Gardarin, Maître de conférences à AgroParisTech**

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Rapporteuse

Rapporteur

Examineur

Examinatrice

À ma famille, à mes ami·es,

Papi, Mamie,

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Résumé en français

La perte d'habitats naturels et l'usage intensif de pesticides contribuent au déclin des pollinisateurs en milieu agricole, menaçant ainsi le service de pollinisation indispensable à de nombreuses cultures. Ce déclin pourrait entraîner une baisse des rendements et fragiliser le fonctionnement des agroécosystèmes. Il est donc essentiel de quantifier la pollinisation, mais aussi la régulation des ravageurs qui est assurée par des groupes d'insectes souvent différents, qui peuvent aussi être impactés par les pratiques agricoles. Comprendre les relations entre ces deux services est essentiel pour renforcer la résilience des systèmes agricoles et préserver la biodiversité. Ma thèse s'inscrit dans cette démarche en développant des méthodes simplifiées pour évaluer et cartographier le service de pollinisation et mieux comprendre ses liens avec les pratiques agricoles, le paysage et le contrôle des ravageurs dans les grandes cultures.

Le premier axe compare différents proxys de pollinisation pour évaluer leur pertinence. Des expérimentations sur un réseau de parcelles du bassin parisien ont combiné des observations non destructives de l'abondance et de la diversité de morphogroupes de pollinisateurs sur colza et flore spontanée, avec des mesures de pollinisation sur plantes phytomètres (fraisiers) et des composantes du rendement du colza. Ces approches non destructives et facilement répliquables constituent une contribution originale. Les résultats de ces différents proxys montrent que l'usage de pesticides réduit la pollinisation, tandis que la diversité du paysage semble la favoriser.

Le deuxième axe étudie l'efficacité des fraisiers comme indicateurs de pollinisation le long d'un gradient d'anthropisation incluant l'urbanisation, en collaboration avec deux doctorants. Comme attendu, la masse des fraises est plus élevée en pollinisation libre qu'avec exclusion des pollinisateurs, mais uniquement en milieu agricole. De plus, l'environnement immédiat influence la pollinisation. Toutefois, le fraisier ne permet pas de détecter finement les variations liées aux composantes paysagères.

Le troisième axe compare des indicateurs de pollinisation à l'échelle du territoire. Un indicateur basé sur le rendement est testé et comparé à un indice fondé sur l'occupation du sol. Les deux indices sont positivement corrélés et se valident ainsi mutuellement, suggérant que l'on capture bien le même service écosystémique. Une corrélation négative significative est observée entre estimation de la pollinisation basée sur les rendements et l'usage de pesticides à l'échelle de la parcelle.

Enfin, le quatrième axe élargit le prisme d'analyse en considérant à la fois service de pollinisation et service de régulation des ravageurs du colza pour explorer leurs déterminants et corrélations. Nous avons évalué le service de régulation biologique par conservation, en nous

intéressant au parasitisme des méligèthes et des altises, ainsi qu'à la régulation des pucerons. Nos résultats montrent des corrélations globalement positives entre pollinisation et régulation des ravageurs, notamment entre la régulation des altises et la pollinisation, même si les autres corrélations restent d'intensité modérée. Les composantes paysagères et pratiques agricoles ont des effets variés sur les services, même s'il est à noter que l'usage de pesticides a un effet négatif, limitant la fourniture simultanée des services. La variation des services selon le paysage et les pratiques souligne la complexité de leur gestion conjointe.

Ces travaux ouvrent des perspectives pour des protocoles de suivi simplifiés, voire automatisés, permettant d'évaluer la pollinisation à différentes échelles spatiales et temporelles. Ils fournissent aussi un cadre pour mesurer l'efficacité des infrastructures agroécologiques ou changements de pratiques visant à améliorer pollinisation et contrôle biologique et contribuent à l'aménagement du territoire en identifiant les zones prioritaires pour ces interventions.

Abstract in English

The loss of natural habitats and the intensive use of pesticides contribute to the decline of pollinators in agricultural landscapes, thereby threatening the pollination service that is essential for many crops. This decline could lead to yield reductions and weaken the functioning of agroecosystems. It is therefore crucial to quantify pollination, but biological pest control, which is ensured by often different groups of insects that are also affected by agricultural practices. Understanding the relationships between these two services is key to strengthening the resilience of farming systems and conserving biodiversity. My PhD fits within this framework by developing simplified methods to evaluate and map pollination services, and by exploring their links with farming practices, landscape features, and pest control in large-scale crops.

The first axis compares different proxies of pollination to assess their relevance. Field experiments on a network of plots in the Paris Basin combined non-destructive observations of the abundance and diversity of pollinator morphogroups on oilseed rape and spontaneous flora, with pollination measurements on phytometer plants (strawberries) and yield components of oilseed rape. These non-destructive and easily replicable approaches represent an original contribution. Results from the different proxies show that pesticide use reduces pollination, while landscape diversity appears to enhance it.

The second axis investigates the effectiveness of strawberries as indicators of pollination along a gradient of anthropization, including urbanization, in collaboration with two fellow PhD students. As expected, fruit mass was higher under open pollination than under pollinator

exclusion, but only in agricultural environments. Moreover, the immediate surroundings influenced pollination. However, strawberries proved unable to finely detect variations related to landscape components.

The third axis compares pollination indicators at the territorial scale. A yield-based indicator was tested and compared with a land-cover-based index. The two indices were positively correlated and thereby validated each other, suggesting that they indeed capture the same ecosystem service. A significant negative correlation was observed between the yield-based pollination indicator and pesticide use at the plot scale.

Finally, the fourth axis broadens the scope of analysis by jointly considering pollination and biological pest control services in oilseed rape, in order to explore their drivers and correlations. We evaluated conservation biological control services by measuring parasitism of pollen beetles and flea beetles, as well as the regulation of aphids. Our results reveal generally positive correlations between pollination and biological control, particularly between flea beetle regulation and pollination, although other correlations were of more moderate intensity. Landscape components and farming practices had diverse effects on the services, but pesticide use consistently showed a negative impact, limiting the simultaneous provision of both. The variation of services across landscapes and practices highlights the complexity of their joint management.

This work opens perspectives for simplified, and potentially automated, monitoring protocols to evaluate pollination across spatial and temporal scales. It also provides a framework to measure the effectiveness of agri-environmental schemes or practice changes aimed at enhancing pollination and biological control, and contributes to land-use planning by identifying priority areas for such interventions.

Table of content

Acknowledgements

Publications and communications

0. General Introduction	1
1. Anthropogenic pressures are a major driver of biodiversity loss	2
2. Implications for ecosystem processes and services	7
3. Rethinking agroecosystem models: bridging biodiversity and production through agroecology	13
Objectives of this PhD	20
I. General Material and Methods	25
1. Presentation of the study sites	26
2. Sampling protocols and experimental designs	29
II. Comparing complementary measurements of pollination in association with landscape composition and pesticide use	43
1. Introduction	46
2. Materials and methods	47
3. Results	57
4. Discussion	65
Supplementary materials	70
III. Studying pollination along an agricultural–urban gradient	83
Are strawberries reliable phytometers for studying pollination across agricultural, suburban and urban landscapes?	85
Abstract	86
1. Introduction	86
2. Materials and methods	88
3. Results	94
4. Discussion	98
Conclusion	102
Supplementary materials	103

IV. Application of a crop yield–based pollination index to a small agricultural landscape: comparison with land-use indicators and pesticide use	111
A crop yield-based pollination index reveals the impacts of land cover and pesticide use on realized pollination at a landscape scale	114
Abstract	115
1. Introduction	116
2. Materials and methods	119
3. Results	127
4. Discussion	134
Conclusion	139
V. Complementarity between pollination and biological control	147
Pollination and conservation biological control are positively correlated but driven by contrasting landscape composition and agricultural practices	149
Abstract	149
1. Introduction	150
2. Material and methods	152
3. Results	161
4. Discussion	165
Conclusion	169
VI. General Discussion	189
1. Overview of the methods developed and implemented	191
2. Drivers and spatial dynamics of pollination services in intensive agricultural landscapes	195
3. Perspectives opened by this work and possible integration in public policies	201
4. More general thoughts opened during this thesis	204
References	
Appendix	

Table of abbreviation

LCLU: Land Cover and Land Use

OSR: Oilseed Rape

PC: Pollinator community

PPI: Potential Pollination Index

RPI: Realized Pollination Index

SNE: Semi-natural elements

TGW: Thousand grain weight

Use of AI tools

Artificial intelligence–based tools (such as DeepL and ChatGPT) were used exclusively to improve the grammatical accuracy and clarity of the English text. These tools were employed after the scientific content had been finalized, and no modifications were made to the results or interpretations. Their use was limited to language refinement purposes only.

Picture credits

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Participation to other PhD student works

Duarte S., Desutter-Grandcolas L., **Gandara T.**, Ropars L., Machon N. Contrasting responses of pollinators to urbanization and local management in urban farms of Havana. *In preparation*.

Reviews for peer-reviewed journals

2 reviews performed with Emmanuelle Porcher for *Agriculture Ecosystem and Environment*

Publication in non-indexed journals

Clélia Sirami, Emmanuelle Porcher, **Thibault Gandara**, Solène Agnoux, 2024. Agriculture et pollinisateurs : vers une nouvelle alliance ? Pour la Science

<https://www.pourlascience.fr/sd/ecologie/agriculture-et-pollinisateurs-vers-une-nouvelle-alliance-26651.php>

Communications

International Congresses (2 presentations)

November 2022 | Metz | SFE² GfÖ EEF International Conference on Ecological Sciences "Ecology and Evolution: New perspectives and societal challenges" | *Evaluation and comparison of pollination service indicators at agricultural landscape level*

October 2024 | Lyon | SFE² International Congress in Ecology and Evolution | Poster: Evaluation/Assessment of pollination services across farmed landscapes reveal negative impacts of pesticide use and habitat loss on pollination

National Congresses (2 presentations)

October 2023 | Bordeaux | 5ème réunion annuelle du GDR Pollineco | Evaluation de l'abondance et la diversité de pollinisateurs en milieu agricole en fonction des pratiques et du paysage.

October 2024 | Dijon | 6ème réunion annuelle du RT Pollineco | New approaches to assess pollination services across farmed landscapes reveal negative impacts of pesticide use and habitat loss on pollination

Scientific outreach (5 presentations)

2023 – 2025 | Paris | A full teaching assignment divided between lectures for M1 and M2 students and outreach workshops for school pupils.

November 2023 | Besançon | 3e Assises nationales des insectes pollinisateurs | Conference: *Quels indicateurs pour évaluer l'état des pollinisateurs et le service de pollinisation ?*

March 2024 | Paris | Webinaire Be CREATIVE - Les indicateurs de biodiversité pour l'évaluation des systèmes agricoles et des territoires | *Mesurer la pollinisation*

February 2025 | AgroParisTech, Palaiseau | Meeting with Rocco Bommarco | Evaluation of the pollination service in intensive agricultural landscapes and correlations with the biological pest control service

0

General Introduction



Zygaena rhadamanthus, in the Cévennes, 2021, © Thibault Gandara

1. Anthropogenic pressures are a major driver of biodiversity loss

1.1 The sixth mass extinction is underway

Current biodiversity loss is occurring at an unprecedented rate, with scientists warning of a sixth mass extinction impacting a broad range of taxa on Earth (Ceballos et al., 2015; Cowie et al., 2022). This current crisis is marked by rapid declines in population sizes, geographic ranges, and ecological functions of countless species, driven primarily by anthropogenic pressures such as habitat destruction, climate change, pollution, and overexploitation with rates of extinction estimated 1000 times faster than estimated background rates of extinction (Pimm et al., 2014). Currently, the IUCN Red List reports over 47,000 species, equivalent to 28% of evaluated species, threatened with extinction (IUCN, 2025). Such alarming figures have raised huge concerns in the scientific community and a growing consensus on the urgent need to act to slow this process down. In addition, beyond fulfilling functional roles in ecosystems, species are increasingly valued for their intrinsic value, emphasizing the ethical requirement for action to conserve biodiversity (Vucetich et al., 2015).

Land-use change is recognized as one of the primary drivers of biodiversity loss on a global scale (de Chazal and Rounsevell, 2009; Newbold et al., 2015). When natural ecosystems are converted into agricultural, urban, or industrial areas, the resulting habitat fragmentation disrupts essential ecological processes and puts many species at risk of decline or extinction. Furthermore, these land-use changes are often accompanied by polluting factors, whose combined effects aggravate the consequences for biodiversity. The Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) reports that these alterations cause a cascade of direct and indirect drivers, leading to cumulative negative effects on biodiversity (Figure 1). This is for example true for urbanization, which is accompanied by heat island effects and air pollution in urban areas (Romero et al., 1999). Similarly, land conversion for intensive agriculture can result in an increased use of fertilizers and pesticides when converting semi-natural areas or extensive agricultural land to intensive farming (Urruty et al., 2016). Intensification of agriculture is pointed out at a global scale as the major driver in the transgression of several planetary boundaries, making it a key sector to work on global sustainability for both biodiversity preservation, but also human health.

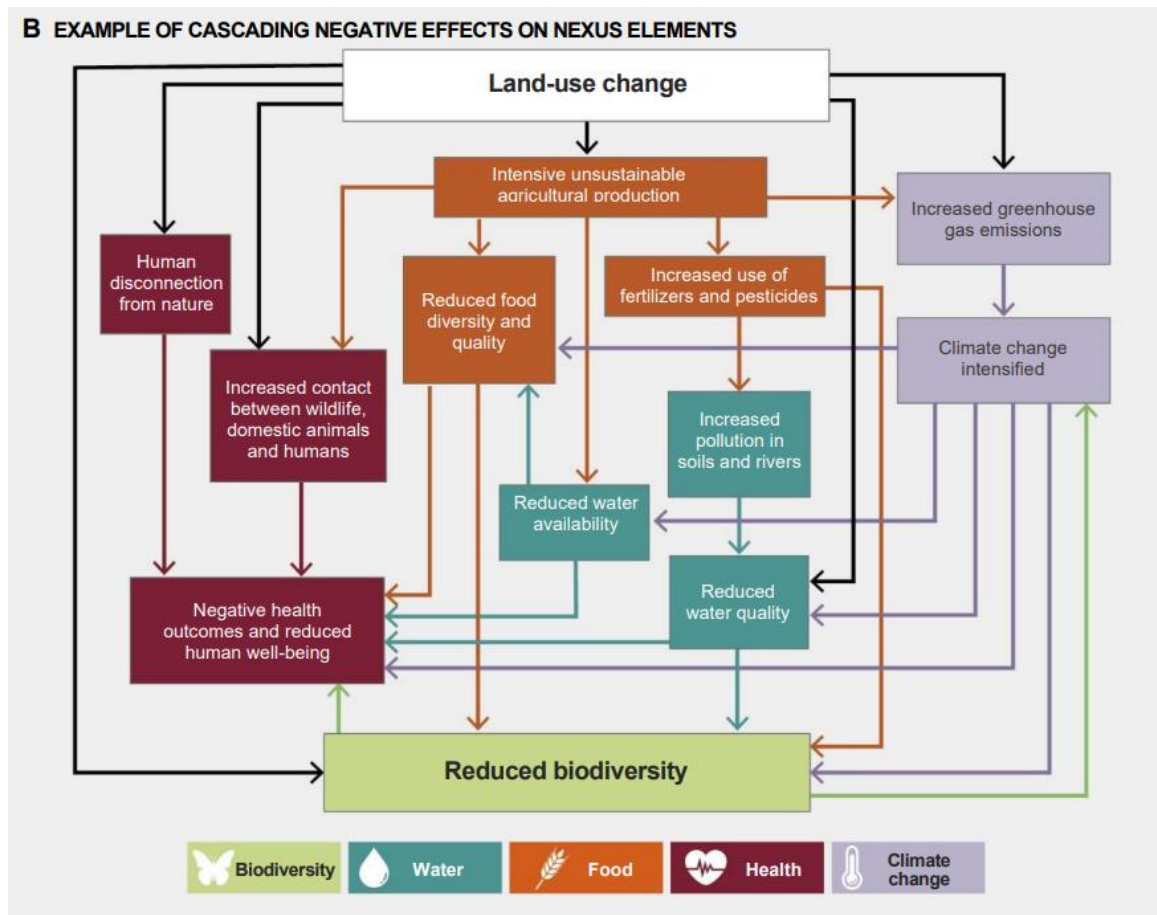


Figure 1. Example of negative cascading effects on Nexus elements. Source : McElwee et al. (2025)

1.2. Agricultural areas are particularly affected by biodiversity decline

The loss of biodiversity is not only a result of land-use change once, but also of the historical, consistent shift toward simpler and more intensive land management techniques. Thus, anthropic landscape simplification can disturb natural balances and jeopardize the ecological interconnections between ecosystems, human systems and society particularly in agricultural ecosystems. Rachel Carson first brought up this problem in the early 1960s in her seminal book *Silent Spring*, which awakened the public to the devastating consequences of modern agriculture on nature.

“Nature has introduced great variety into the landscape, but man has displayed a passion for simplifying it. Thus, he undoes the built-in checks and balances by which nature holds the species within bounds.” This early warning by Rachel Carson in 1962 captures a key driver of biodiversity loss: the widespread simplification and degradation of habitats as shown in Figure 2. Since the end of World War II, the mechanized agricultural revolution has profoundly transformed farmers’ practices and the functioning of agroecosystems itself (Devienne, 2018).

The acceleration of mechanization with possible external inputs pushed landscapes toward increasing specialization, with the removal of semi-natural elements (Box 1)—such as hedgerows—to support bigger machinery (Van Den Berge et al., 2019; Montgomery et al., 2020). These new practices enabled substantial yield gains (Calderini and Slafer, 1998), but came at a high ecological cost. Intensified land use, homogenization of landscapes, and replacement of semi-natural areas with monocultures have significantly reduced spatial and structural heterogeneity of the agricultural landscapes, disrupting their ecological functioning (Tsiafouli et al., 2015; Kehoe et al., 2017; Cabernard et al., 2024). Thus, semi-natural habitats become more and more lost or fragmented, triggering cascading effects on species richness, ecosystem services, and the long-term resilience of agroecosystems (Diyaolu and Folarin, 2024), including a possible collapse of the ecological networks they support.

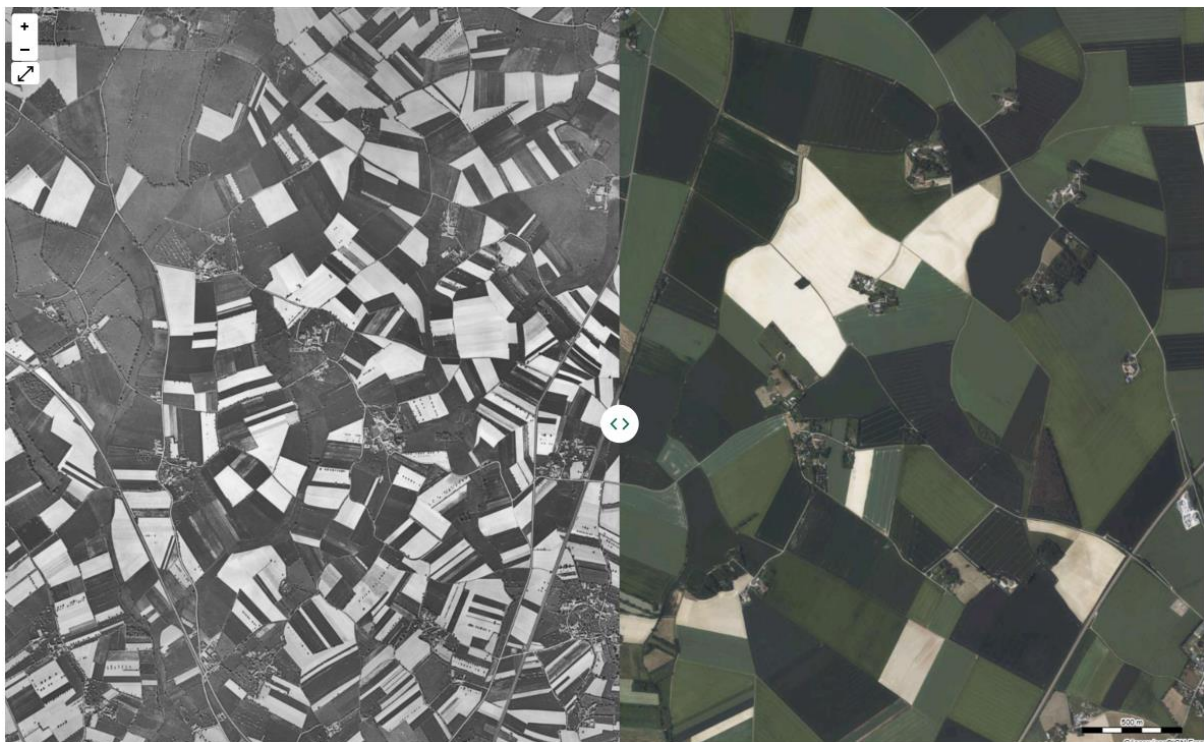


Figure 2. The effects of land consolidation, farm specialization, and enlargement in the Beauce region. The left aerial photograph was taken between 1950 and 1965, and the right one was taken after 2020. Image sourced from the IGN tool *Remonter le temps*.

This agricultural simplification, which shortens crop rotations and reduces area of semi-natural elements, has profound implications for biodiversity, especially for pest dynamics and, thus often leads to increased pesticide use (Meehan et al., 2011). As Rachel Carson wrote in 1962 in *Silent Spring*, “Where do pesticides fit into the picture of environmental disease? We have seen that they now contaminate soil, water, and food, that they have the power to make our streams fishless and our gardens and woodlands silent and birdless. Man, however much he may like to pretend the contrary, is part of nature. Can he escape a pollution that is now so

thoroughly distributed throughout our world?”. Decades later, her warnings are more relevant than ever. Pesticides affect survival, reproduction, and ecological functions of many non-target species (Wan et al., 2025). This is particularly concerning given the current global increase in pesticide use across agricultural ecosystems (Basu et al., 2024) and the re-authorization of neonicotinoids that are known to have severe consequences on insect population such as acetamiprid in France (Ligtelijn et al., 2024). In France, within the framework of the Ecophyto 2030 program, the recent decreases reported in pesticide use appear to result more from changes in calculation methods than from an actual reduction in use (Garnault et al., 2024).

Box 1. Semi-natural elements

Any site within or around an agroecosystem that supports spontaneous vegetation—mainly composed of biennial, perennial, or long-lived plant species—or that hosts intentionally sown, non-harvested cover crops (also known as "service crops"), and that are not disturbed for several years in a row, can serve as a semi-natural habitat. These areas provide essential resources or shelter—either permanently or temporarily—for a wide range of organisms constituting ecosystems, supporting key biological functions such as reproduction, foraging, overwintering, and refuge. They host diverse life forms across multiple domains, including microorganisms, fungi, plants, and animals. In this thesis, the main types of semi-natural elements studied include hedgerows, woodland patches, field margins, and permanent grasslands.

1.3. Insects, a group particularly affected by this decline

When I first mentioned the topic of my PhD to my grandparents, the first thing they discussed with me was the decrease of insects splattered on their car windshields. They remembered that their holiday road trip required frequent stops to clean the windshield, which was quickly covered with insect splashes. Today, such occurrences are rare. This personal anecdote mirrors a broader and shared perception that I heard of during my PhD as the windscreen phenomenon. It is the observed reduction in the number of insects hitting vehicle windshields over time. Although anecdotal and subjective at first, this phenomenon became a symbol of insect decline, prompting public concern to the 6th mass extinction concerning insects.

Few isolated empirical observations of the windscreen phenomenon alone cannot serve as a quantitative measure, this is why some scientists are trying to analyse this phenomenon quantitatively (Møller, 2019; Ball et al., 2022). These studies showed up to 80% decrease in the biomass of insects hit by cars (Whitehouse et al., 2025). To go further than this specific windscreen phenomenon, a large part of the scientific literature confirms that insect populations

are indeed declining at alarming rates. This consensus is supported by both local, long-term monitoring efforts and large-scale syntheses. For instance, (Hallmann et al., 2017)) reported a dramatic 77% decrease in flying insect biomass over 27 years in protected areas across Germany. At a global level, reviews confirm that insect declines are widespread across Europe, North America, and beyond, with only a few exceptions (Sánchez-Bayo and Wyckhuys, 2021). Among the group of insects, pollinators have received particular attention due to their direct relevance to agriculture and ecosystem resilience. Studies such as (Dicks et al., 2021) highlighted not only the widespread decline of pollinators, but also the complex set of pressures—including habitat loss, pesticide use, and climate change—that contribute to pollinator loss (Figure 3).

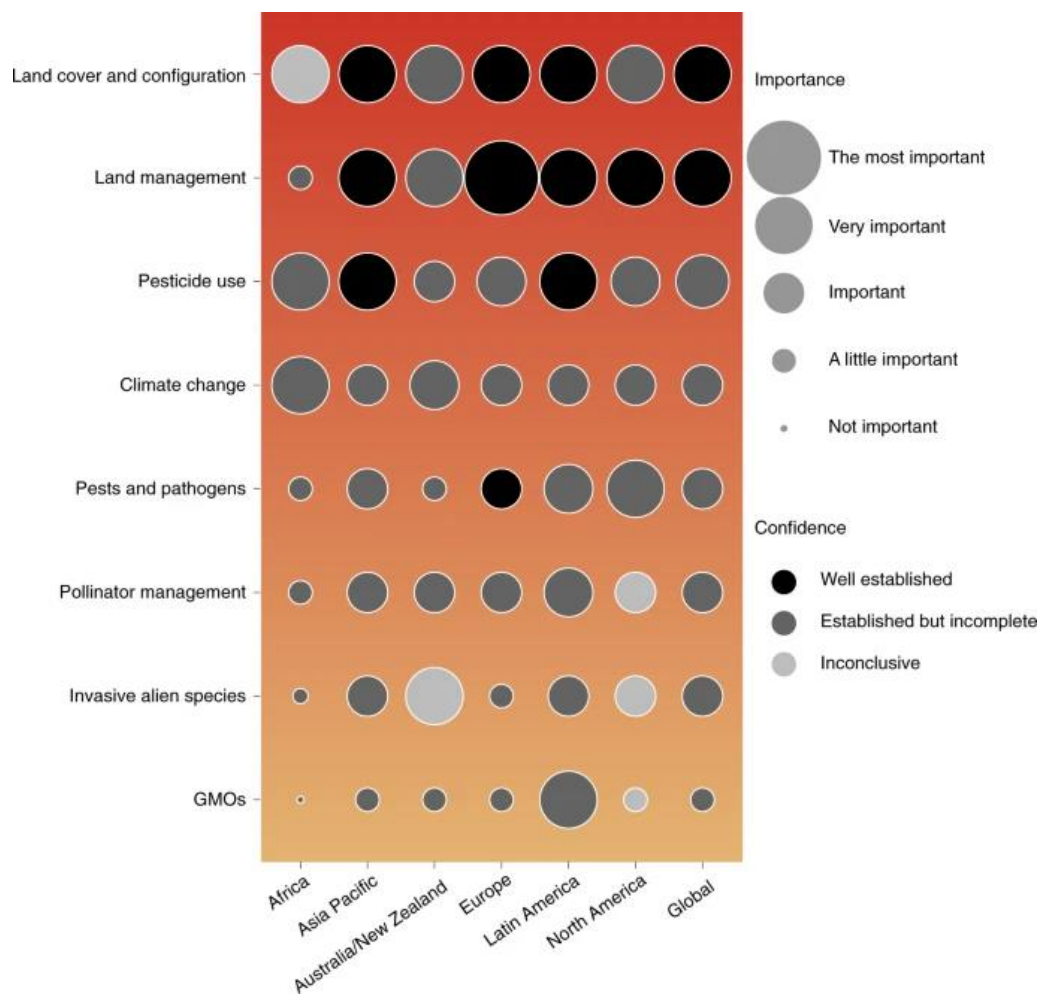


Figure 3. Assessment of the importance of eight major drivers of pollinator decline, for six regions and a global median (right). Source : (Dicks et al., 2021)

Although the negative impacts of agricultural intensification on insects are now well documented, with multiple components of intensification identified as major drivers of insect decline, some uncertainties remain regarding how pesticides specifically shape pollinator

communities (Dicks et al., 2021). This issue is particularly concerning given recent findings suggesting that agricultural landscapes can, under certain conditions, still provide valuable habitats for pollinators (Desaegher et al., 2023). The aim of this PhD is to partly address this issue, by adopting a spatial rather than temporal perspective, owing to the three years duration of the study. We will specifically focus on how agricultural practices (through pesticide use) and landscape composition jointly shape insect communities in large-scale cropping systems, with a focus on pollinators, and the consequences for important ecological functions, as justified below.

2. Implications for ecosystem processes and services

Multiple anthropogenic pressures collectively contribute to the erosion of biodiversity at all levels: genes, species, and ecosystems (Newbold et al., 2015; Bowler et al., 2020). As functional biodiversity declines, the integrity and resilience of ecosystems are also at risk, potentially undermining key ecological processes and the services they provide to human societies (Cardinale et al., 2012). In the context of this thesis, we focus on two key ecological functions that contribute to ecosystem service provision within the category of regulating services: pollination and biological pest control. Both functions play a central role in agroecosystem functioning by mediating biotic interactions that influence crop productivity and the sustainability of agroecosystems.

2.1. Ecological functions addressed in this thesis

2.1.1. Pollination

Pollination plays a fundamental role in terrestrial ecosystems by making the sexual reproduction of seed-producing plants possible. This function corresponds to the transfer of male gametophytes (pollen) to female reproductive structures (carpels), enabling fertilization and then seed development. This process is essential for the sexual reproduction of Spermatophyta, a division including both Gymnosperms and Angiosperms. While Gymnosperms rely exclusively on wind for pollination, Angiosperms—also called flowering plants—evolved floral structures that facilitate pollen transfer, often mediated by animals. This animal-mediated pollination allows pollen transfer on different distances thereby allowing fertilization and the reproduction of plants (Figure 4).

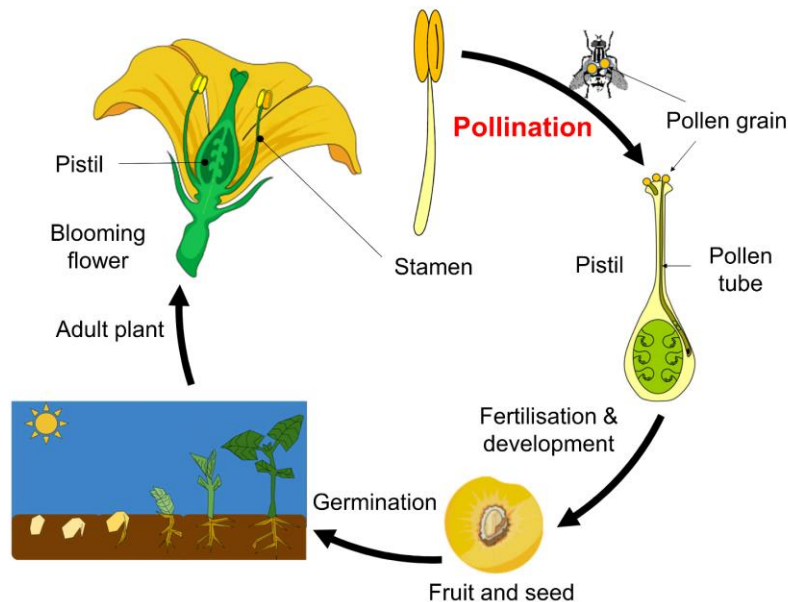


Figure 4. Reproductive cycle of animal-pollinated flowering plants. Credits: Emmanuelle Porcher and <https://commons.wikimedia.org> (Vierge Marie, Mariana Ruiz, Aslyntodd).

In this PhD, we focus on Angiosperm pollination mediated by animals, especially insects, which are the primary pollinators in the world and almost the only animal pollinators in temperate areas. In these ecosystems, pollination is mainly ensured by Hymenoptera (bees, bumblebees, wasps), Diptera (particularly hoverflies), Lepidoptera (butterflies and moths), and Coleoptera (beetles). Among them, wild bees and hoverflies are often highlighted as highly efficient pollinators and the most frequently studied (Kennedy et al., 2013; Osterman et al., 2021), despite other groups also being effective yet largely overlooked. (Orford et al., 2015). Natural selection and coevolution between flowering plants and their pollinators have resulted in widespread animal mediated cross pollination: 87.5% of Angiosperm species are pollinated by animals (Ollerton et al., 2011). In most cases, this relationship is mutualistic: pollinators transfer pollen between flowers while collecting floral resources—such as nectar or pollen—as a food reward (Willmer, 2011). These interactions vary in their degree of specialization, ranging from highly generalized to highly specialized relationship between plants and pollinators (Johnson and Steiner, 2000) as a result of a long history of coevolution. These numerous interactions collectively form complex plant–pollinator networks (Bosch et al., 2009). However, these complex network structures are threatened by rapid, anthropic environmental changes (Burkle and Alarcón, 2011). In the long term, the extinction of pollinators can initiate coextinction cascades, where the loss of dependent plant species leads to further pollinator extinctions, potentially creating a feedback loop of biodiversity loss (Biesmeijer et al., 2006; Vieira et al., 2013) and affecting the functioning of networks and thus ecosystem themselves. For example, we are witnessing a shift towards wind-pollinated plants

and interactions involving generalist pollinators, while species that rely on specific partnerships are declining (Abrahamczyk et al., 2022). Altogether, human-driven landscape change, pollution, and climate change combined with an increasing competition between wild pollinators and managed honey bees (Ropars et al., 2022; Geslin et al., 2023), are reshaping plant–pollinator networks—particularly in agricultural ecosystems (Osterman et al., 2021)—and threatening their stability and long-term persistence.

2.1.2. Parasitism and predation

Predation and parasitism are interactions that benefit one organism to the detriment of another one. These antagonistic interactions are essential to maintain natural ecosystem balance (Combes, 1996; Ripple et al., 2025). Predation, defined as the direct consumption of prey by predators, often results in immediate death, and limits prey abundance, thus preventing outbreak dynamics (Pimentel, 1975; Dwyer et al., 2004). For example, in agroecosystems, syrphidae act as predators, and thus regulators, of aphids populations (Walters et al., 2003; Toft, 2005), but other organisms also parasite aphids (Schmidt et al., 2003). Parasitism is a biotic interaction in which a parasite exploits a host over time, often reducing its fitness. Parasitoids are a specific form of parasites—typically an insect such as a wasp or fly— *“which develops on or in another single (“host”) organism, extracts nourishment from it, and kills it as a direct or indirect result of that development”* (Eggleton and Gaston, 1990; Eggleton and Belshaw, 1997).

2.2. Pollination and predation/parasitism contribute to necessary services in agricultural landscapes

Ecosystem services were formally conceptualized in the *Millennium Ecosystem Assessment* (Millennium Ecosystem Assessment, 2005) as the benefits humans derive from ecosystems, linking ecological processes to human well-being. As they are various ways to define ecosystem services, we will use the following definition here: *“Ecosystem services (ES) are ecological processes or elements of ecosystem structure from which humans derive benefits, either actively—by mobilizing material capital (e.g., energy, water, agrochemicals) and/or cognitive capital (e.g., knowledge, such as agricultural practices)—or passively (e.g., benefit derived from the climate regulation service). The benefits obtained from ES, functionally disconnected from the ecosystem, may be material (goods) or immaterial (socioeconomic services). A single ES can give rise to multiple benefits.”* (Tibi A., Therond O., 2017). To symbolize this link between human and nature through ecosystem services, (Haines-Young and Potschin, 2010) proposed a cascade effect model that provides a clear picture of ecosystem services as the interface between ecological functions and benefits for humans as well as the retroactive impacts humans can have on this cascade (Figure 5).

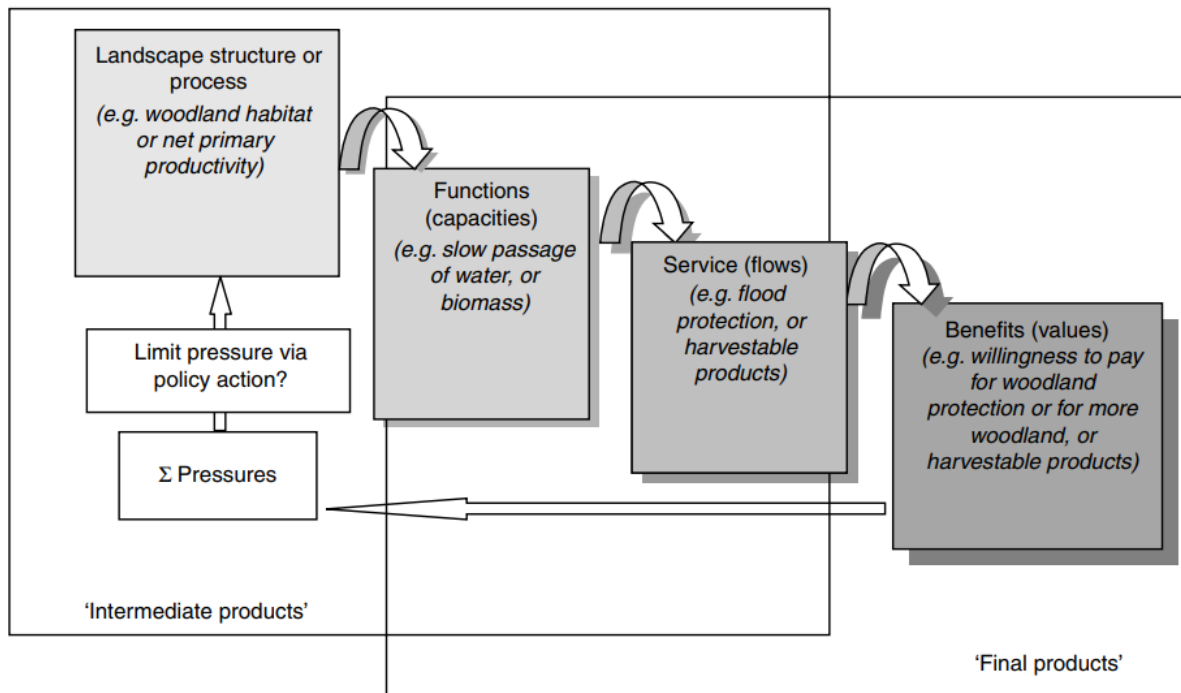


Figure 5. The relationship between biodiversity, ecosystem function and human well-being.
Source : Haines-Young and Potschin (2010)

In this thesis, we will work on several services considered as Regulating Ecosystem services by the FAO (*Biodiversity for food and agriculture and ecosystem services*, 2020). Pest control and pollination are two essential ecosystem services for agricultural ecosystems, supporting crop productivity and sustainability through natural regulation and reproduction processes

2.2.1. Animal pollination service

Pollination considered as an ecosystem service has multiple definitions, each of them being associated with different estimation methods. Five different definitions of pollination service were given by (Liss et al., 2013) considering it from pollinator abundance and diversity to crop yields and linking them to different ecosystem components. It was shown that even within each definition of the pollination, metrics were not the same. The work of (Bartholomée and Lavorel, 2019)) put together this variety of definitions and metrics, analyzing both the diversity of indicators and the methods used to quantify them. This conceptual framework structures the different ways to measure pollination and the associated components as a retroactive loop between ecological functions and social relevance (Figure 6).

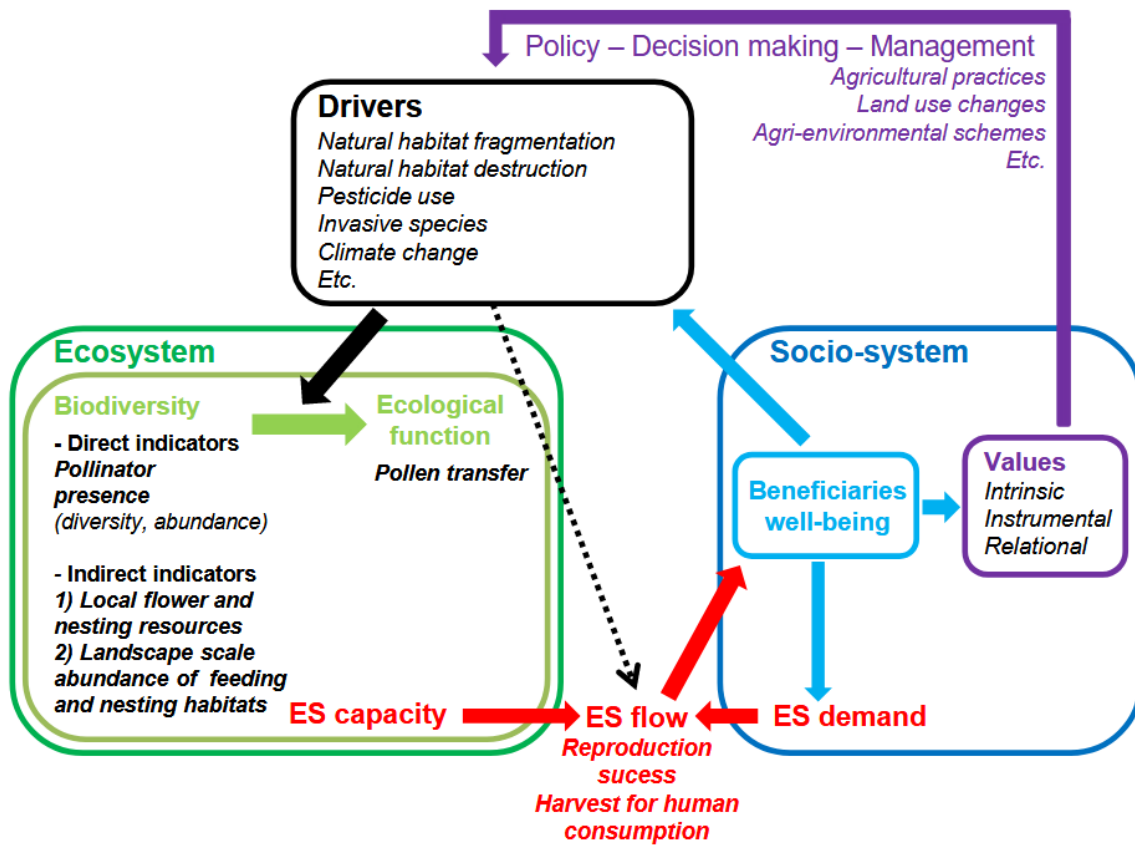


Figure 6. Conceptualisation of the pollination ecosystem. Green boxes and arrows represent ecosystem components; blue boxes and arrows represent socio-system components; red terms and arrows represent ES; purple elements represent ES values and resulting decisions/actions on ecosystems; the black box and arrows represent drivers of ecosystem state and of ES flow. Source : Bartholomée and Lavorel (2019).

Animal pollination is a key ecological process that ensures both the maintenance of diversity in communities of wild plants (Biesmeijer et al., 2006; Thomann et al., 2013; Ehlers et al., 2021) and the quantity and quality of human food (Klein et al., 2007; Lucas A. Garibaldi et al., 2013; Potts et al., 2016). In agrosystems, 70% of cultivated plants depend on pollinators, representing 35% of the annual global production (Klein et al., 2007). Furthermore, the increase of pollinator-dependent crops since the beginning of the 1960s (Aizen et al., 2019) is leading to an increased global demand for pollination services, while simultaneously amplifying the risk of pollination shortfall caused by biodiversity loss, a direct consequence of a less diversified agriculture. Some economists estimated the global value of animal pollination benefit between 235 and 577 billion USD, highlighting the critical importance of pollination services for agricultural ecosystem functioning. In the sixth mass extinction context, considering all the positive outcomes that animal pollination can bring to agricultural systems is essential to influence policies for pollinator conservation.

Despite substantial progress in understanding pollination ecology, knowledge gaps remain. For example, (Senapathi et al., 2017) highlight that, although bee ecology is well studied, we still lack understanding of how other pollinator groups respond to landscape factors, land-use changes and chemicals, emphasizing the need for larger monitoring schemes to produce efficient conservation strategies. Second, the importance of pollination services is well established, but the direct relationship between pollinator abundance and diversity and ecosystem services remains unclear. Theoretically, a higher diversity of pollinators should support complementary pollination of both crops and wild flowers (Woodcock et al., 2019; Katumo et al., 2022). In some agricultural ecosystems, introduction of dominant species such as honey bees provides the majority of pollination services (Fikadu, 2019), shadowing the effects of potential species loss. As even these species are under threat and their provision of pollination services is falling (Breeze et al., 2011), it is more important than ever to understand how biodiversity loss leads to a decline in service provision (Paudel et al., 2015).

The primary objective of this thesis is therefore to assess pollination services in agricultural landscapes through a range of complementary methods. These approaches consider not only the ecological capacity of ecosystems to supply pollination, but also the extent to which this service is useful for humans, especially through its contribution to crop yields. Particular attention will also be given to identifying and quantifying the key ecological and anthropogenic drivers that may modulate the provision of pollination and other ecosystem services across agricultural landscapes. As illustrated in Figure 6, humans can play a role on many drivers to reduce their impact on pollination services.

2.2.2. Conservation biological control

Conservation biological control is an essential ecosystem service in agricultural landscapes, referring to the natural suppression of crop pests by their natural enemies—such as predators and parasites—which regulate pest herbivore population dynamics and pressure on plants, thus contributing to plant protection (Abdala-Roberts et al., 2019; Shameer and Hardy, 2024). This ecosystem service plays a critical role in reducing pest population, thereby contributing to crop protection without systematically relying on pesticide use (Jacquet et al., 2022). Integrated pest management is a concept that is incorporated in many public policies and is based on the balance between targeted pesticide use and natural pest control (Stenberg, 2017). This concept is evolving to integrate more natural control as pests become more and more resistant to pesticides (Bommarco, 2024).

Understanding the ecological and landscape factors that drive the dynamics of these interactions is essential for a broader comprehension of species interactions and manage agroecosystems sustainably (Abdala-Roberts et al., 2019; Brévault and Clouvel, 2019;

Shameer and Hardy, 2024). This is particularly relevant when some natural enemies—such as hoverflies—also provide key ecosystem services like pollination (Shackelford et al., 2013).

2.3. Towards an integrative understanding of pollination and biological control services

Although both functions are essential to agroecosystem sustainability and have received a lot of attention separately, their potential interactions and the extent to which they are interdependent are still understudied. Most studies either focus on a single ecosystem function, typically pollination (e.g. Cole et al., 2022; Crochard et al., 2022), or biological pest control (Rusch et al., 2011; Serée et al., 2022) and new studies that explore multifunctionality (Leroy et al., 2025) do not always examine the interactions between the functions studied. In addition, the mechanisms driving variation in these functions across landscapes remain poorly understood. Consequently, the extent to which these two key functions are correlated and jointly influenced by landscape composition and semi-natural habitat types needs to be studied further. These gaps are particularly relevant in intensively managed agricultural landscapes, where simplification of habitats, pesticide use, and other anthropogenic pressures may alter both the magnitude and spatial distribution of ecosystem services (Vanbergen, 2014).

By addressing these gaps, this thesis aims to provide a mechanistic understanding of how biodiversity and landscape composition jointly shape the provision of pollination and biological control services. Ultimately, this work seeks to provide simple repeatable approaches to guide management strategies that enhance the resilience and sustainability of agroecosystems, by identifying conditions under which both services can be maintained or improved.

3. Rethinking agroecosystem models: bridging biodiversity and production through agroecology

In the face of the dramatic decline in biodiversity, particularly insects, in farmland (Outhwaite et al., 2022) and regarding the need to reduce the use of synthetic inputs in agriculture (Rani et al., 2021), agroecology offers a promising framework by integrating biodiversity-based strategies into the management of agricultural systems (Lundin et al., 2021).

3.1. Enhancing synergetic ecosystem services

Scientists urge for a transformation of the agricultural system from food production to transformation and consumption in order to ensure global food security. Scenarios are proposed, combining shifts in consumption patterns with more sustainable agricultural

practices, which is intrinsically linked to the development of agroecology across farming landscapes (Billen et al., 2021). This agroecological approach integrates multiple ecosystem services and aims to optimize their synergistic functioning, to reduce the use of synthetic inputs while maintaining economically viable farming systems. Building on the two ecosystem services discussed above, Integrated Pest and Pollinator Management (IPPM) is a concept that incorporates pollinator conservation into an already well-established decision-support framework for crop management (Lundin et al., 2021). The underlying idea is that some landscape drivers and agricultural practices influence both pollinators and predators. In this PhD work we will investigate the link between pollination and biological pest control and how they are influenced by landscape structure and agricultural practices, as illustrated in Figure 7.

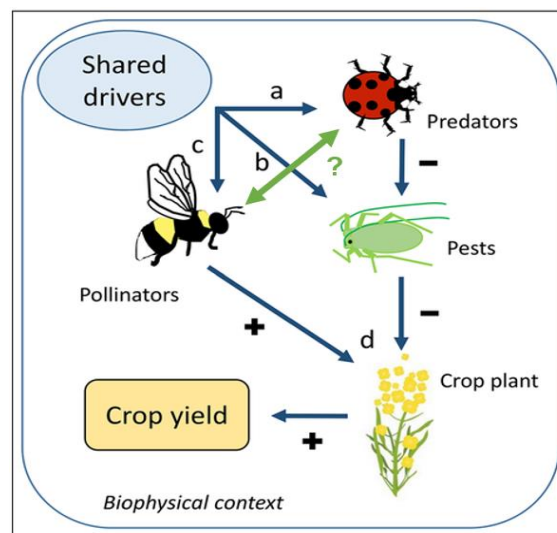


Figure 7. Ecological interactions among pests, natural enemies (predators), pollinators, and crop plants influence crop yield. Interdependence of pest and pollinator management is created by two distinct mechanisms: (a–c) shared drivers and (d) effects of the organism groups on one another’s functioning. These interactions can be modified by the biophysical context (e.g., climate or geographic region). Arrows indicate links between drivers, organisms, and crop yield. Plus (+) and minus (–) signs indicate positive and negative relationships, respectively. The green arrow indicates the possible link between pollination and biological pest control services. Source : Lundin et al. (2021)

3.2. Designing biodiversity-friendly landscapes for resilient pollination services

Designing more heterogeneous and ecologically mindful agricultural landscapes offers a promising pathway to reconcile food production with biodiversity conservation. Landscape heterogeneity refers to the diversity and spatial arrangement of land-use types and habitats, often enhanced by increasing semi-natural elements, but also by greater crop heterogeneity such as smaller field sizes and more diverse crop types. (Sirami et al., 2019) showed that such

within-crop mosaic diversity can support a wide range of species across trophic levels, with effects comparable to or stronger than those of seminatural elements, even in simplified landscapes. These structural changes can be reinforced by local practices such as sowing flowering cover crops or allowing spontaneous flowering weeds to grow between seasons, which provide valuable nectar and pollen resources for pollinators (Petit et al., 2011; Crochard et al., 2022). In addition, smaller fields can facilitate the reintroduction of hedgerows and other linear elements that serve as habitats and continuous corridors for many beneficial species (Dover, 2019). However, such practices remain marginal in conventional systems, as they often conflict with prevailing agronomic norms and objectives: spontaneous weeds are typically viewed as undesirable, and their presence tends to reflect a failure to fully control the field rather than an intentional ecological strategy (Petit et al., 2011; MacLaren et al., 2020).

Ecological designs for more biodiversity-friendly farming systems therefore need to be considered at both the level of local practices and landscape-level habitat availability (Lacombe et al., 2018; Cheng et al., 2020; Tschamntke et al., 2022). For example, Kennedy et al. (2013) highlighted the importance of addressing both of these complementary scales to preserve the abundance and diversity of wild bees, and this is also true for natural enemies (Rusch et al., 2010). Biodiversity gains for common biodiversity can be achieved at the farm level when environmental standards are respected but there is still work to do on landscape scale interventions to preserve threatened species (Aviron et al., 2009). This underscores the need to identify areas where services such as pollination and biological control are most limited, in order to strategically target conservation efforts. Agroecological planning should operate at multiple scales, combining local actions (such as pesticide reduction within farms) and broader landscape-level interventions, including the enhancement of semi-natural elements, increased crop diversity, and overall reduction in pesticide use, to effectively support biodiversity. This supports land-sharing and land-sparing as complementary strategies, both essential to reconcile agricultural productivity with the conservation of biodiversity and ecosystem services (Grass et al., 2019). This perspective is in line with the ambition of this thesis, which is to improve our understanding of the conditions under which pollination services and biological control can be maintained or restored in intensive agricultural landscapes. By identifying how landscape structures and farming practices support or limit pollination, we aim to inform the spatial prioritization of agroecological interventions and help create designs of resilient cropping systems for pollinator-dependent crops.

Box 2. Land-sparing and land-sharing

Land-sparing and land-sharing represent two contrasting strategies to reconcile agriculture and biodiversity conservation. Land-sparing separates intensive agricultural production from areas set aside for nature, while land-sharing integrates biodiversity-friendly practices within farmland.

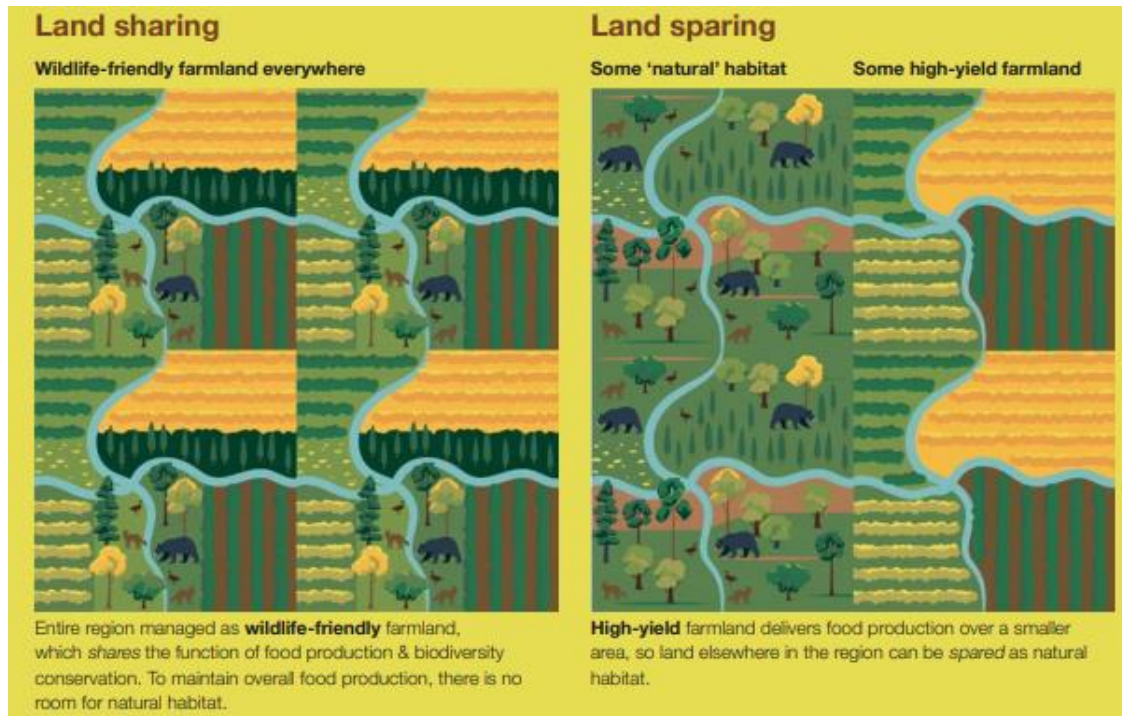


Figure 8. Presentation of land sharing and land sparing approaches (Meijaard et al., 2024).

3.3. How to measure ecosystem services? The example of pollination services.

Understanding why pollination services are limited in intensive landscapes and spatializing this information requires reliable methods to assess both pollinator communities and their contribution to crop production. Ecological infrastructures and agroecological practices offer promising solutions to protect pollinators, but their effectiveness must be evaluated through appropriate measurements for pollination and biological control as ecosystem services (Bartholomée and Lavorel, 2019; Albrecht et al., 2020). To study pollinators and pollination services, which is the main objective of this thesis, scientists and naturalists have developed a variety of protocols to monitor pollinators and pollination, ranging from simple to highly technical approaches. Lethal methods remain the most commonly used to study pollinator communities and thus an indirect proxy of pollination, as they allow species-level identification

through pan traps or sweep netting followed by lab identification. These approaches are time-consuming, demanding expert knowledge for taxonomical determination, and often destructive which raises ethical concerns, especially when insect populations are already threatened by human activities (Barrett and Fischer, 2024). Non-lethal alternatives, such as direct observation of floral visits or photographic monitoring, are gaining interest for their potential to track pollinator activity without harming individuals. For example, harmonizing systematic professional and participatory monitoring schemes across Europe could be a good way to adopt non-lethal methods to monitor both plant and pollinator populations, as well as their interactions (Porcher et al., 2024).

Pollinator monitoring as a proxy for pollination has also led to the development of modelling approaches that estimate the service based on expert knowledge of habitat resources. For example, Lonsdorf et al. (2009) introduced a model that uses information on pollinator nesting resources, floral resources, and foraging distances to predict the potential relative abundance of pollinators within nesting habitats. From these nesting areas, the model then infers the relative abundance of pollinators in nearby croplands requiring pollination services. However, other approaches rely directly on the measurement of the pollination service itself, through its outcome on plant reproduction and crop yield. This is the case for phytometer plants, which are used to quantify pollination by comparing the reproductive success between pollinator-excluded and open-pollinated flowers (Woodcock et al., 2014). Such reasoning linking pollination to yield has also led to the development of large-scale indices that integrate the dependence of different crops on pollinators and their respective yields, providing estimates of a landscape-level pollination index (Martin et al., 2019). A balance between precision, feasibility, and ecological responsibility is increasingly important to improve the spatial and temporal resolution of biodiversity and ecosystem services monitoring and guide the implementation of agroecological structures effectively.

In this thesis, the large cereal plains of the Paris Basin, especially oilseed rape fields (see box 3), serve as a study system to test non-lethal methods for assessing pollination services. These methods aim to evaluate both pollinator populations and the pollination services they provide, while identifying their landscape- and practices-related drivers. In addition, for a more automated approach to the spatial modelling of pollination services, existing crop yield datasets collected by INRAE Dijon were mobilized to explore how service provision can be mapped across agricultural landscapes.

Box 3. Oilseed rape

In large Jurassic cereal-growing regions of France, agricultural systems are predominantly based on a wheat–barley–oilseed rape rotation. This rotation is widely adopted due to its combined agronomic and economic benefits while associated with wheat (*Triticum aestivum*) and barley (*Hordeum vulgare*), cereals that provide high yields and incomes. In cereal-dominated rotations, oilseed rape (*Brassica napus*) introduces functional diversity into the system serving as a break crop that reduces cereal disease pressure, particularly root and stem diseases and also releasing bioactive compounds (e.g., glucosinolates) that suppress soilborne pathogens when residues are left in place in the field. It is a winter crop with a deep rooting system, making it relatively tolerant to water stress and particularly well suited to shallow soils with low water-holding capacity, such as those found on Jurassic plateaus, where spring or summer crops are less viable. Additionally, oilseed rape contributes to improved soil organic matter and carbon inputs, enhancing soil structure, nutrient retention, and water-holding capacity. Its biomass return to the soil exceeds that of most other crops, especially when combined with cover crops or long fallow periods (Terres Inovia, 2019). From an economic perspective, oilseed rape is primarily cultivated for biodiesel production, as well as for vegetable oil markets.

Pollination of oilseed rape

Oilseed rape (*Brassica napus*) is a partially pollinator-dependent crop: while it is capable of self-pollination, a significant proportion of yield can be influenced by animal-mediated pollination. The degree of dependence varies depending on environmental conditions and cultivar characteristics. Accordingly, estimates of the contribution of insect pollination to oilseed rape yield range widely, from negligible to as much as 50% (e.g. (Stanley et al., 2013; Bartomeus et al., 2015; Perrot et al., 2018; Siopa et al., 2024)). It is considered a mass-flowering crop, as it blooms over a short period of time, mainly few weeks between March and May, during which it provides a large and concentrated supply of floral resources for insect pollinators (Westphal et al., 2003a; Rollin et al., 2015).

Biological pest control of oilseed rape

Oilseed rape is also exposed to strong pest pressure, particularly from insects such as the pollen beetle (*Brassicoglyphus aeneus*, Coleoptera: Nitidulidae) and the cabbage stem flea beetle (*Psylliodes chrysocephala*, Coleoptera: Chrysomelidae) making oilseed rape sensitive to pest pressures and diseases leading to the strongest pesticide use in cereal plains with a mean Treatment Frequency Index (TFI)* of 6,3 (Chayre et al., 2024). Chemical control has

become increasingly challenging due to rising insecticide resistance (Bruce, 2010; Hervé, 2018). Although most OSR pests can be partly regulated by specialist parasitoids (Gagnon, 2017; Riggi et al., 2017) and generalist predators (Gagnon, 2017), this natural control may not be sufficient to replace insecticides, especially in areas where no agroecological practices favour them. In some cases, farmers are left with few options and may even abandon OSR. Nevertheless, agroecological practices such as flower strips or companion cropping show promising potential to support conservation biological control and reduce pesticide reliance (Serée et al., 2022).

* TFI is the cumulative dose of each active substance applied throughout the crop cycle (from the previous crop harvest to the actual harvest), divided by the maximum authorized dose under French national guidelines.

To conclude on this section, current methods to assess pollination largely rely on indirect proxies, such as insect abundance or land-cover data to predict pollinator presence (Lonsdorf et al., 2009). Moreover, direct approaches, comparing open versus pollinator exclusion or hand-pollinated flowers, remain time-consuming, limited to small numbers of plants, and are rarely applied at large landscape scales. To address this, we combine measurements of in-field pollinator communities with open- versus caged-flower experiments and evaluate a yield-based pollination index, allowing direct estimation of pollination services across landscapes. By testing these approaches at both fine and broad spatial scales, and examining their relationships with landscape structure, agricultural practices, and temporal variation, we aim to provide scalable tools and actionable insights for mapping pollination and guiding decisions to preserve pollinators and pollination services in intensive farming systems. Finally, this work also explores how agricultural practices can modulate the yield benefits ensured by pollination, thereby highlighting opportunities to enhance both crop production and biodiversity conservation.

Objectives of this PhD

Large intensive agricultural landscapes, especially cereal farming regions, are among the most hostile environments for pollinators. These landscapes are often characterized by intensive monocultures, dominated by crops whose flowers provide little or no resources for pollinators, widespread pesticide use, and only few semi-natural elements, leading to limited availability and continuity of floral and nesting resources. Evaluating pollination services becomes crucial in these landscapes, particularly for mass-flowering crops such as oilseed rape and sunflower, which are already integrated into largely widespread crop rotations. It also aligns with more sustainable agricultural scenarios that aim to relocate food production while preserving ecological functions (e.g. Billen et al., 2021; Mora et al., 2023).

The ambition of this thesis is to go beyond existing knowledge on pollination in oilseed rape by testing complementary approaches to assess this service: non-lethal in-field observations of pollinators, experiments on yields with pollinator exclusion, and a yield-based pollination index that allows direct estimation of services at large spatial scales. By combining these methods across multiple years and spatial resolutions, and by explicitly linking pollination services to landscape structure and farming practices, this work aims to provide new insights into the spatial variability of pollination and its drivers in simplified cereal landscapes. The four objectives are structured as follows and represented graphically in Figure 9.

1. In-field assessment of pollination and pollinator interactions across habitats.

We will compare two simple and repeatable methods to quantify pollination services directly within crop fields: pollinator-exclusion experiments on phytometer plants, namely oilseed rape and strawberry plants placed in the field, and pollinator interaction observations conducted within oilseed rape fields, along paths or field edges, and on strawberry flowers. Yield components, such as number of siliques, seeds per silique, and fruit set, will also be measured to link pollinator activity to plant reproductive success. This approach will allow us to examine how pollinator communities differ between crops and adjacent field margins and to what extent margin-associated pollinators contribute to visitation rates, pollination, and crop yields. We expect that pollinator communities will differ between crops and margins, with margin-associated pollinators contributing significantly to crop pollination and yield, particularly in simplified landscapes.

2. Landscape-scale assessment of pollination using standardized phytometers.

Strawberry plants are used as standardized phytometers across multiple sites over two years to measure pollination services, with fruit traits such as mass and deformations serving as direct indicators of flower pollination. This approach enables quantification of how variations in landscape composition and land use affect pollination services across different contexts, including urban, peri-urban, and intensive agricultural environments. We anticipate that sites with more diverse landscapes and greater semi-natural habitat availability will exhibit higher fruit mass and fewer malformations, reflecting more effective pollination.

3. Development of a yield-based pollination indicator.

We aim to develop a simple and reproducible pollination indicator based on crop yields, using data from the Fénay long-term landscape observatory. This tool is designed to capture spatial variation in pollination services across large-scale agricultural areas where crops differ in their dependence on pollinators. The indicator can potentially be extended to other arable regions, provided suitable yield and landscape data are available, to identify areas where pollination is limited and guide the implementation of targeted agroecological measures. We expect that lower pollination services will be detectable through yield-based metrics, offering a scalable and practical tool for informing conservation and management strategies.

4. Linking pollination and biological control services.

We explore how landscape structure and farming practices jointly influence pollination and natural pest control, and how these co-responses impact crop yields. Understanding the conditions under which multiple ecosystem services are simultaneously enhanced is crucial for promoting productive and ecologically resilient agricultural systems. We hypothesize that certain landscape configurations and management practices, such as the presence of semi-natural habitats and reduced pesticide use, will support both pollination and biological control, thereby improving overall crop productivity and agroecosystem resilience.

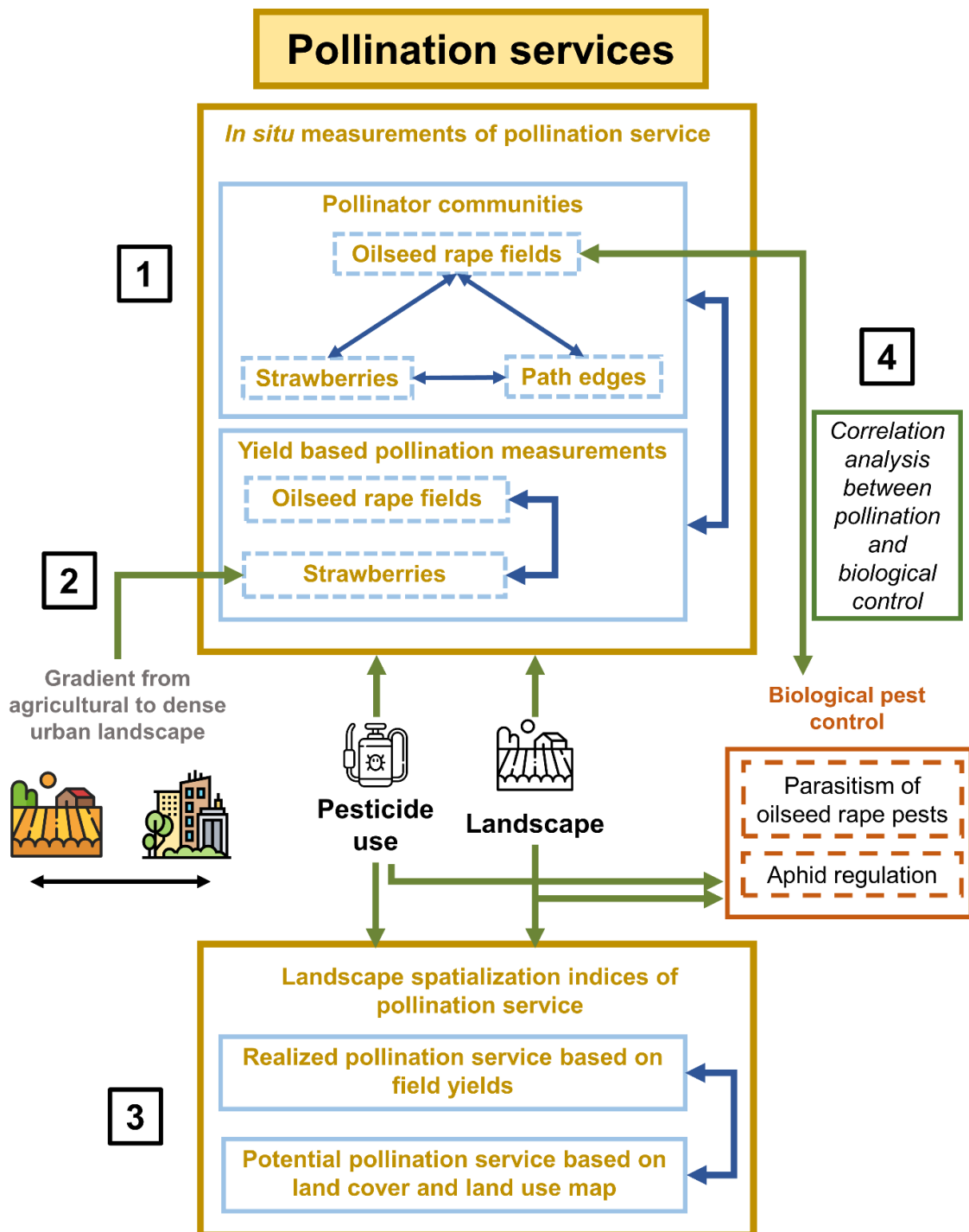


Figure 9. Summary diagram of the different research axes of the thesis and the variables investigated within each. This figure will be reused and adapted at the beginning of each chapter to illustrate the relationships analysed in each of them. The blue arrows indicate the links between the pollination measurements, while the green arrows represent the links with environmental variables or with other ecosystem services.

1

General Material and Methods



Bombus morphotype terrestris, in the Cévennes, 2021, © Thibault Gandara

This thesis is based on two main datasets: an experimental study conducted by me in 2023 and 2024 in the Paris Basin, and a long-term dataset on crop yields and farming practices in the Féney experimental platform covering the period 2007 to 2019. In this section, we present the two study areas and the protocols used to collect field data. As this thesis is structured in the form of articles, descriptions of experimental protocols are repeated within the “Materials and Methods” sections of the different chapters, depending on the protocols mobilized. Analytical methods are detailed throughout the "Materials and Methods" sections of each chapter, depending on the specific questions addressed.

1. Presentation of the study sites

1.1. The SCARABEE study site in the arable plain of the Parisian cereal plain

To study the effects of diverse practices and landscape contexts on ecosystem services, we relied on a network of farmers in the Paris Basin (SCARABEE), coordinated by Antoine Gardarin. This network covers the administrative departments of Eure-et-Loir (28), Yvelines (78), and Essonne (91). This region is predominantly agricultural, with arable crop production with few semi-natural elements (Figure 1.1) and limited livestock farming.

Sixteen farmers were selected (Figure 1.2) to capture a wide range of pesticide uses, from conventional high pesticide use to organic farming. Several of these farmers are already involved in biodiversity- or pesticide-reduction-focused groups (e.g. DEPHY), coordinated by local Chambers of Agriculture. This diversity of farms ensures a representative gradient of management intensities and landscape contexts, providing a solid foundation to assess how farming practices and landscapes can influence biodiversity and ecosystem service provision across real-world agricultural systems.



Figure 1.1. Typical landscape of the Beauce region, characterized by large open fields with few semi-natural elements. An oilseed rape field is visible on the left.

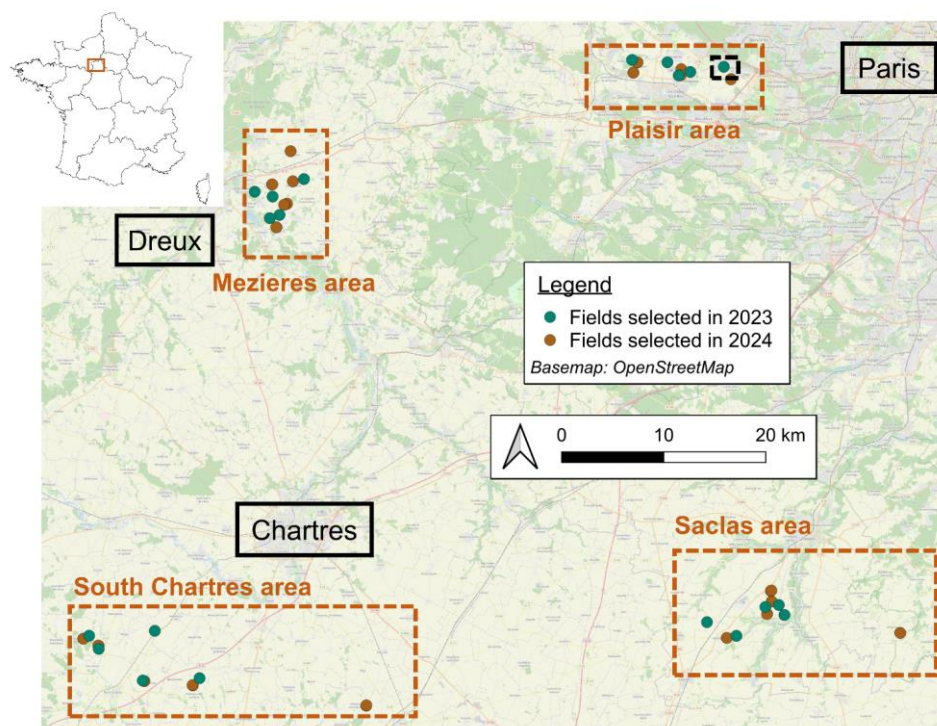


Figure 1.2. Location of study sites clustered into four main areas.

1.2. The Fénay landscape platform

The Fénay platform is a 1,000-hectare area of contiguous arable fields located in the plains south of Dijon, eastern France. It is managed by 25 commercial farmers without any imposed management protocols (Figure 1.3). The Agroecology research unit (UMR Agroécologie, INRAE Dijon) has conducted annual monitoring of the platform, collecting detailed agronomic and biological data integrated into a spatialized database. We used the data collected between 2007 and 2019, provided by Sandrine Petit-Michaud.

This platform aims to investigate how farming systems and the spatial and temporal arrangement of crop fields and semi-natural elements influence community structure, ecosystem functions, and the provision of ecosystem services. It serves as a model to study multiple biological communities, including weed flora, soil microbial communities, and natural enemies of crop pests. Functional analyses of these communities are used to assess associated ecosystem services—such as food resource availability for pollinators and seed-eating fauna, soil denitrification potential, and soil pathogen pressure—in relation to agricultural production and management practices across the landscape.

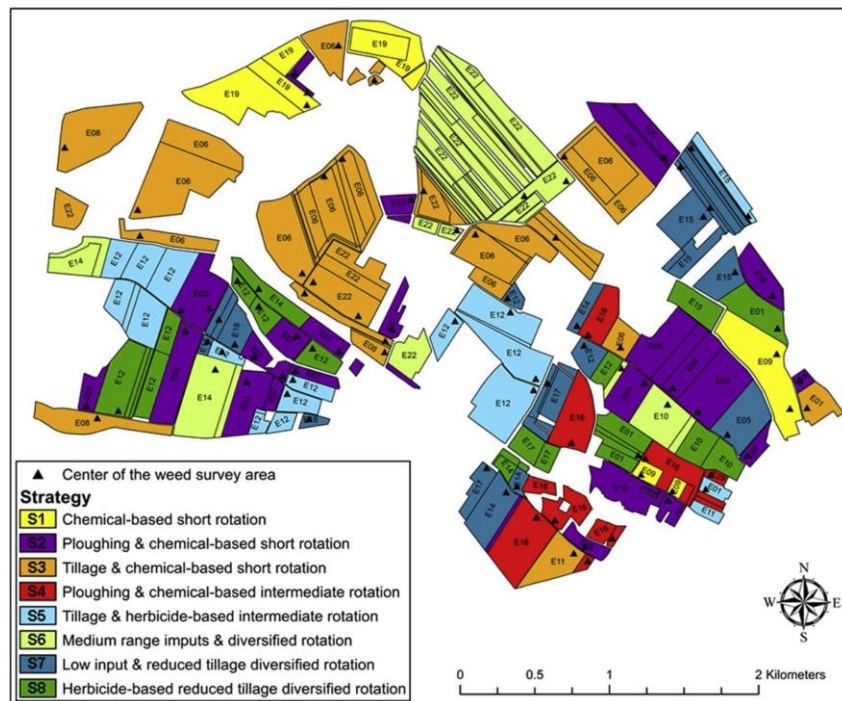


Figure 1.3. Geographical distribution of the 8 crop management strategies and the location of weed surveys (triangle) across the Fénay platform. A field on the map corresponds to the smallest homogeneous unit where management, including crop rotation and farming practices associated, was the same between 2004 and 2016. Blanks represent villages or semi-natural elements (woods, ditches) (Luc Biju-Duval and Séverin Yvoz © 2019 from Yvoz et al., 2020).

2. Sampling protocols and experimental designs

2.1. Selection of fields

In Chapters 2, 3, and 5 of this thesis, we investigate how landscape composition, particularly the area of oilseed rape and semi-natural elements in landscapes, and agricultural practices, affect pollination services. To do so, we selected study fields along two gradients. The first gradient is one of pesticide use intensity obtained from farmer interviews. The second gradient is one of semi-natural habitat cover calculated from landscape features characterization within a 1 km radius around each selected oilseed rape field using agricultural land-use data (Land Parcel Identification System available at <https://geoservices.ign.fr/rpg>) and topographic maps (BD TOPO®, available at <https://geoservices.ign.fr/bdtopo>). Care was taken to avoid collinearity between these gradients (Figure 1.4), to ensure, for example, that low pesticide use did not systematically coincide with high semi-natural elements area, under the assumption that both factors can positively influence biodiversity. Multicollinearity analyses were conducted for all statistical models to verify that the two gradients were not confounded. This approach allowed us to maximize the range of variation for each landscape descriptor while minimizing correlations between variables, thereby meeting the statistical requirements for assessing both their individual effects and potential interactions with ecological variables (Pasher et al., 2013). Finally, we focused our efforts on four main geographic regions to facilitate logistical coordination and ensure the feasibility of fieldwork within the available timeframe.

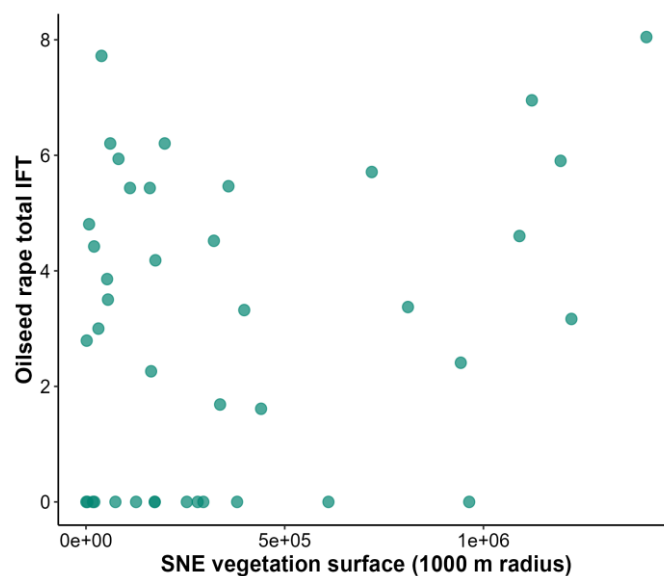


Figure 1.4. Graph showing the distribution of selected fields according to the surrounding semi-natural area or pesticide use on oilseed rape plots.

2.2. In situ estimation of pollination services

To better estimate pollination services under real field conditions, we adopted a multi-method approach based on simple, field-applicable protocols. The aim was to compare several in situ methods that can be easily implemented by non-specialists and assess whether they provide consistent results. By combining complementary techniques, we sought to improve the reliability and robustness of pollination service assessment, while ensuring that the protocols remain accessible for broader use in applied or participatory monitoring contexts.

2.2.1 Pollinator morphogroup observations

Pollination services were assessed by evaluating the ecosystem's capacity to support pollination (Bartholomée and Lavorel, 2019). This capacity was defined based on the organisms responsible for the pollination function, with a focus on both the diversity of pollinator morphogroups and their interactions with plant reproductive structures. For ethical reasons, we adopted a non-lethal monitoring method, given that pollinator populations are already under severe pressure in intensively managed landscapes.

Quadrat observation and positions

Pollinator observations were conducted directly within oilseed rape fields (Figure 1.5.A), at a distance of 30 meters from the field edge, using two 2×2 m quadrats spaced 20 meters apart in areas representative of the local floral density. To assess pollinator communities in the broader agricultural landscape and to investigate whether pollinators present in field margins may influence pollination within oilseed rape crops, we also established observation points at 500 ± 150 m and 1000 ± 150 m from each sampled field, located at the edge between agricultural paths and cereal fields without adjacent oilseed rape (Figure 1.5.B and C).

Observation sessions

In each quadrat, pollinator activity was recorded over a 5-minute period under standardized weather conditions during the oilseed rape flowering period (March to May): sunny conditions, temperature above 12 °C, and average wind speed ≤ 20 km/h. In 2023, data were collected over three sessions between April 5th and May 5th, yielding 360 observations ($20 \text{ fields} \times 2 \text{ quadrats} \times 3 \text{ sessions} \times 3 \text{ locations}$). In 2024, two sessions were conducted between March 20th and April 29th, resulting in 244 observations ($20 \text{ fields} \times 2 \text{ quadrats} \times 2 \text{ sessions} \times 3 \text{ locations} + 1 \text{ additional field without sampling in borders}$).



Figure 1.5. Pictures representing the different observation sites. (A) Observation site within an oilseed rape field, with one of the 2 meters woody folding rule used to delimit the 2×2 m quadrats in the foreground. (B) Field margin along a grassy path bordering a cereal crop. (C) Close-up of an interaction between a solitary bee and *Veronica persica* flower, illustrating a typical plant–pollinator (large wild bee) contact recorded during field observations.

Morphogroup list

During each session, all interactions between insect visitors—visually identified and assigned to one of 13 predefined morphogroups—and the reproductive organs of flowers were recorded. The morphogroups included: small wild bees (<1 mm), large wild bees, honeybees, bumblebees, wasps, parasitoid Hymenoptera (e.g., *Tersilochus* spp. associated with oilseed rape biological control), other Hymenoptera, hoverflies, bee-flies, other Diptera, beetles, butterflies, and other insect pollinators (Figure 1.6). All interactions involving pollen beetles were excluded, regardless of the plant species.

This simplified morphogroup-based protocol was deliberately chosen to ensure reproducibility and ease of application across different observer profiles, including non-entomologists. It was

designed to be accessible to people such as students with no prior taxonomic expertise, and in the long term, it would be ideal for farmers willing to monitor their fields. For instance, within Diptera, the protocol only required distinguishing easily recognizable groups such as hoverflies (Syrphidae) and bee-flies (Bombyliidae), while all remaining flies were grouped as "other Diptera." Similarly, beetles were not identified beyond the order level. When supervised by an experienced observer, novices appropriated rapidly the protocol and reported it as easy to apply, highlighting its suitability for broader participatory monitoring. Examples of typical representatives for each morphogroup are provided in Table 1. We are aware of the limitations associated with using morphogroups, as these groups can differ in their ecological traits and we also acknowledge that not all flower visitors are effective pollinators. Yet, for sake of clarity and consistency, in the following we name 'pollinators' all insects for which we recorded interactions with the reproductive parts of flowers.

Floral area

To account for variation in pollinator visitation rates, we quantified total floral area at each morphogroup observation session. It follows the assumption that greater floral abundance and diversity generally lead to higher pollinator visitation rates (Mahon and Hodge, 2022; Neumann et al., 2024). Given the low diversity of flowering plants typically observed in intensive cereal-dominated landscapes, we focused primarily on total floral area rather than species richness for our work.

In each 4 m² quadrat, all entomophilous flowers were counted individually. Flower counts were based on floral units, defined specifically for each species following (Michelot-Antalik et al., 2025). For example, *Veronica persica*, each single flower was considered a unit, whereas for Apiaceae, the secondary umbel was used as the unit. For oilseed rape, due to the high flower density, we applied a subsampling method: the number of flowering stems (inflorescences) was counted within 1 m², and for a random subset of eight stems, we recorded the number of flowers per stem. The total number of flowers was then extrapolated to the full 4 m² area.

Total floral area per quadrat was calculated as the sum of the product of the number of floral units and the mean floral area per floral unit per flowering species. To estimate mean floral area per species, we measured the diameter of 20 floral units in the field using a digital caliper, assuming a circular or rectangle shape depending on the floral unit to calculate surface area. When field measurements were missing, mean floral area values were retrieved from the species databases of Alice Michelot-Antalik and Antoine Gardarin.

Guide used for morphogroups identification

Hymenoptera

Small wild bees
(< 1 mm)



Lasioglossum dialictus
© Dimitri Bénon

Large wild bees
(≥ 1 mm)



Andrena cineraria
© Patrick Lahoreau

Honeybees



Apis mellifera
© Thibault Gandara

Bumblebees



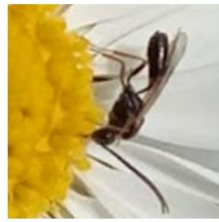
Bombus terrestris
© Thibault Gandara

Wasps



Vespula germanica
© Paul Cools

Parasitoid Hymenoptera of
oilseed rape pests



Tersilochus microgaster
© Antoine Gardarin

Other Hymenoptera



Ichneumonidae spp.
© Quirin

Diptera

Hoverflies



Eristalis spp.
© Thibault Gandara

Bee-flies



Bombylius major
© Kim Kuntze

Other Diptera



Sarcophagidae spp.
© Benoît Janichon

Butterflies



Pieris rapae
© Thibault Gandara

Beetles



Oedemera nobilis
© Babette Köhler

Others



Synema globosum
© Gilberto Sánchez Jardón

Figure 1.6. Examples of representative taxa for each insect morphogroup used in pollinator observations. For each morphogroup, one commonly observed representative is provided.

2.2.2. Quantifying pollination services in oilseed rape fields using a paired Cage–Control design

In 2023, a field experiment was conducted to assess the contribution of pollination to oilseed rape yield. In each of the 20 study fields, we established two treatments: a pollinator exclusion cage and an open control zone, resulting in a total of 40 samples. At the onset of OSR flowering, two cages of 2.25 m² (1.5 × 1.5 m) were installed per field. One was fully enclosed with a fine PVC mesh (0.3 mm) to exclude all pollinators and natural enemies, while the control cage was left open on the sides but covered with the same mesh on top to replicate shading conditions. Cages were placed approximately 10 ± 5 m apart and positioned 30 ± 5 m from the field edge, depending on operational constraints related to machinery for farmers. Before flowering, we geolocated the position of each cage, counted the number of plants per zone, and ensured no pollinators were trapped inside (Figure 1.7). Cages were removed at the end of flowering to allow subsequent plant development under comparable conditions.



Figure 1.7. Cage installation process. Wooden stakes placed at the centre of each cage helped hold the mesh and prevent tearing during heavy rainfall. Metal brackets were attached at the corners to reduce the risk of damage by wild boars. (A) Fixing the vertical supports for the exclusion cages. (B) View of installed exclusion and control cages.

Sampling was conducted on 1 m² quadrats within each treatment area, selecting plots slightly inside the zone to avoid edge effects. The number of plants within each quadrat was recorded. Plants were carefully uprooted with their taproot when possible or cut with pruning shears if necessary. If fewer than 10 plants were present, additional individuals were sampled from just outside the quadrat (within the same treatment zone) and stored separately. These "supplemental" samples were used to ensure we had at least 10 individuals per sample for analysis. Plants were placed in labelled bags and stored at 4 °C prior to processing.

In the laboratory, fresh weight was measured separately for the main and supplemental samples. When more than 10 plants had been collected, a subsample of 10 individuals (or 15 in the case of particularly small or weak plants) was selected at random. Each plant was then dissected, with observers dividing up the branches and proceeding from the base upward. On each branch and sub-branch, we recorded yield-related traits, including the number of full siliques, aborted siliques (empty or containing undeveloped seeds), shattered siliques, as well as short and long pedicels. Fifty siliques were randomly selected from across the entire sample to later count the number of seeds per silique. These were dried separately.

All plants and siliques were oven-dried at 80 °C for 48 hours. Yield components were then estimated for each treatment for each field, including total dry biomass, number of seeds per silique, and thousand-grain weight (TGW). To ensure seeds were fully developed, TGW was measured using mature siliques collected from the remaining cage and control zones just before harvest. A seed counter was used after drying to obtain precise measurements.

Importantly, this experiment was conducted in a year of high aphid pressure, which provided a unique opportunity to evaluate a second ecosystem service: aphid regulation. By comparing aphid colony length between closed (exclusion) and open (control) treatments, we were able to estimate the effect of natural enemies on aphid populations. Colony length was measured on each branch of the selected plants using a large ruler and summed per plant to provide an integrative measure of aphid infestation. Closed cages prevented the access of natural enemies, serving as a baseline for maximum aphid pressure. The difference observed in aphid pressure between exclusion and control treatments was therefore interpreted as a proxy for natural biological control occurring within fields.

2.2.3. Monitoring pollination service using strawberry plants as phytometers.

To assess pollination services just after the massive oilseed rape flowering, we used *Fragaria × ananassa* (cv. Charlotte) as a phytometric tool. This is an experimental estimation of insect-mediated pollination, using phytometers which are sentinel plants produced under controlled conditions and temporarily placed in the field to quantify pollination levels (Blareau et al., 2023; Steffan-Dewenter et al., 2002). Strawberries are an insect-pollinated crop known to rely on pollinators for a substantial portion of fruit development, with approximately 19% to 55% of fruit weight depending on insect pollination (Siopa et al., 2024; Gudowska et al., 2024). The Charlotte cultivar was selected due to its extended flowering and fruiting period (May–October).

Strawberry plants were sourced from a single commercial nursery (SARL Nicolas le Jardinier) in March. All plants were grown in 5 L pots filled with standard potting compost, received

uniform organic nitrogen input between 2023 and 2024 (10 g of DCM ECOR4® per plant), and were regularly watered to prevent water stress. This controlled setup was designed to minimise environmental variation related to soil properties, nutrient availability, or irrigation practices, thereby isolating the effect of pollinator activity on fruit development. Plants were installed in the fields in mid-spring, approximately two to three weeks prior to the expected peak flowering period.

Four distinct pollination treatments were applied to flowers, following the FAO protocol for assessing pollination deficits in crops (Vaissière et al., 2011):

Pollinator Exclusion (E): Flowers were enclosed in fine-mesh bags (mesh size < 1 mm) to exclude all pollinator visits and received no supplementary pollination.

Open Pollination (O): Flowers were left unbagged and exposed to ambient pollinator communities, with no manual intervention.

Open Pollination + Hand Supplementation (O+H): Flowers were exposed to pollinators and additionally received hand pollination to maximize pollen deposition.

Pollinator Exclusion + Hand Supplementation (E+H): Flowers were bagged as in the E treatment but received manual cross-pollination using pollen collected from designated donor plants (plants 7 to 10), placed nearby to facilitate controlled pollen transfer.

At each site, potted strawberry plants were deployed in an open area, avoiding direct shade and ensuring flower accessibility to pollinators. In 2023, six plants were installed per site, with two of them bagged to apply the exclusion treatments (pollinator exclusion with one third of the flowers completed by hand supplementation), and the remaining four left unbagged to implement the open pollination treatments (open pollination with one third of the flowers completed by Hand Supplementation). These treatments allowed us to assess both the baseline pollination level provided by the local insect communities, defined as the difference between open vs. exclusion treatments, and the pollination deficit, defined as the difference between open and hand-supplemented pollination outcomes. Bagging treatments served two main purposes: first, to quantify the degree of plant dependence on insect pollination by comparing fruit production under complete pollinator exclusion (reflecting only self- and wind-pollination); and second, to estimate the full pollination potential under optimal pollen deposition, using hand supplementation as a theoretical maximum.

However, following several instances of plant theft and in order to simplify and secure the process of cross-pollination between donor and recipient plants during hand-pollination treatments, the 2024 protocol was adjusted. Pollinator Exclusion (E) was applied to three potted

plants (plants 1–3 in Figure 1.8.A and 1.8.B), with approximately one third of their flowers hand-pollinated to obtain the E+H treatment. Open Pollination (O) was applied to plants 4–6 (Figure 8.A and 8.B), and again about one third of the flowers were hand-pollinated to obtain the O+H treatment. The remaining four strawberry plants were used for plant–pollinator observations. The remaining four strawberry plants were used for plant–pollinator observations.



Figure 1.8. Experimental setup for assessing pollination services using strawberry phytometers (*Fragaria × ananassa*, cv. Charlotte).

Each experimental unit consisted of ten potted strawberry plants arranged outdoors during the end of the flowering period of oilseed rape. Among them, three plants were enclosed under insect-exclusion nets (plants 1–3; pollinator exclusion), three were left open for subsequent fruit mass measurements (plants 4–6; open pollination), and four served both as pollen donors and observation units for insect visitation surveys (plants 7–10). (A) Setup at the margin of a cereal field; (B) Setup at the margin of an oilseed rape field; (C) Aggregated setup with all

strawberry plants from all sites placed together at a single location, for fruit ripening and collection.

On each plant, approximately 25% of the flowers were manually pollinated. Cross-pollination was performed using an identical paintbrush, transferring pollen from at least two donor flowers to receptive stigmas, with priority given to freshly opened flowers. Each pollinated flower was individually marked with a unique identifier (see Figure 1.9.A), allowing precise tracking of treatment application and ensuring that only flowers exposed during the intended experimental window were included in subsequent measurements. This experimental design allowed us to isolate the contribution of insect pollinators to fruit quantity and quality, and to detect potential pollination deficits under real-world agricultural conditions.

After field exposure, all potted strawberry plants were relocated to a common site for fruit development—at the Arboretum de Versailles-Chèvreloup in 2023, and on the rooftop of the Muséum national d'Histoire naturelle (MNHN) in 2024 (Figure 1.8.C). This centralized setup ensured uniform post-pollination growing conditions across all experimental sites. After fruit maturation, ripe strawberries were harvested (Figure 1.9.B) and weighed (Figure 1.9.C) on the same day to ensure consistency and avoid post-harvest water loss. Strawberries development is regulated by fertilized achenes, which produce auxin, a plant hormone essential for receptacle growth (Tian et al., 2022). As a result, well-pollinated flowers typically produce larger, well-formed fruits, while insufficient pollination often leads to smaller and misshapen strawberries due to a lack of fertilization. In addition to fresh weight, each fruit was measured for length, from base to petiole insertion (Figure 1.9.D) and two perpendicular widths (one along the longest axis and one orthogonal to it) and photographed for post hoc assessment of achene number and distribution, as well as to evaluate symmetry and deformation as proxies for pollination quality.

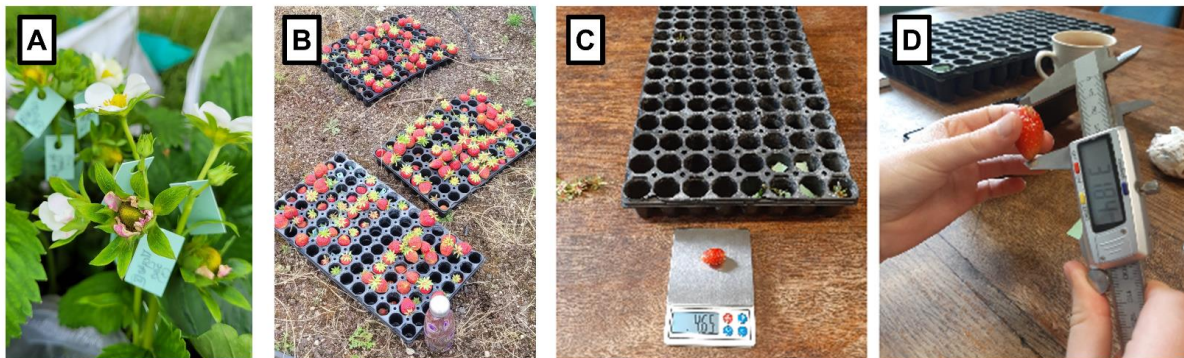


Figure 1.9. Stepwise protocol for measuring strawberry yield components in the field. (A) Individual marking of each flower with unique identifiers on the field (B) Harvesting of ripe strawberries on the day of maturation (C). Measurement of fruit fresh mass (D). Measurement of fruit length and width on the day of harvest.

2.3 In situ parasitism assessment of two major oilseed rape pests: pollen and flea beetles

Conservation biological control was assessed for parasitoids of two key herbivores of oilseed rape (Figure 1.10.A and 1.10.B). These two pests are the cabbage stem flea beetle (*Psylliodes chrysocephala*) and the pollen beetle (*Brassicogethes aeneus*). These species exhibit distinct life cycles, as illustrated in Figure 1.11, and effects of parasitism on their control are not immediate. As shown in Figure 1.11, parasitism typically occurs after crop damage has already taken place. Therefore, parasitoids do not directly reduce herbivory during the current season but rather contribute to the long-term biological control of pest populations by limiting the number of larvae reaching maturity, thereby reducing pressure in the following year. The hosts larvae drop to the soil and pupate, forming cocoons (Figure 1.10.C) within the same oilseed rape field where parasitism occurred (Figure 1.11). As such, parasitoid populations partially develop within the crop, and their persistence and effectiveness may depend on oilseed rape presence across years. To account for this, both current-year and previous-year oilseed rape cover were included in our analyses: the former may dilute parasitoid activity, while the previous may enhance overwintering success and spring emergence. Moreover, adult parasitoids often rely on floral resources to complete their life cycles, suggesting that the presence of insect-attractive flowering plants—particularly in semi-natural habitats—could support their survival and reproductive success. Landscape elements providing such resources are therefore also expected to influence parasitism rates and the strength of natural pest control.



Figure 1.10. Photography of parasitoids involved in the biological control of oilseed rape pests © Antoine Gardarin. (A) *Tersilochus heterocerus*, a dominant larval parasitoid of pollen beetles (*Brassicogethes aeneus*), observed on an oilseed rape flower next to adult beetles. (B) Adult parasitoid of the cabbage stem flea beetle (*Psylliodes chrysocephala*) foraging on a daisy at the field margin. (C) Cocoons of pollen beetle parasitoids formed after consumption and development within the host larva.

Parasitism of *P. chrysocephala* was monitored in early April. Late-instar larvae were collected from the leaf petioles at the base of oilseed rape plants along two transects, located 5 and 30 meters from the field edge and intersecting pollinator observation points. When possible, at least 100 larvae were sampled per field. These were placed in one rearing box per field and distance, where they spontaneously burrowed to pupate. Boxes were incubated at room temperature (20–25°C), and adult flea beetles were counted three weeks later. To allow for parasitoid emergence, boxes were then placed at 5°C for four months to simulate winter, followed by a second incubation phase during which emerging parasitoids were recorded daily. The parasitism rate per transect was calculated as the number of emerged parasitoids divided by the total number of adult beetles and parasitoids recovered.

In parallel, parasitism of *B. aeneus* larvae was assessed at the end of the flowering period (late April), along the same transects. At least 100 fully developed larvae (> 4 mm) were collected per field from oilseed rape flowers and preserved in 70% ethanol. Parasitism by *Tersilochus heterocerus*, the dominant species in the region, was later determined under a binocular microscope by detecting translucent eggs visible through the larval cuticle. When large larvae were scarce, medium-sized larvae ($\approx$ 3 mm) were included. In total, 20 fields were monitored in 2023, and 17 (for flea beetles) or 19 (for pollen beetles) in 2024, depending on field accessibility and compatibility with pollinator observations.

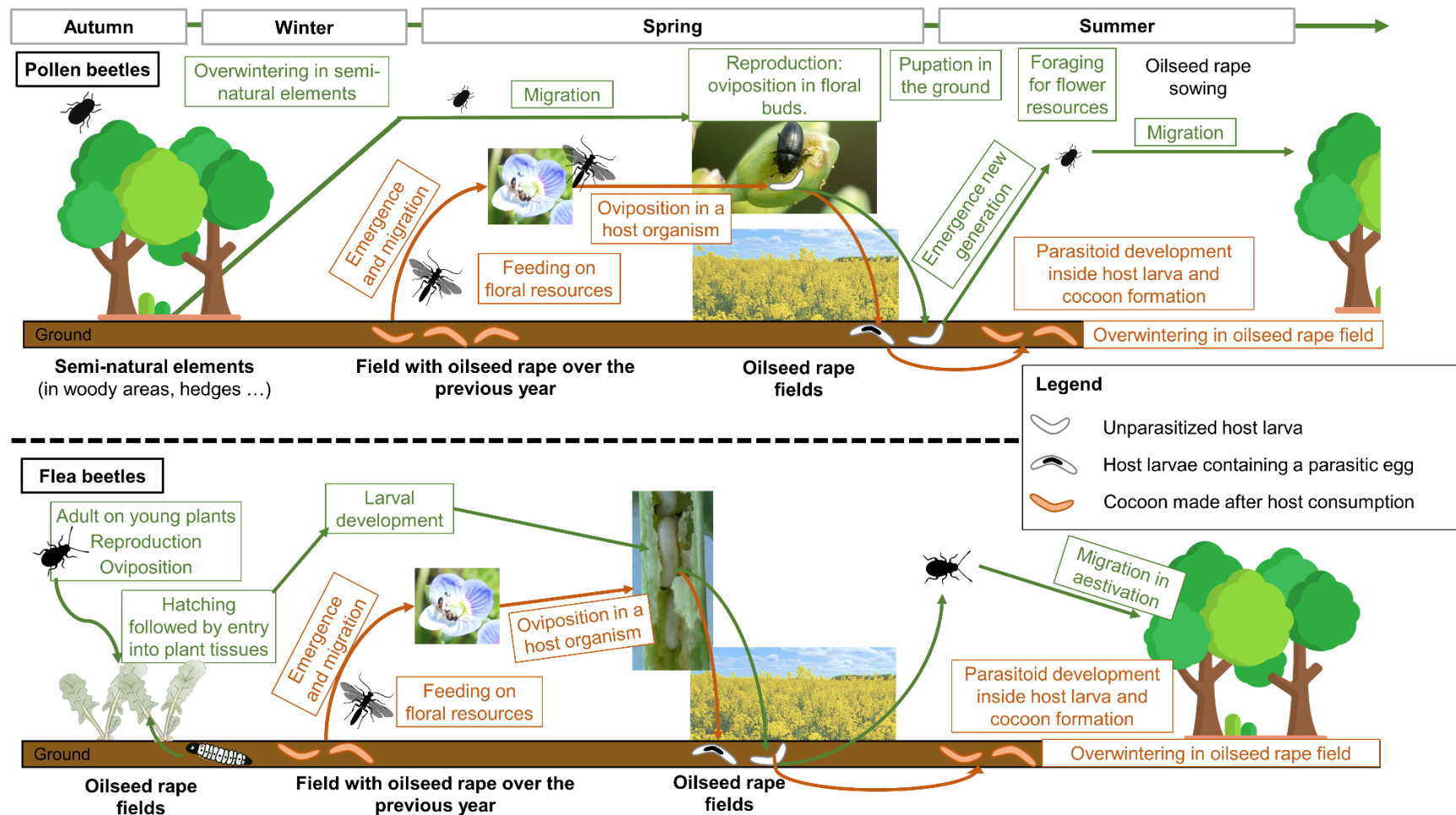
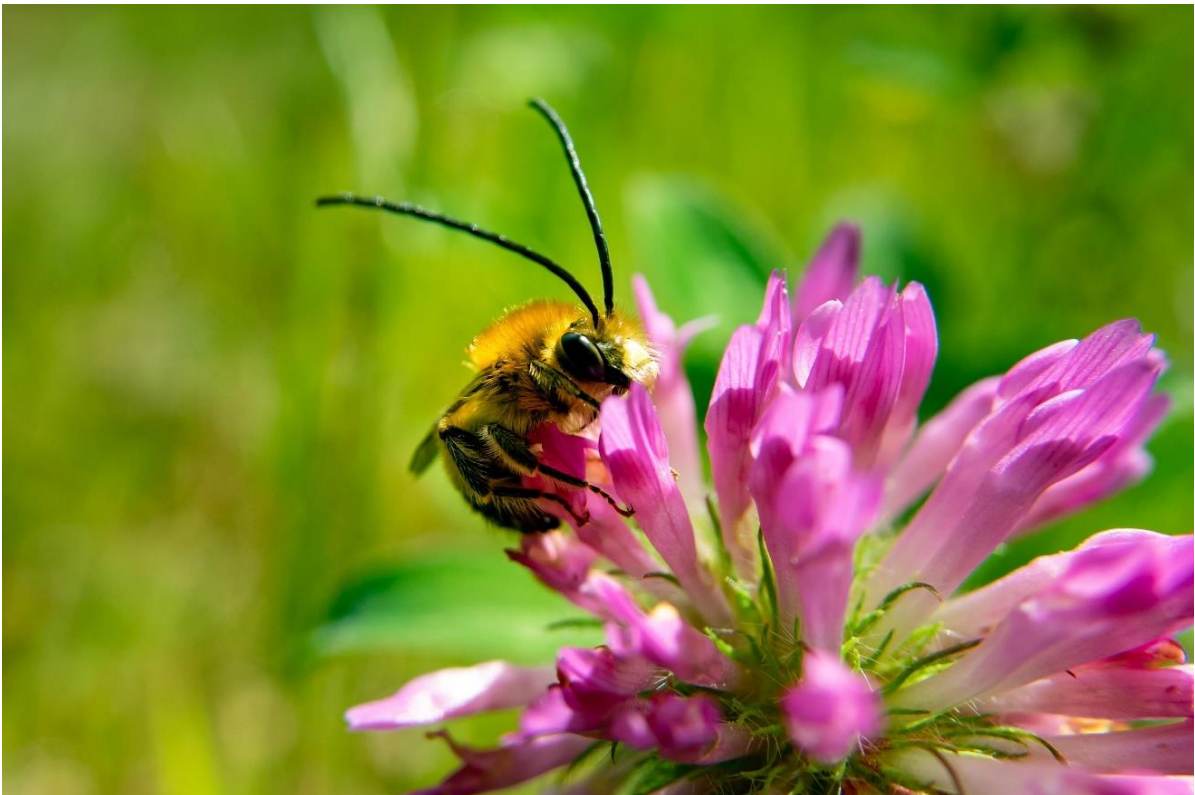


Figure 1.11. Life cycles of the two major oilseed rape pests studied in this thesis: pollen beetles (top) and flea beetles (bottom). Pest life stages are shown in green, while those of their hymenopteran parasitoids are shown in orange adapted from (Seree, 2022). Drawing of oilseed rape © Justine Pigot.

2

Comparing complementary measurements of pollination in association with landscape composition and pesticide use



Eucera sp. in the Cévennes, May 2021, © Thibault Gandara

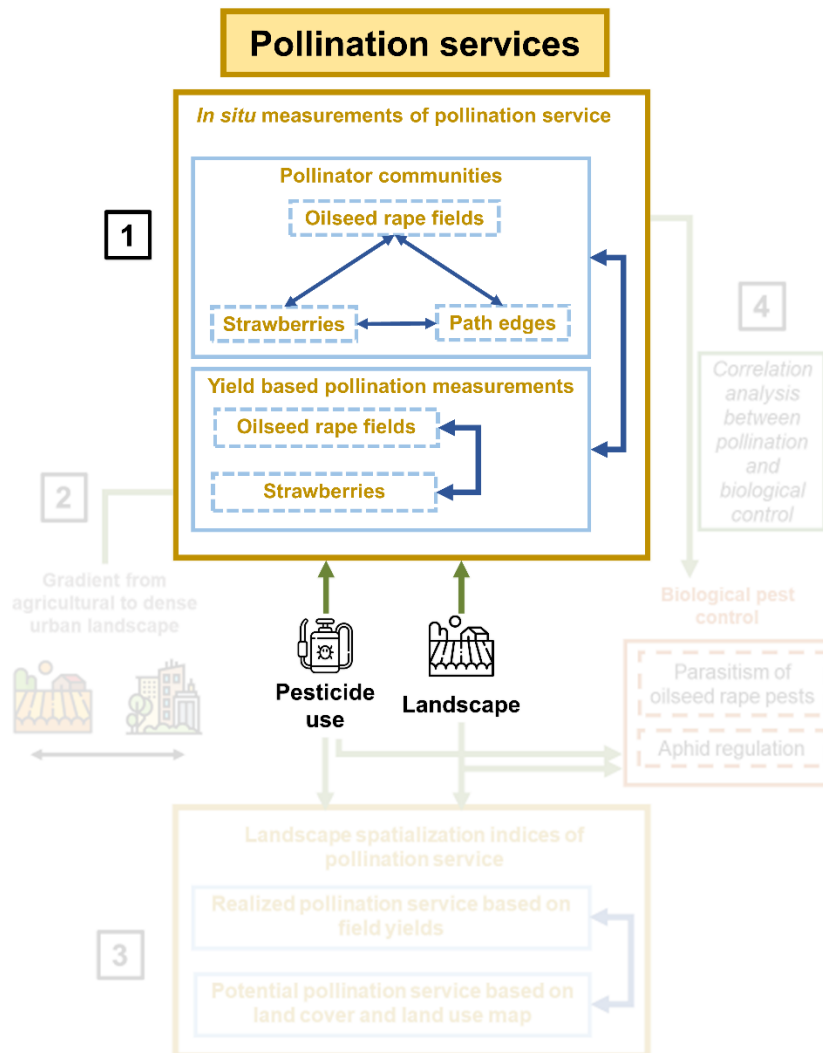


Figure 2.0. First research axis within the general diagram summarizing the whole thesis.

Chapter overview

The primary goal of this study was to implement a set of complementary methods to measure pollination across a common landscape framework. This approach was designed to capture the multiple dimensions of pollination, following the conceptual framework proposed by Bartholomée and Lavorel (2019), which distinguishes between the ecological process, the ecosystem services, and the resulting benefits. By combining different levels of observation— from plant–pollinator interactions to crop yield— we aimed to better understand how pollination operates within real agricultural landscapes. Through this integrative design, our objective was to link the diversity and activity of pollinators to the effective delivery of pollination services and their tangible outcomes for angiosperm reproductive success.

From pollinators to yield: comparing complementary measurements reveals the benefits of landscape diversification and low pesticide use on pollination

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FOREWORD

Note for the members of the jury: the first chapter of this manuscript is written in the form of a scientific article, but it also serves to present the main dataset collected in the field by myself and to provide a brief overview of the preliminary analyses that could be conducted. For the final publication, a narrower selection of methods and results will be prepared.

1. Introduction

Animal pollination is a key ecological function, essential to the reproduction of 78% of temperate wild plants (Ollerton et al., 2011) and to 70% of cultivated plant species at a global scale (Klein et al., 2007), that is yet under increasing threats. High pollinator diversity is known to enhance the reliability and complementarity of pollination services across both crops and wild plants (Woodcock et al., 2019; Katumo et al., 2022). However, agricultural intensification, through habitat loss and pesticide use, is a major contributor to declines in pollinator diversity and abundance (Potts et al., 2010), affecting both wild and managed pollinators (Kennedy et al., 2013; Paudel et al., 2015). These pressures are concerning given the rapid global expansion of pollinator-dependent crops since the 1960s (Aizen et al., 2019), which has simultaneously increased the demand for pollination services and heightened the risks of pollination deficits. Oilseed rape (*Brassica napus*), for instance, visited both by managed honey bees and wild pollinators, is widely cultivated in intensive agricultural landscapes, where field margins are often the only semi-natural elements providing floral resources outside crop fields. Understanding how plant/pollinator networks connect oilseed rape fields with other flowering plants in the surroundings, such as wildflowers in field margins, is essential to determine whether weeds can act as direct providers of pollinators for crops (Crochard et al., 2022), or of refuges that sustain species unable to persist within intensively managed fields (Hevia et al., 2021). Studying these patterns and their responses to environmental factors is essential to understand the ecological mechanisms that link landscape heterogeneity, pollinator diversity and abundance, and the resulting provision of pollination services.

In addition to understanding the dynamics of plant/pollinator interactions in agroecosystems, defining and quantifying pollination as an ecosystem service remains a challenge. Pollination has been conceptualized in multiple ways, ranging from metrics of pollinator abundance and diversity to measures on phytometer plants or indices directly obtained from crop yields (Liss et al., 2013). Each definition captures different facets of pollination services and often relies on distinct estimation methods. Bartholomée and Lavorel (2019) highlighted this diversity of approaches, showing how different metrics reflect the ecological, agronomic, and socio-economic dimensions of pollination. They introduced a framework linking ecological functions to their social relevance, emphasizing the importance of integrating complementary measures to better capture the multifaceted nature of pollination services. Building on this conceptual background, a central question remains: do the different ways of measuring pollination actually converge in their assessment of the service? It is still unclear whether indicators based on pollinator activity, phytometer performance, or crop yield outcomes correlate with each other and provide consistent results or respond similarly to environmental gradients (Bartholomée and Lavorel, 2019; Rivers-Moore et al., 2023). Few studies have compared multiple metrics

side by side in the same locations, limiting our understanding of their congruence and their common drivers across landscapes and agricultural practices contexts. The elected methods for a given survey shape the picture obtained for pollinator communities and pollination services. For example, focusing on pollinator community composition, pan traps generally collect more species, particularly solitary bees and hoverflies, whereas transects tend to record higher abundances of bumblebees and provide information on plant–pollinator interactions (O’Connor et al., 2019).

Because no single method can fully characterize pollinator diversity, we combined complementary methods to obtain representative and comparable datasets across space and time to assess pollination within the same experimental design, focusing on oilseed rape in the Paris basin. We chose non-lethal methods only, as this choice was both ethically sound and particularly relevant in contexts where pollinators are already under pressure (Lövei et al., 2023; Barrett and Fischer, 2024), such as the Paris basin, an intensively managed arable landscape. Our objectives were (i) to assess whether pollinator communities differ across floral resources and how these different communities respond to landscape composition and agricultural practices, (ii) to assess whether different ways of estimating pollination, from observation of pollinator interactions to yield measurements, reveal similar responses to landscape composition and agricultural practices and finally (iii) to check whether these methods yield proxies of pollination that correlate with each other. By integrating these perspectives, we aim to provide a more comprehensive understanding of how pollination can be measured and varies across agroecosystems.

We hypothesize that pollinator communities differ across floral resources, owing to specialization, but that their main landscape and agricultural practices related drivers are broadly similar. We further expect that pollinator and pollination metrics respond consistently to environmental variables and are positively correlated with each other, reflecting the link between biodiversity and ecosystem service provision.

2. Materials and methods

2.1. Study sites, sampling methods and data collected

The study took place in 2023 and 2024 in the southwestern Paris Basin (Yvelines, Essonne, Eure-et-Loir), a region dominated by large-scale arable systems with sparse semi-natural elements. We implemented three complementary protocols to assess pollination: (i) observations of plant–pollinator interactions within oilseed rape fields, as well as in surrounding herbaceous field margins, adjacent to cereal fields, (ii) a phytometer method using strawberry plants (*Fragaria × ananassa*) placed along perennial field margins, comparing open

pollination vs. pollinator exclusion together, together with observations of strawberry flower–pollinator interactions, and (iii) pollinator exclusion vs. open pollination experiments in oilseed rape fields to quantify pollinator contribution to oilseed rape yield.

2.1.1. Measurement of plant–pollinator interactions in oilseed rape fields, herbaceous field margins and on strawberries

Pollination potential was assessed by recording interactions between pollinators and oilseed rape flowers in crop fields as well as between pollinators and wild plants in herbaceous field margins, between March and May. In oilseed rape fields, observations were conducted in two 2×2 m quadrats, placed 30 m from field edge and 20 m apart, under standardized conditions (sunny or only overcast sky allowing pollinator activity, > 12 °C, average wind speed ≤ 20 km h^{-1}). To assess pollinator communities in the broader agricultural landscape and to investigate whether pollinators present in field margins may influence pollination within oilseed rape crops, we also sampled observation sites at 500 ± 150 m and at 1000 ± 150 m from each oilseed rape field. In these sites, two 2×2 m quadrats were placed in the herbaceous field margin, between an agricultural path and a cereal field (no immediate vicinity of oilseed rape). The exact positioning of the quadrats was adjusted so that they contained more or less the same core list of plant species, common to all observation sites, to limit the effect of the identity of flowering species on pollinator visits. Each observation session lasted 5 min per quadrat. Across all locations, there were three sessions per field in 2023, resulting in 360 observations ($20 \text{ fields} \times 2 \text{ quadrats} \times 3 \text{ sessions} \times 3 \text{ locations}$), and two sessions in 2024, hence 244 observations ($20 \text{ fields} \times 2 \text{ quadrats} \times 2 \text{ sessions} \times 3 \text{ locations} + 1 \text{ additional field without sampling in herbaceous field margins}$). Observed pollinator individuals were assigned to one of 13 morphogroups described in figure 1.6 of the general Material and Methods of this thesis, excluding interactions with pollen beetles. For analyses, observations of the two quadrats of each session and site were pooled into a single 10-min session to obtain a more robust estimate of plant-pollinator interactions and to avoid pseudo-replication.

Within each quadrat of herbaceous field margins, insect-attractive Angiosperms with open flowers were identified to species level, and floral units were counted following (Michelot-Antalik et al., 2025) to estimate a total floral area on the $4m^2$. For oilseed rape, we estimated floral area as the mean number of flowers per inflorescence (averaged over 10 plants) multiplied by the number of inflorescences within the $4 m^2$ quadrat and by the mean surface area of a single oilseed rape flower. For strawberries, floral area was calculated as the number of flowers on the four phytometer plants where pollinator interactions were recorded (see below), multiplied by the average surface area of a strawberry flower.

To visualize the plant–pollinator network, we used the R package *bipartite* (Dormann et al., 2025). The *plotmoduleweb* function was used to identify possible modular structures within the networks. Additionally, we plotted bipartite networks of plant–pollinator interactions using the R package *ggalluvial* (Brunson and Read, 2023) retaining only plant species with more than 25 recorded interactions; the full network is shown in Figure S2.2.

2.1.2. Strawberries as phytometers to evaluate the contribution of pollination to yield components

To assess pollination after oilseed rape flowering, we used strawberry plants (*Fragaria × ananassa*, cv. Charlotte) as phytometers, following established protocols (Steffan-Dewenter et al., 2002; Blareau et al., 2023). Strawberry is an insect-pollinated crop with 19–55% of fruit weight attributed to insect visits (Gudowska et al., 2024; Siopa et al., 2024). Plants were grown under standardized conditions in 5 L pots filled with potting compost, fertilized with 10-g uniform organic fertilizer inputs (DCM ECOR4®) between flowering seasons, and well-watered to minimize variation unrelated to pollinator activity.

During the flowering period of strawberries, we conducted plant–pollinator interaction surveys and applied a set of four complementary treatments on each site to quantify the effects of open and hand pollinated treatments compared to a pollinator excluded treatment. On each site, four treatments were applied to quantify the effect of pollinators and hand-pollination on fruit set, following FAO guidelines (Vaissière et al., 2011): Pollinator Exclusion (E): bagged flowers, no manual pollination; Exclusion + Hand Supplementation (E+H): bagged flowers, hand-pollination using donor plants; Open Pollination (O): unbagged flowers, exposed to pollinators; Open + Hand Supplementation (O+H): exposed and hand-pollinated flowers. : In treatments with hand supplementation, approximately 25% of flowers on each plant were manually cross-pollinated using a sterile paintbrush to transfer pollen from at least two donor flowers to receptive stigmas, prioritizing freshly opened flowers; each treated flower was uniquely tagged for accurate tracking.

In 2023, six potted strawberry plants were placed at the edges of the 20 oilseed rape fields and in 20 herbaceous field margins located 500 m away from these field sites. Two plants were bagged to exclude pollinators, while four remained open to assess ambient pollination and one third of the strawberries were hand pollinated for both exclusion and open pollination. In total, 240 strawberry plants were deployed in the field. Plants were placed for experiments between April 25 and 28 2023, before the onset of their flowering and at the end of the oilseed rape flowering period. They were left in the field for three weeks after the blooming of the first flowers and were removed between June 1 and 4. In 2024, to improve consistency and minimize plant losses due to vandalism or vertebrate grazing, ten potted strawberry plants were

deployed at each site, resulting in a total of 200 plants across 10 oilseed rape fields and 10 cereal field margins. At each site, three plants were bagged to exclude pollinators, while seven remained open to provide a larger floral screen and three were used to collect strawberries. One third of the strawberries were hand pollinated for both exclusion and open pollination. Sites were selected in relatively secure locations and monitored regularly (daily or every two days) to ensure plant maintenance. Plants were placed in the field between May 13 and 17 2024 and retrieved three weeks after the onset of flowering, on June 13–14 2024. During the flowering period of strawberries in the field for both years, plant–pollinator interactions were surveyed on four open strawberry plants for 10 minutes each, following the same observation conditions as described previously in section 2.1.1 and counting the number of open strawberry flowers for the floral area.

After field exposure, all strawberry plants were moved to a common site for uniform fruit development (Arboretum de Versailles-Chèvreloup in 2023 and MNHN rooftop in 2024). Upon ripening, fruits were harvested and processed on the same day to prevent water loss. Several measurements were taken to assess pollination quality: fresh fruit weight using high-precision scales (± 0.01 g), length and mean width using electronic calipers (precision ± 0.1 mm), and visual assessment of deformation. Fruit deformation was classified into five categories: perfect or nearly perfect (0–10%), slightly deformed (10–25%), moderately deformed (25–50%), strongly deformed (50–75%), and severely deformed (75–100%). In this experiment, hand-pollination did not result in any significant increase in strawberry yield; therefore, in the following sections we focus solely on the open and closed pollination treatments.

2.1.3. Evaluation of the contribution of pollinators to yield components in oilseed rape using exclusion cages

In 2023, the contribution of pollination to oilseed rape yield was quantified through a paired cage experiment in 20 fields, where we directly used oilseed rape plants as phytometers. Each field received two treatments: a pollinator-exclusion cage (1.5×1.5 m, mesh size 0.3 mm) and an open control cage with mesh only on top to maintain the same shading conditions as in the closed cages, while allowing insect access. Cages were set up at the beginning of flowering, approximately 30 m from the field edge, and removed once flowering ended one month later to ensure uniform post-flowering development. In June, all plants from a 1 m^2 area within each treatment were collected for yield assessment. For each sample, plants were classified by size and weighted to measure fresh and dry mass. On each branch and sub-branch, we recorded yield-related traits, including the number of full siliques, aborted siliques (empty or containing undeveloped seeds), shattered siliques, as well as short and long pedicels. Fifty siliques were randomly selected from the entire sample and oven-dried to later count the mean number of

seeds per silique. The additional siliques present in the cage or open treatment not collected within the 1m² area were harvested just before farmer's harvest to measure thousand grain weight. The total seed mass per plant was calculated as follows: number of full siliques × mean seed number per silique × mean thousand-grain weight. Additionally, because the experiment coincided with a year of high aphid pressure, we measured aphid colony length on every branch and sub-branch. These data were used as a covariate to control for aphid pressure, ensuring that pollination effects could be detected without bias from this factor.

2.1.4. Characterization of landscape and agricultural practices

We selected landscape and agricultural practices variables known from the literature to influence pollinators or pollination. To quantify landscape composition, we defined three buffer sizes (500 m, 1000 m, and 2000 m) around observation sites. The percentage cover of semi-natural elements was derived from two complementary sources: BD TOPO® (available at <https://geoservices.ign.fr/bdtopo>) was used to extract woody semi-natural elements such as forests, shrublands, and hedgerows, while herbaceous elements, including fallows and grasslands, were obtained from the Land Parcel Identification System (LPIS, available at <https://geoservices.ign.fr/rpg>). We work with the total area of semi-natural elements, i.e. the sum of areas of the abovementioned elements.

Oilseed rape cover from the previous year was included, as it can influence wild pollinator activity and reproduction (Van der Meersch et al., 2022). Other mass-flowering crops (see Table S2.1) in the previous year were also extracted from LPIS, as they may provide important resources that benefit pollinator populations (Beyer et al., 2021). We also retrieved data on oilseed rape cover in the sampling year: in 2023 from LPIS, and in 2024 by manually analysing aerial imagery from the Sentinel program (available at <https://apps.sentinel-hub.com/eo-browser/>), because the LPIS data was not available yet. Crop heterogeneity was calculated as a Shannon diversity index (Alignier et al., 2020), on the basis of the crops cultivated in the fields surrounding the observation sites in a 1000m, excluding fallows and grasslands, which were considered as semi-natural elements in our analyses.

Based on farmers surveys, pesticide use was quantified at field level using the treatment frequency index, computed as the cumulative dose of each active substance applied throughout the crop cycle (from the the previous crop harvest to the actual harvest), divided by the maximum authorized dose under French national guidelines, and weighted by the relative field area treated. Landscape-level pesticide use was estimated at the municipality scale using data provided by Solagro (available at <https://solagro.org>), with the same unit (treatment frequency index) as for field-level pesticide use. A weighted average based on the area of each

municipality within the three buffer sizes was calculated to obtain an overall estimate of pesticide use in the landscape.

2.2. Statistical analysis

All statistical analyses were conducted in R version 4.5.1 (R Development Core Team, 2017). For each model, spatial autocorrelation of residuals was tested using Moran's I statistics, and no significant spatial autocorrelation was detected. Model diagnostics and validation were performed using the DHARMA package (Hartig et al., 2024).

2.2.1. Pollinator community responses to the identity of visited plants and environmental variables

A full dataset of plant-pollinator interactions was obtained by compiling interactions (1) with oilseed rape, (2) with wild flowers in herbaceous field margins and (3) with strawberry plants. This dataset was used (i) to compare pollinator assemblages across the three floral resources, and (ii) to assess how these pollinator communities responded to environmental variables, using both a community composition perspective via multivariate methods, but also examining the response of total pollinator interaction abundance via linear models.

2.2.1.a. Pollinator community composition across flower resources

A comparison of pollinator community composition across the different flower resources was conducted using the R package *vegan* (Oksanen et al., 2025). We used non-metric multidimensional scaling (NMDS) to compare the composition of pollinator communities, classified by major morphogroups (e.g., small wild bees, bumblebees, hoverflies), across the three different flower resources: oilseed rape fields, wildflower communities along field margins and strawberry plants. Data manipulation and aggregation were handled using *dplyr* and *purrr*, while visualizations of NMDS results were produced with *ggplot2*. To further identify taxa specifically associated with each habitat, we performed a multi-level pattern analysis on the pollinator interaction matrix using 10 000 permutations with *multipatt* function of the *indicspecies* R package (Cáceres et al., 2025).

2.2.1.b. Multivariate analyses of the relationship between pollinator community composition and environmental variables

To assess the effects of flower resources, landscape and farming practices on pollinator community composition, we used Bray–Curtis distance-based redundancy analysis (dbRDA) with the *capscale* function in the *vegan* package (Oksanen et al., 2025). The analyses were performed on the entire dataset of plant–pollinator interactions as well as separately for each

flower resource (oilseed rape, wild plants, and strawberry) to explore whether environmental covariates differed among these communities.

The control variables included in the dbRDA were: year, as a factor, to account for interannual variation in pollinator activity (2023 and 2024); the flower resource; total floral area measured during the observation session; wind speed; temperature; decimal hour of observation. In addition, a set of explanatory environmental variables calculated within a 1000-m radius around each site was included in the model: total area of semi-natural elements, mean treatment frequency index in the landscape, oilseed rape area in the previous and current year, crop heterogeneity (Shannon diversity index) in the previous year, and area of flowering crops other than oilseed rape in the previous year. For the plant-specific dbRDA models, the fixed effect of *flower resource (FR)* was omitted.

To validate the results of the dbRDA with an alternative multivariate statistical approach, we also performed a PERMANOVA using the *adonis2* function in *vegan* with 999 permutations. Multicollinearity among explanatory variables was checked using variance inflation factors (VIF) with the *vif.cc* function, and all values were below 4, indicating no problematic collinearity.

2.2.1.c. Environmental covariates of total pollinator abundance

We performed linear mixed models to study the relationship between total abundance of pollinator communities and landscape and agricultural practices variables. Total numbers of interactions per session were modelled using generalized linear mixed-effects models with a negative binomial distribution, *nbinom2()* with *glmmTMB* (Brooks et al., 2025). The equation is the following:

$$(1) \text{logit}(\text{Pollinator}_{ijkl}) = \text{mean} + Y_i + FR_l + \alpha \times FA_{ilk} + \beta \times W_{ijk} + \gamma \times T_{ijk} + \eta \times H_{ijk} + \theta \times SNE_k + \vartheta \times TFI_k + \iota \times OP_k + \kappa \times OC_k + \lambda \times CH_k + \mu \times FP_k + S_k$$

where *Pollinator_{ijkl}* is the mean number of pollinator visits recorded at year *i* and sampling date *j* in site *k* for observation on a flower resource *l*, associated with a given floral area (FA), wind speed (W), temperature (T), hour (H), area of semi-natural element area (SNE), Mean treatment frequency index in the landscape (TFI), Oilseed rape area of the previous year (OP), Oilseed rape area in the year of sampling, Crop heterogeneity of the previous year (CH) and Flowering crop of the previous year (FP); *S_k* is a random intercept accounting for unmeasured variability associated with each site *k*, assumed to follow a normal distribution with zero mean and variance σ_F^2 .

2.2.2. Estimating the contribution of pollinators to yield components in strawberry and oilseed rape, and identifying their environmental covariates

For oilseed rape and strawberry plants, we compared two treatments: open pollination vs. pollinator exclusion. This design allowed us to directly test the effect of pollinator exclusion on yield components in each plant species. Numerous measurements of yield components were carried out for each phytometer. Below, we detail the measurements and the statistical analyses performed on these different components. Hereafter, we refer to this method to characterize animal pollination as yield-based pollination estimation.

2.2.2.a. Strawberries as phytometer

For strawberries, we retained two yield components that are deemed good proxies of pollination: fruit mass (Blareau et al., 2023; Gudowska et al., 2024) and deformation (Wietzke et al., 2018). A quantitative, continuous measure of deformation was estimated using the following equation: $D = \left| \frac{length}{width} - 1 \right|$, with values closer to 1 indicating more deformed fruits and values closer to 0 reflecting regular shapes, as well-developed strawberries have a length/width ratio close to 1. These quantitative estimates were correlated with categorical visual assessments of deformation.

2.2.2.b. Oilseed rape as phytometer

For oilseed rape, we retained three yield components, i.e. the number of siliques, the number of seeds per silique, and thousand dry grain weight. From these data, we estimated seed mass per ramification and per plant. Spearman correlations were used to examine compensatory relationships among yield components, such as the expected trade-off between seed weight and seed number per silique, as these components can be differently influenced by pollinators (Perrot et al., 2018). In addition, comparisons between caged and open-pollinated plants allowed us to assess whether pollination influenced yield components. In the following analyses, we assumed that seed filling, hence thousand grain weight, was influenced by the number of seeds per silique. Likewise, the number of seeds per silique was expected to depend on the total number of siliques produced by a plant, with potential compensatory effects (i.e. fewer siliques bearing more seeds). Finally, we considered that the total seed mass per plant or per plot was driven by the initial number of flowers produced and by aphid pressure, approximated by colony length.

2.2.2.c. Link with environmental variables

We tested whether environmental variables affected the contribution of insects to the pollination of strawberries and oilseed rape. Explanatory environmental variables (collectively grouped as “*Env*” in the models below) included the area of semi-natural elements (meadows, fallows, hedgerows and woody areas), the mean treatment frequency index (pesticide use intensity), the proportion of oilseed rape fields in the previous and sampling years, the crop heterogeneity index in the previous year, and the area of flowering crops other than oilseed rape in the previous year, all calculated within a 1000-m radius around each site. For strawberries, fruit mass and deformation index were modelled as Var_{ijklm} in equation (2), which included year (2023–2024), T_j pollination treatment (Open vs. Exclusion), and their interaction with environmental variables Env_k , with random effects accounting for plant identity within sites.

For oilseed rape, the statistical models did not include year as the experiment only took place in 2023. First, we used generalised linear mixed models to assess how environmental variables influenced the different general yield components of oilseed rape measured once across each treatment per fields, namely thousand grain weight (*TGW*) and the number of grains per silique (*NGS*). We modelled *TGW* as a function of the environmental variables *Env*, but also *NGS* (Equation (3)), because higher grain numbers per silique are generally associated with lower *TGW* (Verocai et al., 2024). *NGS* was modelled as a function of the environmental variables *Env* and the number of full siliques (*NFS*, equation (4)). Finally, an integrative model calculating the total mass of seeds per plant (*M*) combining all yield components, i.e. *TGW*, *NGS* and number of siliques per plant, was fitted (equation (5)). This model additionally included A_l the aphid colony length and F_l the initial flower number on *plant l* as covariates to account for both aphid pressure and plant size. In both models, *Env* represented the six landscape variables described above, and random terms were assumed normally distributed.

We used gaussian distributions, as they provided the best fit to the data compared to alternative distributions except for equation 5, which was better fitted with a Tweedie distribution.

$$(2) Var_{ijklm} = mean + Y_i + T_j + (a_0 + a_j)Env_k + SP_{kl} + \varepsilon_{ijklm}$$

$$(3) TGW_{jk} = mean + T_j + (a_0 + a_j)Env_k + b \times NGS_{jk} + F_k + \varepsilon_{jk}$$

$$(4) NGS_{jk} = mean + T_j + (a_0 + a_j)Env_k + b \times NFS_{jk} + F_k + \varepsilon_{jk}$$

$$(5) M_{jkl} = mean + T_j + F_{jkl} + A_l + (a_0 + a_j)Env_k + F_k + \varepsilon_{jkl}$$

2.2.3. Comparing direct and indirect indices of animal pollination

2.2.3.a. Relating pollination estimation to plant–pollinator interactions

We assessed whether the abundance of plant–pollinator interactions was linked to pollination estimates with phytometer plants, using the same modeling approach described above.

For strawberries, fruit mass and deformation were modeled following equation (2), but replacing the environmental variables with number of pollinator interactions with two predictors: (i) the total number of plant–pollinator interactions recorded at the corresponding site during oilseed rape flowering, and (ii) the total number of interactions observed on strawberry flowers throughout the flowering period in the field.

Oilseed rape yield components were modeled as a function of the total number of interactions observed in the field, and at 500 m and 1000 m on wildflowers in herbaceous field margins. The same control covariates as in the previous models were included in the three models. For total mass of seeds, residuals from plant-level models were not normally distributed, so we calculated the total oilseed rape seed mass per square meter by summing yield components within this area instead, resulting in a total mass per m².

2.2.3.b. Calculation of pollination indices for each site

To compare the two yield based measurements, we calculated two indices of pollination based on yield differences between open- and caged-pollination treatments on similar locations. For strawberries, the pollination index was calculated at each of the 30 observation sites as the difference in mean fruit mass between open and exclusion treatments ($O - E$), retaining only sites with at least two fruits per treatment. For oilseed rape, the pollination index was calculated in 20 fields as the difference in seed yield between open and closed treatments ($O - E$), after correcting yields for initial flower number and aphid pressure. Both pollination indices were standardized (z-transformation across all sites within each crop) to allow comparability across sites.

Direct comparison between the two pollination indices was possible only for the six fields where both oilseed rape and strawberries were jointly monitored, and their relationship was assessed using Spearman's rank correlation.

3.Results

3.1. Analysis of plant–pollinator interaction networks in relation to landscape context and agricultural practices

3.1.1. Plant-pollinator networks

The plant–pollinator interaction network highlights the diversity of pollinator visits observed during the surveys (Figure 2.1), with other Diptera (29.5%) and parasitic wasps (23.7%) the most abundant pollinators overall, but differences across flowering communities. Strawberries were mainly visited by beetles (48.2% of visits) and other Diptera (16%). Oilseed rape was mainly visited by other Diptera (48.1%) and honeybees (27.4%). Wildflower communities were mainly visited by parasitic wasps (41.9%) and other Diptera (27.1%).

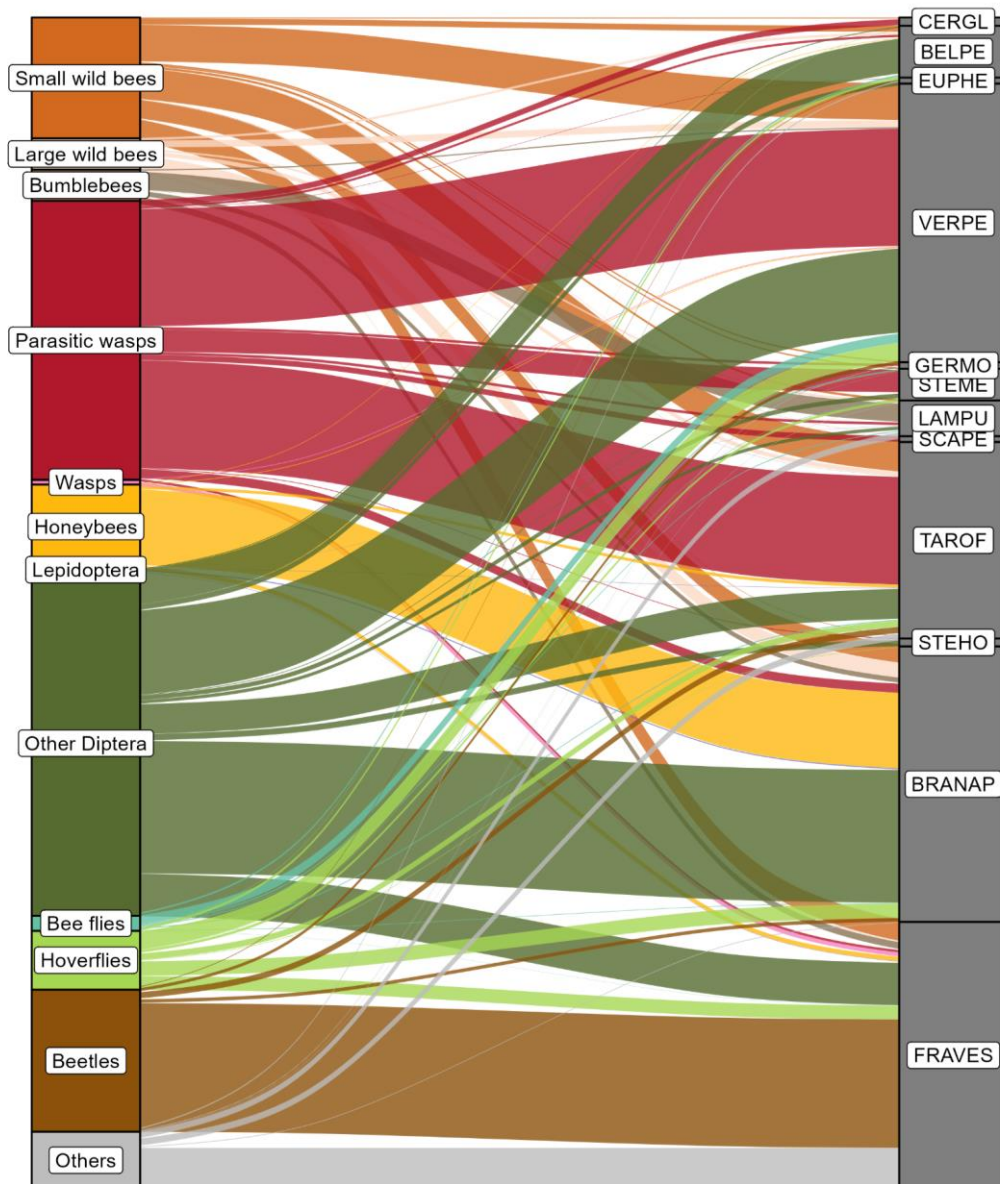


Figure 2.1. Alluvial diagram of plant–pollinator interactions. The diagram shows the distribution of pollinator morphogroups (left) visiting flowering plant species (right). Only plant species with more than 25 recorded interactions are displayed, for clarity. Colors represent the different pollinator morphogroups. The resulting alluvial diagram represents the cumulative dataset across the two sampling years, with a total of 5163 interactions displayed. The flows (alluvia) are proportional to the frequency of interactions. The correspondence between species plant codes and scientific names is provided in Table S2.1.

3.1.2. General differences in pollinator community composition among the studied plants

3.1.2.a. Floral resources-driven differences in pollinator community composition

The non-metric multidimensional scaling analysis revealed clear differences in pollinator communities among the three flowering communities (strawberries, wildflower herbaceous field margins, and oilseed rape fields). This pattern was supported by a one-way ANOSIM, which showed a significant difference between groups ($R = 0.242$, $p = 0.001$), indicating that pollinator communities as a whole differed among habitats (Figure 2.2). On strawberry flowers, we found very strong evidence for associations with beetles (stat = 0.425, $p < 0.001$) and other insects (stat = 0.317, $p < 0.001$), and moderate evidence for associations with wasps (stat = 0.119, $p = 0.030$). In field borders, very strong evidence supported associations with parasitic wasps (stat = 0.289, $p < 0.001$), small wild bees (stat = 0.221, $p < 0.001$), and bee-flies (stat = 0.177, $p < 0.001$). On oilseed rape, honeybees were strongly associated with very strong evidence (stat = 0.353, $p < 0.001$). Large wild bees (stat = 0.111, $p = 0.049$) showed weak evidence of association, while other Diptera (stat = 0.316, $p < 0.001$) exhibited very strong evidence of association with both field borders and oilseed rape.

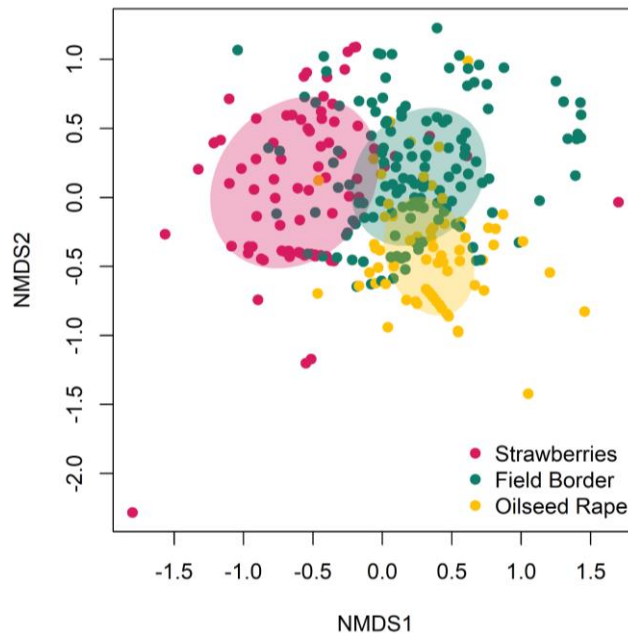


Figure 2.2. NMDS ordination of the plant–pollinator interactions. Points represent individual 10-minute observation sessions, based on the abundance of interactions between each pollinator group and flowering community. Three modalities are shown: interactions observed on strawberries (*pink*), wild flowering plants in field borders (*green*), and oilseed rape (*yellow*).

3.1.2.b. Influence of landscape composition and farming practices on pollinators

The distance-based redundancy analyses (Table 2.1) revealed that, when considering the entire pollinator community (all flowering communities pooled), all tested environmental variables were significantly related to community composition, an association also confirmed by the permanova method (Table S2.4). However, different sets of drivers emerged across flowering communities and for some pollinator morphogroups (Figures S2.3 and S2.4).

We found strong evidence that pollinator communities associated with oilseed rape (OSR) were shaped by pesticide use intensity in the landscape (mean TFI; $F = 3.01$, $p = 0.005$). For visitors of wild flowers in field margins, we detected strong evidence of relationships with semi-natural elements ($F = 2.40$, $p = 0.01$) and crop heterogeneity ($F = 2.12$, $p = 0.018$), and moderate evidence of a relationship with the proportion of OSR in the current year ($F = 2.00$, $p = 0.03$) and the area of flowering crops in the previous year ($F = 2.18$, $p = 0.012$). Concerning visitors of strawberry phytometers, we found strong evidence of a relationship with the area of OSR in the previous year ($F = 3.44$, $p = 0.003$), together with moderate evidence of relationships with crop heterogeneity ($F = 2.06$, $p = 0.036$) and flowering crop area in the previous year ($F = 2.04$, $p = 0.036$).

For the number of plant–pollinator interactions for the entire pollinator community, we found strong evidence of a relationship with semi-natural elements (Estimate = 0.17, $p = 0.02$), moderate evidence of a positive relationship with OSR in the previous year (Estimate = 0.15, $p = 0.03$). We also found moderate evidence of a negative relationship between the number of interactions and pesticide use intensity, specifically for the oilseed rape pollinator community (Estimate = -0.41 , $p = 0.01$) and moderate evidence of a relationship with semi-natural elements on strawberry pollinator communities (Estimate = 0.24, $p = 0.042$). These results highlight that while community composition is shaped by a broad range of environmental variables depending on the flowering community, the overall abundance of plant–pollinator interactions is more consistently driven by semi-natural elements and oilseed rape of the previous year, with pesticide intensity emerging as a negative driver for OSR pollinator assemblages (Figure 2.3).

Table 2.1. Summary of multivariate (Bray–Curtis distance-based redundancy analysis) or univariate (generalized linear mixed models, GLMM) analyses examining the relationships between environmental variables and pollinator communities (PC), over all flower resources (“Whole PC”) or within each flower resource. “Whole PC” corresponds to all pollinator communities combined, with a factorial effect of observation flowering community included in the model; “Osr PC” refers to communities observed on oilseed rape fields, “Wild flo PC” to communities on wildflowers in field margins, and “Straw PC” to communities on strawberry plants. For the dbRDA, F-statistics and their significance levels are reported, whereas for the GLMM, parameter estimates along with their significance levels are presented in the table. Whole tables are in Supplementary materials (Tables S2.2, S2.3, S2.5 and S2.6).

Explanatory variable	Bray distance-based redundancy analysis				GLMM			
	Whole PC	Osr PC	Wild flo PC	Straw PC	Whole PC	Osr PC	Wild flo PC	Straw PC
Area of semi-natural elements	2.76**	1.27	2.40**	0.65	0.17*	0.056	0.15	0.24*
Mean TFI in the landscape	2.16**	3.01**	1.46	1.21	-0.11	-0.41*	-0.031	-0.14
Oilseed rape area N-1	2.20**	1.15	0.95	3.44**	0.15*	0.072	0.066	0.13
Oilseed rape area N	2.21*	1.24	2.00*	0.88	-0.05	-0.048	-0.20.	0.007
Crop heterogeneity N-1	2.27**	1.22	2.12*	2.06*	0.13	0.096	0.153	-0.21
Flowering crop area N-1	1.93*	1.65	2.18 *	2.04*	-0.12	-0.091	-0.158	0.26
Model adjusted R ² for dbRDA R ² C for glmm	0.126	0.042	0.06	0.072	0.97	0.87	0.889	0.878

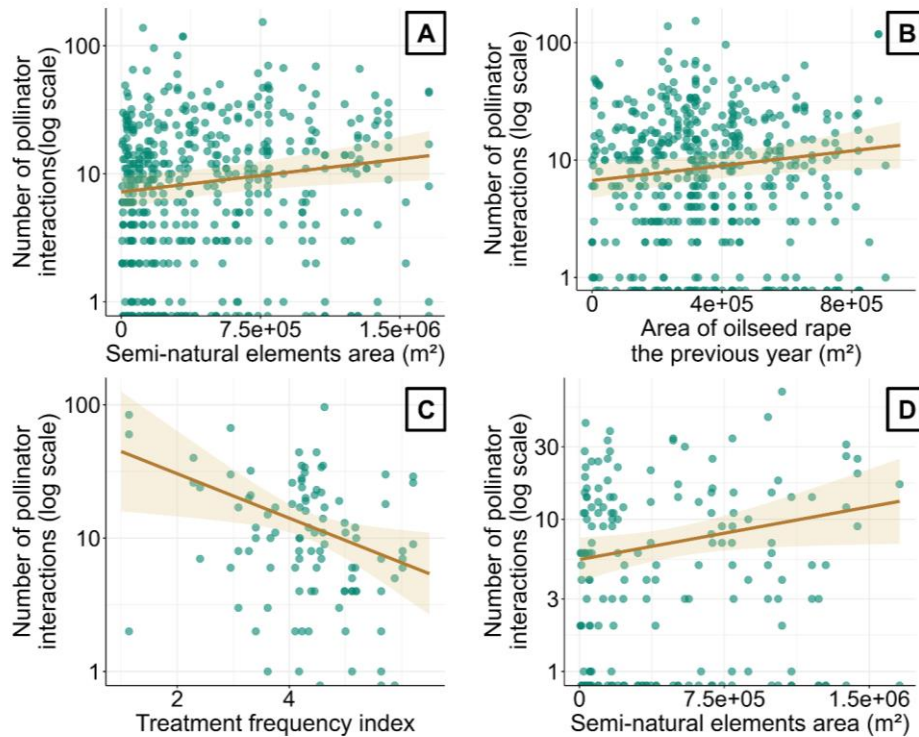


Figure 2.3. Modelled effects of significant relationships between pollinator interaction abundances and environmental variables presented in Table 2.1. Panels A and B show results for the whole pollinator community, panel C for the oilseed rape pollinator community, and panel D for the strawberry pollinator community. Predicted marginal effects (solid lines) and 95% confidence intervals (shaded areas) derived from GLMM, illustrating the influence of landscape variables and farming practices on pollinator interactions. Observed values (counts, green circles) are overlaid to model regressions.

3.2. Estimating pollination services in two phytometer species: *Brassica napus* and *Fragaria × ananassa*

3.2.1. Relationships between yield components in oilseed rape

Thousand grain weight (TGW) was negatively related to the number of seeds per silique (Figure 2.4), but the relationship was marginally significant only ($p = 0.077$), while the pollination treatment (open vs exclusion) and its interaction with seed number had no significant effect ($p > 0.4$). In contrast, total seed mass per plant was significantly higher under open pollination compared to caged plants ($p=3.1e-7$). Finally, aphid colonies were significantly longer inside cages than under open pollination ($p=2.5e-12$) (Figure S2.5).

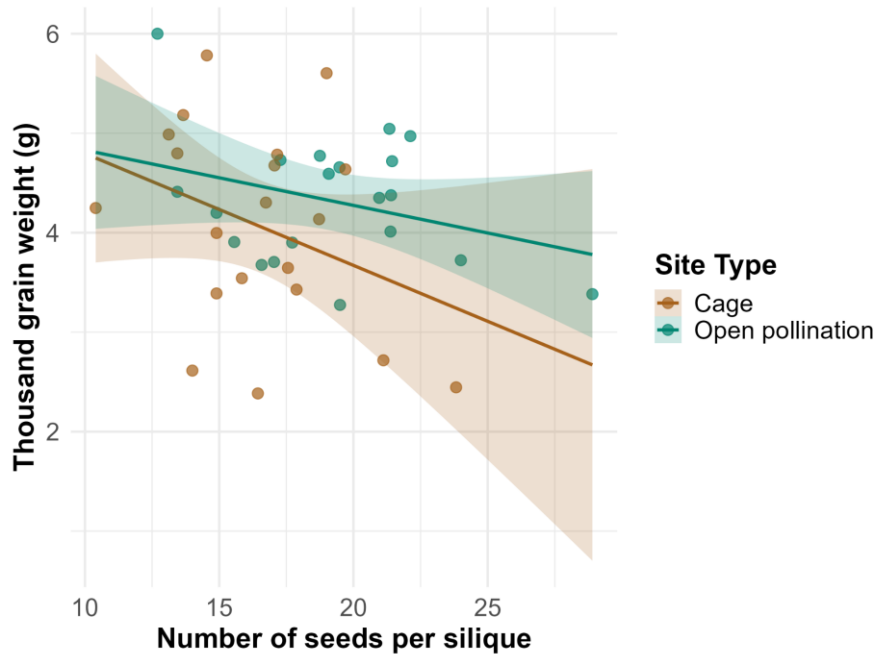


Figure 2.4. Relationship between thousand grain weight and number of seeds per silique under caged and open pollination treatments. Points represent each treatment for each field, colored by pollination treatment. Lines show linear regressions with 95% confidence intervals shaded. Thousand grain weight (TGW) is expressed in grams. Insect-proof cages prevented insect access to the crop, while open pollination allowed all pollinators.

3.2.2. Relationship between yield-based pollination estimation and environmental variables

For strawberries, we found moderate evidence that open pollination had a positive effect on fruit mass (Estimate = 1.61, $p = 0.011$), whereas no association with other environmental variables for both strawberry mass and deformation was observed (Table 2.2).

In oilseed rape, thousand grain weight, the number of seeds per silique and total seed mass per plant were higher under open pollination, compared with exclusion cages. We found strong evidence that, under open pollination, the number of grains per silique increased with the area of surrounding semi-natural elements ($p = 0.003$), and there was moderate evidence for a positive relationship between previous-year oilseed rape fields and grain number per silique. Finally, we found very strong evidence that the total seed mass per plant was positively related to the area of semi-natural elements (Estimate = 0.307, $p < 0.001$), strong to moderate evidence of a relationship with the area of oilseed rape in the previous year (Estimate = 0.265, $p = 0.001$) and in the current year (Estimate = 0.230, $p = 0.021$), whereas there was moderate evidence for a negative relationship with pesticide use (mean TFI: Estimate = -0.270 , $p = 0.034$).

Table 2.2. Mixed-effects models testing the effect of open (O) vs. closed (C) pollination treatments on yield components of two phytometer species (strawberry and oilseed rape abbreviated OSR in the table). The yield components considered were strawberry mass and deformation, OSR thousand grain weight (TGW), number of grains per silique, and seed mass per plant. Explanatory variables include the treatment (T) and its interactions with environmental variables calculated in a 1000m buffer radius. Coefficients correspond to estimates, with significance indicated as * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, and “.” for marginal significance ($p < 0.1$). Model fit is assessed with marginal (R^2_m , variance explained by fixed effects) and conditional (R^2_c , variance explained by both fixed and random effects) R^2 . Whole table results are shown in Supplementary materials (Tables S2.7 and 2.8).

Explanatory variable	Strawberries		Oilseed rape		
	Strawberry mass	Strawberry deformation	OSR TGW	OSR grains per silique	OSR seed mass per plant
Treatment	1.61 *	-0.002	0.41 **	3.03 ***	0.41 ***
O x Semi-natural elements area	-0.78	0.002	0.13	2.90 ***	0.31 ***
O x Mean TFI in the landscape	0.21	-0.008	0.37	-0.97	-0.27 *
O x Oilseed rape area N-1	-0.35	-0.016	-0.06	2.50 *	0.27 **
O x Oilseed rape area N	-0.38	0.034 .	-0.20	-0.17	0.23 *
O x Crop heterogeneity N-1	-0.16	-0.020	0.09	-1.89	-0.04
O x Flowering crop area N-1	0.24	0.018	0.45.	1.64	0.05
Model R^2	$R^2_c = 0.17$ $R^2_m = 0.06$	$R^2_c = 0.37$ $R^2_m = 0.06$	$R^2_c = 0.79$ $R^2_m = 0.40$	$R^2_c = 0.55$ $R^2_m = 0.46$	$R^2_c = 0.75$ $R^2_m = 0.64$

3.3. Comparing the different ways to assess pollination

3.3.1. Comparison of yield-based pollination estimation to pollinator interaction observations

The relationships between pollination services, measured on phytometer plants as yield differences between the open-pollination and the pollinator-exclusion treatments, and pollinator-pollinator interactions did not reveal any consistent pattern. None of the relationships tested were statistically significant, except for moderate evidence of a positive influence of pollinator abundance observed directly in oilseed rape fields (0 m) on the number of seeds per silique in the same fields. Results are shown in Tables S2.9 and S2.10.

3.3.2. Comparison of the pollination indices

Any significant correlation was found between the two pollination indices (Spearman's correlation test, $p = 0.217$).

4. Discussion

4.1. Pollinator and landscape effects on yield components

Using non-lethal protocols, our analyses enabled us to observe pollinator communities across different flowering communities and to estimate their responses to environmental variables.

The differences in yield components between the open pollination and exclusion treatments showed different responses to environmental variables. Strawberry yields showed an increase in fruit mass associated with open pollination, but this effect was not related to local pollinator observations or environmental variables. Oilseed rape yield components were influenced by the interaction between open pollination and environmental variables, particularly total seed mass per plant, which was associated with semi-natural habitats, pesticide use, and the area of oilseed rape in both the current and previous years. No difference was observed for the mean weight of grains, but effects were found for the number of grains per silique and for total seed mass. This is consistent with recent studies showing that pollinators primarily influence the number of grains per silique rather than individual grain mass (Amro, 2021). Other studies showed the opposite pattern (Bommarco et al., 2012) suggesting that more precise information on cultivars and their dependence on pollinators may be needed to improve the model.

4.2. Partitioning of pollinator communities among flowering communities.

The observation of the interaction network seems to reveal the most abundant morphogroups in pollinator communities. Wild bees (small and large bees and bumblebees) accounted for relatively few interactions across all flowering communities. This result highlights a deficit of wild bees, which are considered more effective for pollination (Jauker et al., 2012), in an intensive cropping landscape such as the one studied. Although considered less effective for pollination (Goulnik et al., 2020), the other Diptera represent a significant proportion of pollinators in the three flowering communities, which was mainly observed in semi-natural elements such as permanent grasslands (Lefebvre et al., 2014; Goulnik et al., 2020). We observed a clear preference of honeybees for oilseed rape as in (Gay et al., 2024). Parasitic wasps appeared to forage on wild plants before laying their eggs and did not seem to benefit from the massive floral resource provided by oilseed rape probably due to competition with other pollinator taxa. Strawberry plants are mainly visited by beetles, which are a group of pollinators that generally carry little pollen. Nevertheless, these pollinators seem to have a positive effect on strawberry weight and shape, as reflected in the difference between these two variables in closed and open pollination in our results. This could be explained by the reduced observation time of pollinator morphogroups, which is not necessarily representative of all pollinator visits during the entire flowering period of strawberry plants.

These observed patterns were confirmed multivariate analyses which displayed a clear partitioning of pollinator groups among flowering communities, with certain taxa exhibiting strong specificity for oilseed rape or wild flowers. Wild plants supported pollinator communities that rarely visit oilseed rape within the same landscapes, underscoring their essential role in maintaining pollinator diversity in intensively managed agricultural areas (Bretagnolle and Gaba, 2015; Benvenuti, 2024). This is consistent with previous findings showing that even a small proportion of ruderal plants within sunflower plantations can sustain a more diverse community of pollinators (Carvalho et al., 2011).

4.3. Negative impact of pesticides on pollinators and pollination

Conserving and enhancing wild flowers in fields and herbaceous margins is essential but insufficient on its own to sustain pollinator communities. Indeed, both multivariate analyses and linear models based on the number of interactions within oilseed rape pollinator communities revealed negative responses to pesticide use, a finding consistent with the literature (C. Brittain et al., 2010). Pesticides affect pollinators through both lethal and sub-lethal effects (Basu et al., 2024) as well as by reducing floral resources through mechanisms such as the decline of arable wild plants associated with herbicide use (Nicholls and Altieri, 2013). Therefore, promoting flower strips alone is insufficient; broader changes in agricultural practices are needed to effectively protect insect populations.

These patterns were also reflected in the yield-based pollination estimation of the studied phytometers. While strawberry yields showed an overall increase in fruit mass due to pollination, this effect was not related to local environmental variables or pollinator observations. In contrast, oilseed rape yield components were negatively affected by pesticide use. This suggests that pesticide exposure may directly reduce pollination services for oilseed rape by negatively affecting pollinators as shown above, highlighting the broader consequences of intensive chemical management on pollination-dependent crop production. (Catarino et al., 2019; Perrot et al., 2022).

4.4. Positive effect of semi natural elements on pollinators and pollination

Pollinator communities and oilseed rape yield-based pollination estimation showed constant positive response to the presence of semi-natural elements in the landscape. Semi-natural habitats can have a positive effect on pollination as they provide long-term, stable resources for pollinators (Neumüller et al., 2020), in contrast to oilseed rape whose floral resources are ephemeral. These habitats not only supply nectar and pollen but also offer relatively undisturbed sites for nesting (Quin et al., 2015; Requier and Leonhardt, 2020), supporting pollinator populations across multiple crop cycles. Protecting and integrating such habitats

within agricultural landscapes is thus critical to sustain both pollination services and overall insect biodiversity. They can also help to mitigate negative impacts of pesticides (Park et al., 2015) even if both must be made at the same time to preserve pollinators effectively (Le Féon et al., 2010; Perrot et al., 2022).

4.5. Effects of crops grown during the current and previous year in the landscape

Our multivariate analyses, which account for both species richness and abundance, revealed effects of past crop heterogeneity and the presence of flowering crops on the overall pollinator community and on communities associated with wild flowers, but models based solely on interaction abundance didn't show any response. It is consistent with the pattern that landscape complexity typically affects species richness more strongly than abundances (Marja et al., 2022). In particular, the presence of flowering crops in the previous year had a positive effect on pollinator communities, especially in landscapes dominated by cereals. Oilseed rape, for instance, contributes both directly through its floral resources and indirectly via the spillover of early-season pollinators associated with its flowering (Riedinger et al., 2015). Such spillover dynamics support the maintenance and enhancement of pollinator populations from year to year, particularly species specialized on these crops. Similarly, other mass-flowering crops have been shown to promote pollinator abundance and diversity; for example, higher coverage of mass-flowering crops over consecutive years can enhance wild bee densities in subsequent oilseed rape fields (Beyer et al., 2021; Perrot et al., 2022), highlighting the cumulative benefits of floral resources at the landscape scale.

4.6. Limits of this study

For most analyses, we observed a strong and significant effect of the pollination treatment alone, without interactions with other variables. This suggests that our models may not capture all factors interacting with pollination services, or that there could be a slight bias in plant growth under cages, which might contribute to highlighting this treatment effect.

When linking pollination indices (differences in yield between open and closed treatments) with pollinator observations, no consistent significant relationships emerged as previous studies (Rivers-Moore et al., 2023). This absence of clear correlation is likely related both to the moderate pollinator dependence of the phytometer plants and to the restricted duration of our field observations, which did not capture the full variability of pollinator activity. Future studies could benefit from recent automated monitoring methods, such as acoustic sensors (Ribeiro et al., 2021; Crochard, 2023) or GPS-equipped pollinator tracking (Kratschmer et al., 2025), which allow continuous and fine-scale observation of pollinator movements and activity

across temporal and spatial gradients, providing a more comprehensive picture of community dynamics.

Conclusion

Overall, our study highlights the double importance of conserving pollinators for both biodiversity and ecosystem services. Pollinator communities respond positively to semi-natural elements and landscape complexity, while intensive pesticide use has clear negative effects on both pollinator abundance and pollination services, particularly for oilseed rape. Maintaining continuous floral resources in the landscape, including wild plants and flowering crops, supports diverse pollinator assemblages and enhances pollination-dependent yields. These findings underscore the need for integrated, sustainable agricultural practices that reduce chemical inputs and preserve or restore semi-natural habitats. By promoting such practices, farmers can simultaneously support pollinator conservation and secure reliable pollination services, contributing to more resilient and productive agroecosystems.

Perspectives

Although biodiversity is often assumed to directly enhance ecosystem services, the relationship between the two is far from straightforward. The factors driving biodiversity are not necessarily the same as those that determine the delivery or stability of ecosystem services. For instance, in biological pest control, increasing natural enemy diversity does not always translate into more effective biological control, as shown in several recent syntheses (e.g. Begg et al., 2017; Serée et al., 2022; Vialatte et al., 2023). Similar patterns may apply to pollination, where species composition, functional traits, and landscape context can be more important than species richness alone (Stavert et al., 2016). From the plant-pollinator interactions we observed, it became apparent that many parasitoid micro-wasps interact almost exclusively with wild plants rather than with oilseed rape. This highlights the key role of wild flora as a key resource for insects, providing both pollination and biological pest control services (Stephens et al., 2006). These findings naturally lead into Chapter 5, which will explore in greater detail the potential links between pollination and biological pest control services.

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Supplementary materials

Table S2.1. Correspondence table between plant codes and scientific names

Scientific name	Code	Scientific name	Code
<i>Anthriscus caucalis</i>	ANTCA	<i>Ranunculus acris</i>	RANAC
<i>Barbarea vulgaris</i>	BARVU	<i>Ranunculus ficaria</i>	RANFI
<i>Bellis perennis</i>	BELPE	<i>Ranunculus repens</i>	RANRE
<i>Capsella bursa-pastoris</i>	CAPBP	<i>Scandix pecten-veneris</i>	SCAPE
<i>Cardamine hirsuta</i>	CARHI	<i>Senecio vulgaris</i>	SENVU
<i>Cerastium fontanum</i>	CERFO	<i>Silene latifolia</i>	SILLA
<i>Cerastium glomeratum</i>	CERGL	<i>Stellaria holostea</i>	STEOH
<i>Brassica napus</i>	BRANAP	<i>Stellaria media</i>	STEME
<i>Erodium cicutarium</i>	EROCI	<i>Taraxacum officinale</i>	TAROF
<i>Euphorbia helioscopia</i>	EUPHE	<i>Valerianella sp.</i>	VALLO
<i>Fumaria officinalis</i>	FUMOF	<i>Veronica arvensis</i>	VERAR
<i>Geranium dissectum</i>	GERDI	<i>Veronica chamaedrys</i>	VERCA
<i>Geranium molle</i>	GERMO	<i>Veronica persica</i>	VERPE
<i>Geranium pusillum</i>	GERPU	<i>Vicia hirsuta</i>	VICHI
<i>Lamium album</i>	LAMAL	<i>Vicia sativa</i>	VICSA
<i>Lamium purpureum</i>	LAMPU	<i>Viola arvensis</i>	VIOAR
<i>Matricaria discoidea</i>	MATOD		
<i>Matricaria recutita</i>	MATRE		
<i>Medicago arabica</i>	MEDAR		
<i>Myosotis ramosissima</i>	MYOHE		

Table S2.2. Results of the dbRDA assessing the effects of environmental variables across all the pollinator communities.

Explanatory variable	Df	SumOfSqs	F-statistic	p-value	Global adj. R ²	Significance
Semi-natural elements area	1	1.0576580	2.759	0.003	0.126	**
Mean TFI in the landscape	1	0.8106519	2.115	0.010	0.126	**
Oilseed rape area N-1	1	0.8436335	2.201	0.010	0.126	**
Oilseed rape area N	1	0.8486421	2.214	0.013	0.126	*
Crop heterogeneity N-1	1	0.8703672	2.270	0.009	0.126	**
Flowering crop area N-1	1	0.7406430	1.932	0.030	0.126	*
Cloud cover	1	0.6590125	1.719	0.047	0.126	*
Temperature	1	1.3321974	3.475	0.001	0.126	***
Wind	1	0.5304823	1.384	0.148	0.126	
Flower area	1	0.4202720	1.096	0.328	0.126	
Plant type	2	14.2384733	18.570	0.001	0.126	***

Table S2.3. Results of the dbRDA assessing the effects of environmental variables for all pollinator communities individually.

Explanatory variable	Df	SumOfSqs	F-statistic	p-value	Global adj. R ²	Significance
Strawberries						
Semi-natural elements area	1	0.2386562	0.646	0.795	0.072	
Mean TFI in the landscape	1	0.4480659	1.213	0.235	0.072	
Oilseed rape area N-1	1	1.2695538	3.437	0.003	0.072	**
Oilseed rape area N	1	0.3244306	0.878	0.531	0.072	
Crop heterogeneity N-1	1	0.7601670	2.058	0.036	0.072	*
Flowering crop area N-1	1	0.7516502	2.035	0.036	0.072	*
Cloud cover	1	0.6420815	1.738	0.072	0.072	.
Temperature	1	0.6833501	1.850	0.045	0.072	*
Wind	1	0.3956798	1.071	0.352	0.072	
Flower area	1	0.781898	2.116	0.029	0.072	*
Oilseed rape						
Semi-natural elements area	1	0.3720887	1.268	0.221	0.042	
Mean TFI in the landscape	1	0.8839003	3.013	0.005	0.042	**
Oilseed rape area N-1	1	0.3359351	1.145	0.305	0.042	
Oilseed rape area N	1	0.3623404	1.235	0.252	0.042	
Crop heterogeneity N-1	1	0.3577512	1.219	0.247	0.042	
Flowering crop area N-1	1	0.4851938	1.654	0.098	0.042	.
Cloud cover	1	0.4419588	1.506	0.139	0.042	
Temperature	1	0.5687875	1.939	0.059	0.042	.
Wind	1	0.2066285	0.704	0.703	0.042	
Flower area	1	0.2832015	0.965	0.468	0.042	
Wild flower						
Semi-natural elements area	1	0.8574900	2.403	0.010	0.060	**
Mean TFI in the landscape	1	0.5213571	1.461	0.144	0.060	
Oilseed rape area N-1	1	0.3374103	0.946	0.511	0.060	
Oilseed rape area N	1	0.7120019	1.996	0.028	0.060	*
Crop heterogeneity N-1	1	0.7570014	2.122	0.018	0.060	*
Flowering crop area N-1	1	0.7762364	2.176	0.012	0.060	*
Cloud cover	1	0.4547082	1.274	0.213	0.060	
Temperature	1	1.6788102	4.705	0.001	0.060	***
Wind	1	0.5738891	1.609	0.090	0.060	.
Flower area	1	0.8576949	2.404	0.007	0.060	**

Table S2.4. Results of the Permanova assessing the effects of environmental variables across all the pollinator communities.

Explanatory variable	Sum of Squares	R ²	F-statistic	p-value	Significance
Semi-natural elements area	0.969	0.007	3.316	0.003	**
Mean TFI in the landscape	0.717	0.005	2.452	0.007	**
Oilseed rape area N-1	0.757	0.005	2.587	0.010	**
Oilseed rape area N	0.755	0.005	2.581	0.009	**
Crop heterogeneity N-1	0.756	0.005	2.585	0.008	**
Flowering crop area N-1	0.643	0.004	2.201	0.019	*
Cloud cover	0.584	0.004	1.996	0.038	*
Temperature	1.251	0.009	4.278	0.001	***
Wind	0.454	0.003	1.554	0.110	
Flower area	0.358	0.002	1.225	0.256	
Plant type	14.107	0.098	24.126	0.001	***

Table S2.5. Results of the mixed linear model assessing the effects of environmental variables on the abundance of pollinator–plant interactions across the whole dataset.

Explanatory variable	Estimate	Std. Error	z-value	p-value	Significance
Semi-natural elements area	0.168	0.070	2.383	0.017	*
Treatment frequency index in the landscape	-0.106	0.087	-1.211	0.226	
Oilseed rape area N-1	0.154	0.071	2.160	0.031	*
Oilseed rape area N	-0.059	0.078	-0.756	0.450	
Crop heterogeneity N-1 (Shannon index)	0.107	0.096	1.114	0.265	
Flowering crop area N-1	-0.106	0.087	-1.225	0.221	
Cloud coverage	0.029	0.055	0.530	0.596	
Temperature	0.107	0.053	2.004	0.045	*
Wind	-0.176	0.052	-3.373	0.001	***
Number of flowers	0.077	0.067	1.149	0.251	
Plant type: path edges	0.666	0.148	4.514	0.000	***
Plant type: oilseed rape fields	0.460	0.193	2.380	0.017	*

Table S2.6. Results of the mixed linear model assessing the effects of environmental variables on the abundance of pollinator–plant interactions across each dataset for each observation plant type.

Explanatory variable	Estimate	Std. Error	z-value	p-value	Significance
Oilseed					
Semi-natural elements area	0.056	0.144	0.391	0.696	
Treatment frequency index in the landscape	-0.408	0.165	-2.464	0.014	*
Oilseed rape area N-1	0.072	0.144	0.504	0.615	
Oilseed rape area N	-0.048	0.147	-0.323	0.747	
Crop heterogeneity N-1 (Shannon index)	0.096	0.200	0.478	0.633	
Flowering crop area N-1	-0.091	0.182	-0.500	0.617	
Cloud cover	0.164	0.094	1.747	0.081	.
Temperature	-0.099	0.088	-1.131	0.258	
Wind	-0.077	0.088	-0.880	0.379	
Flower area	0.196	0.108	1.806	0.071	.
Border					
Semi-natural elements area	0.153	0.095	1.610	0.107	
Treatment frequency index in the landscape	-0.031	0.119	-0.259	0.796	
Oilseed rape area N-1	0.066	0.097	0.682	0.495	
Oilseed rape area N	-0.201	0.108	-1.864	0.062	.
Crop heterogeneity N-1 (Shannon index)	0.153	0.124	1.241	0.215	
Flowering crop area N-1	-0.158	0.113	-1.403	0.161	
Cloud cover	0.016	0.069	0.237	0.813	
Temperature	-0.125	0.060	-2.083	0.037	*
Wind	-0.076	0.072	-1.051	0.293	
Flower area	0.270	0.075	3.621	0.000	***
Straw					
Semi-natural elements area	0.241	0.118	2.036	0.042	*
Treatment frequency index in the landscape	-0.142	0.151	-0.940	0.347	
Oilseed rape area N-1	0.127	0.122	1.035	0.301	
Oilseed rape area N	0.007	0.125	0.053	0.957	
Crop heterogeneity N-1 (Shannon index)	-0.206	0.166	-1.243	0.214	
Flowering crop area N-1	0.259	0.153	1.694	0.090	.
Cloud cover	-0.021	0.104	-0.201	0.841	
Temperature	0.473	0.105	4.514	0.000	***
Wind	-0.078	0.091	-0.851	0.395	
Flower area	0.412	0.095	4.335	0.000	***

Table S2.7. Responses of oilseed rape yield components to environmental variables, with associated covariates shown for each component. In addition to the interactions between open pollination and environmental variables, individual responses are also reported.

Explanatory variable	Estimate	Std. Error	z-value	p-value	Significance
Mass					
Year (ref=2023)	2.187	0.880	2.485	0.013	*
Open pollination	1.617	0.634	2.550	0.011	*
Semi-natural elements area	0.472	0.642	0.734	0.463	
Mean TFI in the landscape	0.310	0.741	0.418	0.676	
Oilseed rape area N-1	0.361	0.661	0.546	0.585	
Oilseed rape area N	0.600	0.661	0.908	0.364	
Crop heterogeneity N-1 (Shannon index)	1.200	0.958	1.253	0.210	
Flowering crop area N-1	-0.232	0.829	-0.279	0.780	
Open pollination x Semi-natural elements area	-0.775	0.801	-0.967	0.334	
Open pollination x Mean TFI in the landscape	-0.548	0.923	-0.594	0.553	
Open pollination x Oilseed rape area N-1	-0.465	0.795	-0.585	0.558	
Open pollination x Oilseed rape area N	-0.810	0.829	-0.978	0.328	
Open pollination x Crop heterogeneity N-1 (Shannon index)	-1.436	1.196	-1.201	0.230	
Open pollination x Flowering crop area N-1	0.637	0.962	0.662	0.508	
Deformation					
Year (ref=2023)	-0.009	0.018	-0.503	0.615	
Open pollination	-0.002	0.013	-0.139	0.889	
Semi-natural elements area	-0.028	0.013	-2.121	0.034	*
Mean TFI in the landscape	0.012	0.015	0.787	0.431	
Oilseed rape area N-1	-0.007	0.014	-0.496	0.620	
Oilseed rape area N	-0.038	0.014	-2.815	0.005	**
Crop heterogeneity N-1 (Shannon index)	-0.009	0.019	-0.461	0.644	
Flowering crop area N-1	-0.015	0.017	-0.890	0.373	
Open pollination x Semi-natural elements area	0.002	0.016	0.119	0.905	
Open pollination x Mean TFI in the landscape	-0.008	0.019	-0.396	0.692	
Open pollination x Oilseed rape area N-1	-0.016	0.016	-0.981	0.327	
Open pollination x Oilseed rape area N	0.034	0.017	1.949	0.051	.
Open pollination x Crop heterogeneity N-1 (Shannon index)	-0.020	0.024	-0.821	0.411	
Open pollination x Flowering crop area N-1	0.018	0.020	0.929	0.353	

Table S2.8. Responses of oilseed rape yield components to environmental variables, with associated covariates shown for each component. In addition to the interactions between open pollination and environmental variables, individual responses are also reported.

Predictor	Estimate	SE	t/z value	p-value	Signif.
TGW (thousand-grain weight)					
Open pollination	0.412	0.146	2.818	0.005	**
Semi natural elements area	-0.195	0.180	-1.084	0.278	
Mean TFI in the landscape	-0.168	0.291	-0.578	0.563	
Oilseed rape area N-1	-0.426	0.217	-1.966	0.049	*
Oilseed rape area N	0.127	0.243	0.522	0.602	
Crop heterogeneity N-1	0.011	0.265	0.043	0.966	
Flowering crop area N-1	-0.714	0.273	-2.611	0.009	**
Number of grains per silique	-0.215	0.110	-1.954	0.051	.
Open pollination x Semi natural elements area	0.130	0.175	0.745	0.456	
Open pollination x Mean TFI in the landscape	0.370	0.249	1.485	0.137	
Open pollination x Oilseed rape area N-1	-0.056	0.200	-0.281	0.779	
Open pollination x Oilseed rape area N	-0.204	0.204	-0.997	0.319	
Open pollination x Crop heterogeneity N-1	0.088	0.231	0.382	0.703	
Open pollination x Flowering crop area N-1	0.451	0.232	1.945	0.052	.
Number of grains per silique					
Open pollination	2.743	0.826	3.321	< 0.001	***
Semi natural elements area	-0.686	0.780	-0.880	0.379	
Mean TFI in the landscape	0.911	1.329	0.685	0.493	
Oilseed rape area N-1	-1.023	0.936	-1.093	0.274	
Oilseed rape area N	0.534	1.092	0.489	0.625	
Crop heterogeneity N-1	1.120	1.172	0.955	0.340	
Flowering crop area N-1	-0.298	1.261	-0.236	0.813	
Initial estimated flower number per plant	-0.384	0.606	-0.634	0.526	
Open pollination x Semi natural elements area	3.109	1.036	3.000	0.003	**
Open pollination x Mean TFI in the landscape	-1.751	1.653	-1.060	0.289	
Open pollination x Oilseed rape area N-1	3.002	1.252	2.398	0.016	*
Open pollination x Oilseed rape area N	0.423	1.449	0.292	0.770	
Open pollination x Crop heterogeneity N-1	-1.999	1.513	-1.321	0.186	
Open pollination x Flowering crop area N-1	1.017	1.547	0.658	0.511	
Mass per ramification					
Open pollination	0.410	0.062	6.597	< 0.001	***
Semi natural elements area	-0.155	0.106	-1.458	0.145	
Mean TFI in the landscape	0.524	0.178	2.950	0.003	**
Oilseed rape area N-1	-0.257	0.124	-2.082	0.037	*
Oilseed rape area N	-0.059	0.144	-0.411	0.681	
Crop heterogeneity N-1	0.028	0.147	0.191	0.849	
Flowering crop area N-1	0.009	0.162	0.056	0.955	
Aphid pressure per plant	0.018	0.032	0.578	0.563	
Initial estimated flower number per plant	0.559	0.028	20.289	< 0.001	***
Open pollination x Semi natural elements area	0.307	0.073	4.228	< 0.001	***
Open pollination x Mean TFI in the landscape	-0.270	0.128	-2.115	0.034	*
Open pollination x Oilseed rape area N-1	0.265	0.081	3.274	0.001	**
Open pollination x Oilseed rape area N	0.230	0.100	2.310	0.021	*
Open pollination x Crop heterogeneity N-1	0.048	0.094	0.510	0.610	
Open pollination x Flowering crop area N-1	0.028	0.111	0.254	0.800	

Table S2.9. Responses of strawberry yield components to pollinator visits. In addition to the interactions between open pollination and pollinator visitations, individual responses are also reported.

Predictor	Estimate	SE	t/z value	p-value	Signif.
Fruit mass					
Year (ref=2023)	2.595	0.670	3.871	< 0.001	***
Open pollination	3.178	1.375	2.312	0.021	*
Pollinator interactions on site during oilseed rape flowering	0.015	0.019	0.820	0.412	
Pollinator interactions with strawberries	-0.002	0.022	-0.110	0.912	
Open pollination: Pollinator interactions on site during oilseed rape flowering	-0.034	0.023	-1.485	0.137	
Open pollination: Pollinator interactions with strawberries	-0.014	0.028	-0.491	0.624	
Fruit deformation					
Year (ref=2023)	-0.026	0.015	-1.772	0.076	.
Open pollination	0.001	0.014	0.062	0.950	
Pollinator interactions on site during oilseed rape flowering	0.003	0.011	0.270	0.787	
Pollinator interactions with strawberries	0.000	0.011	-0.037	0.970	
Open pollination x Pollinator interactions on site during oilseed rape flowering	-0.007	0.013	-0.567	0.570	
Open pollination x Pollinator interactions with strawberries	-0.002	0.014	-0.114	0.909	

Table S2.10. Responses of oilseed rape yield components to pollinator visits. In addition to the interactions between open pollination and pollinator visitations, individual responses are also reported.

Predictor	Estimate	SE	t/z value	p-value	Signif.
Number of grains per silique					
Open pollination	-2.641	2.237	-1.180	0.238	
Pollinators at 0m	-0.026	0.019	-1.385	0.166	
Pollinators at 500m	-0.029	0.028	-1.055	0.292	
Pollinators at 1000m	0.018	0.042	0.438	0.661	
Number of siliques per plant	-0.344	0.510	-0.674	0.500	
Open pollination × Pollinators at 0m	0.051	0.026	1.972	0.049	*
Open pollination × Pollinators at 500m	0.021	0.039	0.529	0.597	
Open pollination × Pollinators at 1000m	0.091	0.060	1.529	0.126	
Thousand grain weight					
Open pollination	0.281	0.381	0.739	0.460	
Pollinators at 0m	-0.005	0.005	-0.980	0.327	
Pollinators at 500m	-0.002	0.007	-0.338	0.735	
Pollinators at 1000m	0.002	0.011	0.201	0.840	
Number of grains per silique	-0.305	0.122	-2.496	0.013	*
Open pollination × Pollinators at 0m	0.002	0.005	0.543	0.587	
Open pollination × Pollinators at 500m	-0.002	0.006	-0.307	0.759	
Open pollination × Pollinators at 1000m	0.006	0.010	0.573	0.567	
Total estimated mass					
Open pollination	34.580	51.955	0.666	0.506	
Pollinators at 0m	-0.830	0.574	-1.446	0.148	
Pollinators at 500m	-0.396	0.838	-0.473	0.636	
Pollinators at 1000m	-0.473	1.285	-0.368	0.713	
Number of flowers	153.819	15.285	10.063	< 0.001	***
Aphid pressure	-50.077	16.683	-3.002	0.003	**
Open pollination × Pollinators at 0m	-0.326	0.611	-0.533	0.594	
Open pollination × Pollinators at 500m	0.731	0.895	0.816	0.414	
Open pollination × Pollinators at 1000m	0.776	1.355	0.572	0.567	

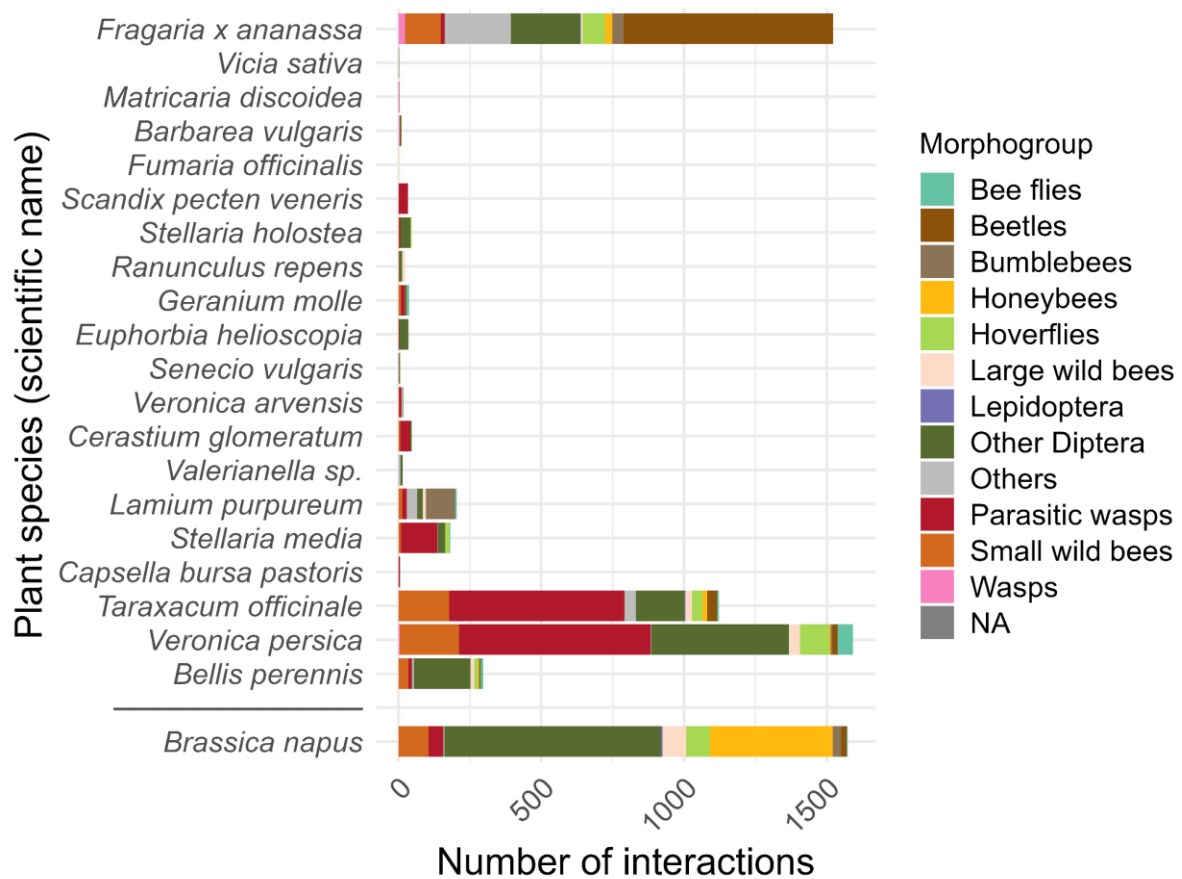


Figure S2.1. Cumulative number of pollinator interactions recorded per plant species, categorized by insect morphogroups.

Interaction data are pooled across all observation sessions. The cultivated crop species *Brassica napus* (oilseed rape) is displayed at the bottom separately from the other plant species to emphasize that it is the only cultivated crop.

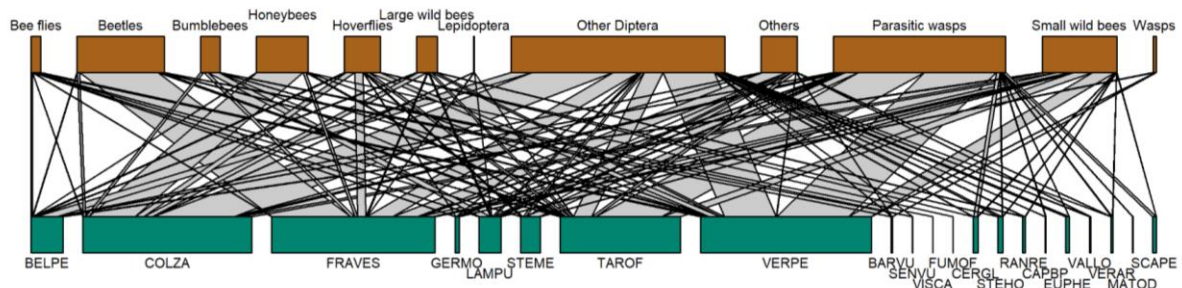


Figure S2.2. Global pollinator network including all observed interactions between plants and pollinators. The width of the links corresponds to the frequency of interactions. Plant species are shown on the lower axis and pollinator groups on the upper axis.



Figure S2.3. Graphical representation of the first two axis of the distance-based redundancy analysis (dbRDA) of pollinator communities and environmental variables. Points represent individual sampling sessions. Orange dashed arrows indicate the pollinator groups most strongly associated with the first two dbRDA axes, while green solid arrows show the environmental variables driving community composition. This combined visualization illustrates relationships between pollinator assemblages and environmental gradients but does not capture the full n-dimensional structure of the dbRDA.

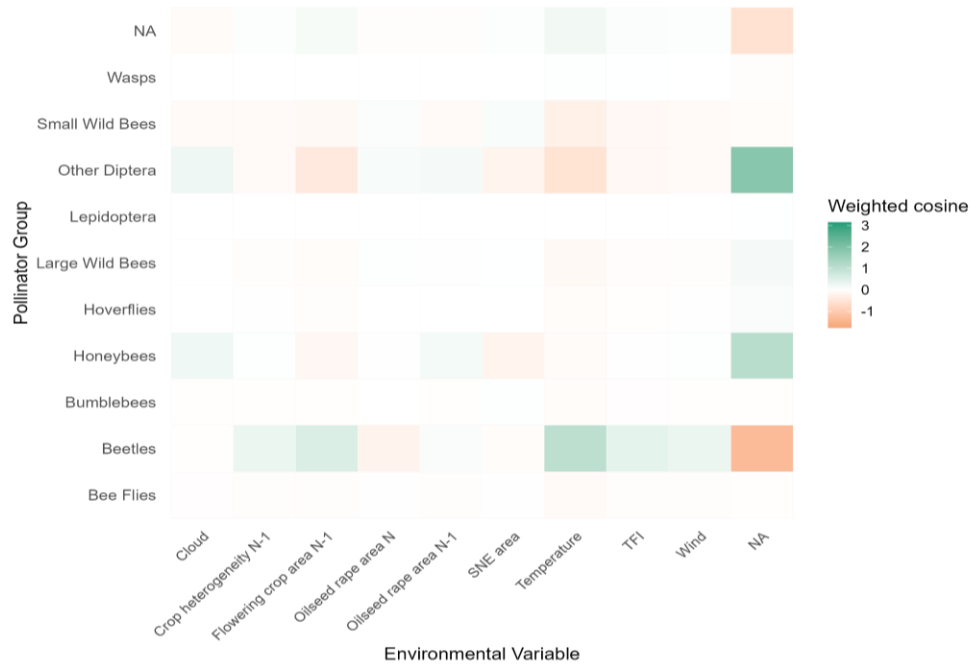


Figure S2.4. Heatmap illustrating the associations between pollinator morpho-groups and environmental variables, derived from the first two axes of the dbRDA. Associations were calculated as the cosine of the angle between species vectors and environmental vectors on CAP1 and CAP2, weighted by arrow lengths. Stronger positive associations are indicated by greenish colors, while negative associations are indicated by orange colors.

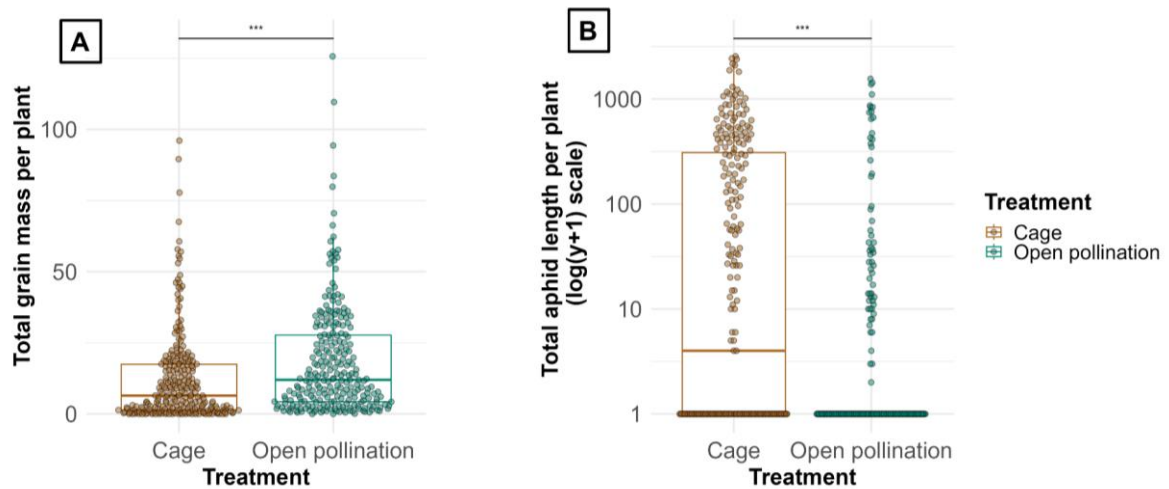
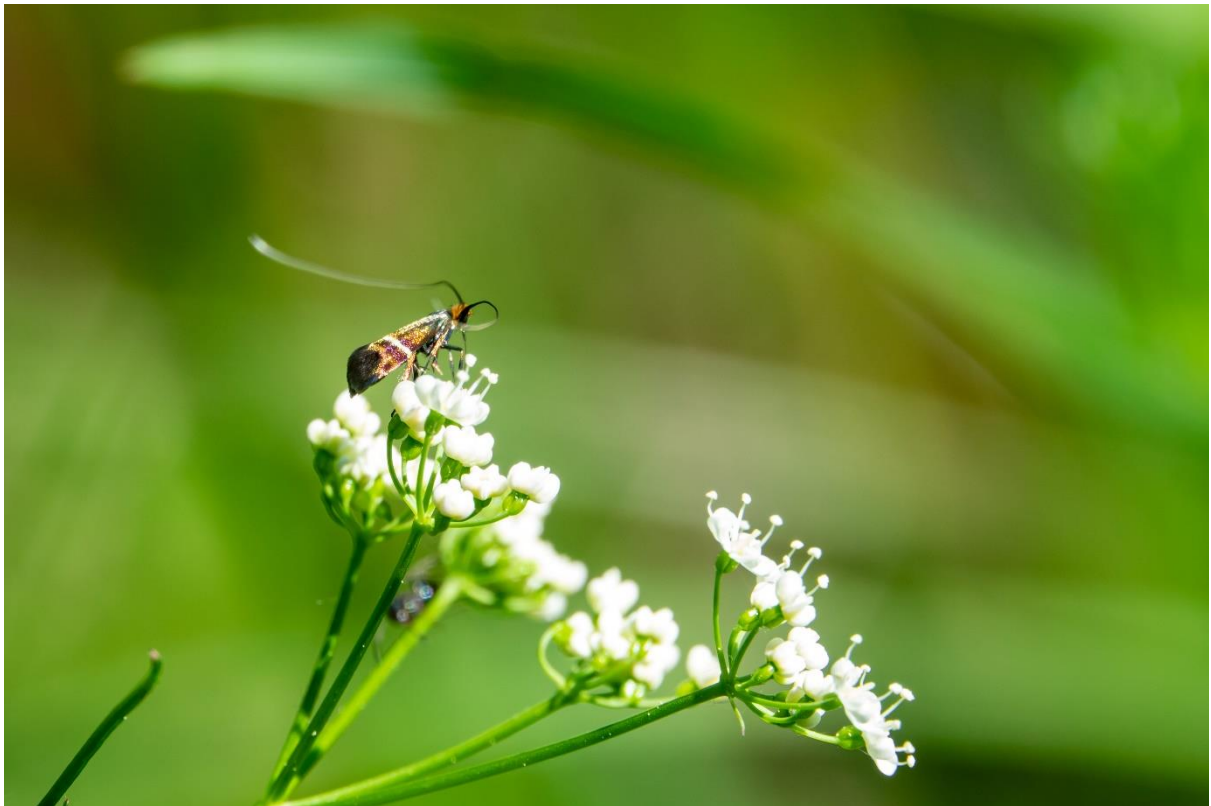


Figure S2.5. Effects of pollination treatment on seed production and aphid colonies in oilseed rape. (A) Total seed mass per plant, calculated as the product of the number of full siliques $\times$ mean seed number per silique $\times$ mean thousand-grain weight, in relation to treatment. (B) Total aphid colony length per plant in relation to treatment. In both cases, Wilcoxon rank-sum tests were performed to assess differences between treatments.

3

Studying pollination along an agricultural–urban gradient



Adela sp. In the Cévennes, May 2021, © Thibault Gandara

Integrating individual experiments into a collaborative framework on pollination services

Having presented the results of my individual experiments, it is important to note that the use of strawberry plants as phytometers was part of a broader collaborative effort. Building on previous successful experiments conducted by Elsa Blareau, we chose strawberries (*Fragaria* × *ananassa*, var *Charlotte*) as a standardized study system to quantify pollination services. Together with two other PhD students, Elsa Blareau and Mathieu Lachaise, all working simultaneously on pollination, we were able to combine our datasets to cover a wide environmental gradient, from highly intensive agricultural landscapes to densely urbanized areas. This collaborative approach enabled us to combine our datasets to gain a more comprehensive understanding of how contrasting landscapes influence pollination, and to evaluate the suitability of strawberry plants as phytometers for assessing pollination services. The results of this integrated analysis, based on the pooling of our experimental data, are presented in the following chapter.

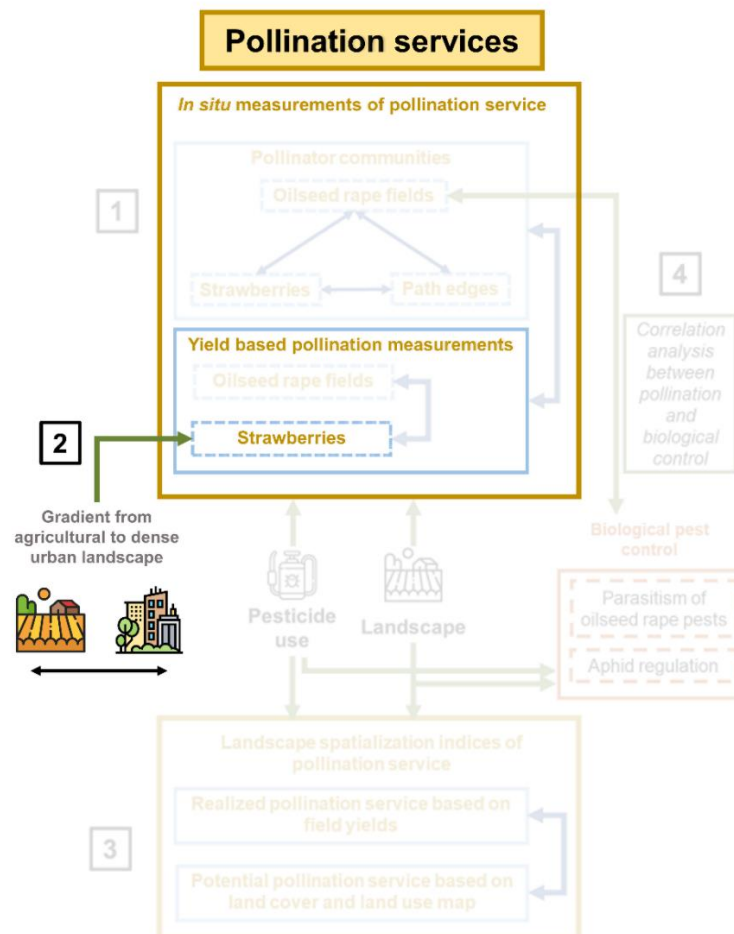


Figure 3.0. Second research axis within the general diagram summarizing the whole thesis

Are strawberries reliable phytometers for studying pollination across agricultural, suburban and urban landscapes?

Auteurs

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Abstract

Environmental pressures in urban and agricultural areas adversely impact insect pollinator communities, leading to biotic homogenisation of these communities. However, the consequences of such changes for pollination, a key ecological function and service, are still poorly estimated across different landscapes. Here, we carried out a two-year field experiment on 65 study sites to investigate the potential effects of urban, suburban and agricultural landscapes on pollination services, using strawberry (*Fragaria x ananassa*) as a phytometer. By characterising landscapes either as three discrete categories or as gradients of different land-use types at 100, 200, 500 and 1000m radii, we showed that pollination services, as measured by fruit weight, were higher in agricultural vs. suburban or urban areas when they are considered as discrete landscape categories, but did not vary along the agricultural land-use gradient. We also showed that, for the Charlotte strawberry cultivar, fruit weight depended more strongly on land use gradients than on insect pollination. Moreover, fruit deformation did not vary among pollination treatments or landscape when defined as discrete categories or land-use gradients. We discuss the relevance of using strawberry plants as phytometers for pollination and propose more suitable methods for characterising landscapes to better capture the fine-scale responses of pollinators and pollination to land-use pressures.

1.Introduction

Insect pollinators are threatened worldwide, with declines in abundance and diversity documented across the globe for wild pollinator species (Biesmeijer et al., 2006; Winfree et al., 2009; Potts et al., 2010), and high rates of honey bee colony losses *Apis mellifera* (Bruckner et al., 2023; Gray et al., 2019; Potts et al., 2010; Requier et al., 2024; Sibaja Leyton et al., 2025). The environmental pressures threatening bees are related, among others, to land use change, in particular agricultural intensification and urbanisation (Goulson et al., 2015; Potts et al., 2016). On the one hand, in intensive agricultural environments, pesticide use and habitat simplification reduce the availability and quality of nesting habitats as well as the diversity of floral resources (Dicks et al., 2021). On the other hand, in urban areas, soil sealing limits ground nesting opportunities and native floral communities, while the urban heat island effect impacts plant and pollinator phenology, altering their interactions (Baldock, 2020; Wenzel et al., 2020).

These pressures act as filters on pollinator communities according to their functional traits, excluding specialist species while maintaining generalist species (Fauviau et al., 2022), thus leading to biotic homogenisation in both urban (Banaszak-Cibicka and Żmihorski, 2020) and agricultural landscapes (Gámez-Virués et al., 2015). This could lead to detrimental effects on the quality of pollination services, since these are positively linked to the diversity and

composition of pollinator communities (Albrecht et al., 2012; Lucas A. Garibaldi et al., 2013; Katumo et al., 2022). Indeed, pollinators differ in their pollination efficiency, for example because some pollinators transfer more conspecific pollen than others due to differences in behaviour and morphology (Roquer-Beni et al., 2022). In particular, generalist pollinators such as the Western honey bee are not always the most efficient pollinators (Page et al., 2021). More generally, functional diversity leads to complementarities among different pollinators, which in turn leads to better pollination services (Woodcock et al., 2019).

Since highly human-modified landscapes (such as cities or intensive agricultural landscapes) tend to filter pollinator communities, several studies report that gradients of impervious surfaces have negative effects on pollinator diversity (Birdshire et al., 2020; Deguines et al., 2016; Geslin et al., 2016), or that intensive agricultural environments host pollinator communities with a low diversity (Baldock et al., 2015). Moreover, a recent study using landscape gradients on a national scale in France found that urbanisation decreased pollinator species richness overall, in particular when the urban areas were surrounded by agricultural landscapes (Desaegher et al., 2023). Interestingly, responses were found to vary when considering taxa separately (Desaegher et al., 2023). Finally, suburban areas are thought to benefit pollinators, with a review finding that areas with 20% to 50% impervious surfaces, associated with urban sprawl, favoured pollinator populations compared to agricultural landscape and dense cities (Wenzel et al., 2020).

The consequences of contrasting urban vs. agricultural pollinator communities on pollination are still little documented, although pollinators are required both for crop yields in agricultural landscapes and in urban agricultural areas (e.g. for private gardens, community gardens, rooftop farms, and periurban farms; (Orsini et al., 2020). In light of pollinator declines in agricultural and urban landscapes, pollination deficits could emerge due to a lack of diverse pollinator communities (Garratt et al., 2021). Although pollination deficits have been documented independently in urban areas (Bennett et al., 2020) and in intensive agricultural areas (Garibaldi et al., 2011), they have rarely been compared in the same study that combines both landscape gradients (but see Renaud et al. 2022).

Here we carried out a field experiment combining urbanisation and agricultural gradients to assess the potential effects of urban, suburban and agricultural landscapes on pollination services. We based our approach on the FAO Protocol to Detect And Assess Pollination Deficits Crops (Vaissière et al., 2011) using phytometer plants (Theodorou et al., 2020). Different plants have been used as phytometers for pollination, such as white mustard (*Sinapi alba*) (Zaninotto et al., 2020), red clover (*Trifolium pratense*) (Theodorou et al., 2020), aubergine (*Solanum melongena*), cucumber (*Cucumis sativus*), coneflower (*Echinacea purpurea*) (Lowenstein et al., 2015) or *Symphytotrichum* spp. (Woodcock et al. 2014). We chose

strawberry (*Fragaria x ananassa*), which is known to depend partly on insect pollination to bear fruit (Klein et al., 2007; Gudowska et al., 2024). As a phytometer, strawberry has previously been used to measure pollination in urban (Dietzel et al., 2023; Nicholls et al., 2023), suburban (Nicholls et al., 2023) and agricultural (Castle et al., 2019) landscapes. We consider landscape types either as three discrete categories, or as two quantitative land-use gradients of increasing urban land cover and increasing agricultural land cover, measured in buffers of various radius sizes around the studied sites. We expect discrete categorical dense urban and conventional agricultural landscapes to exhibit low pollination services, with suburban landscapes showing higher levels of pollination. Similarly, in the land-use gradient approach, we hypothesise that increasing urban surface cover and agricultural land cover will negatively impact pollination success, but that the intensity of these effects could differ between the two landscape gradients and with the radius of buffers used to characterize the surrounding landscape.

2. Materials and methods

2.1. Study sites and discrete landscape categories

We selected 65 sites in the southwestern Paris basin, France, a region characterised by a temperate oceanic climate and a mosaic of urban (Paris metropolitan area) and agricultural landscapes dominated by cereal crops. The sites were distributed across three discrete landscape categories: agricultural (n = 51), suburban (n = 11), and densely urban (n = 3). This classification was based on the geographical context of each site, irrespective of the immediate land cover in their surroundings. Thus, sites located in field margins within large-scale crop production areas were considered as agricultural. Sites located in private gardens within predominantly residential neighborhoods and in experimental facilities in semi-natural areas were classified as suburban. Sites located in urban greenspaces within densely urbanised areas were considered as densely urban (Figure 3.1).

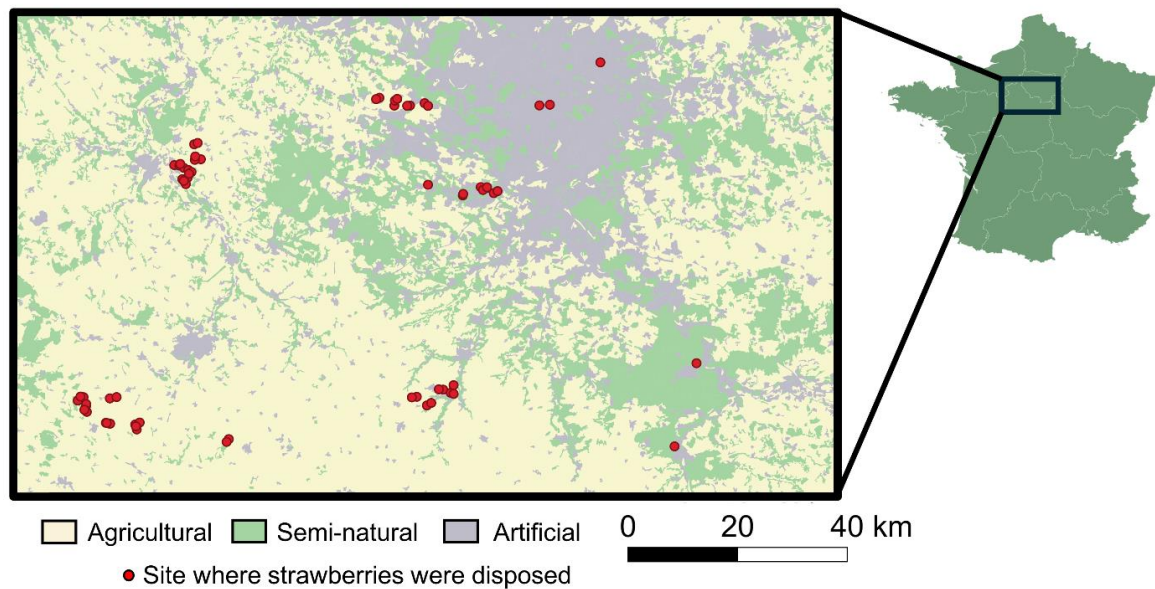


Figure 3.1. Map of the study sites in three contrasting landscape contexts.

2.2. Characterisation of land-use cover with continuous variables

We characterised land-use cover around each site using buffer zones with radii of 100, 200, 500, and 1000m, in QGIS (QGIS Development Team, 2024). This range of distances was within the typical foraging range of pollinators, from a few hundred meters to a few kilometers (Zurbuchen et al., 2010; Rader et al., 2020; Kendall et al., 2022). Land cover was determined through the superimposition of two GIS layers. The 2023 CoSIA layer from the National Institute of Geographic and Forestry Information (IGN) classifies land cover into 16 categories at a resolution of 20 cm × 20 cm, using artificial intelligence. We also used the French Land Parcel Identification System (RPG) from 2022–2023, provided by IGN and the Ministry of Agriculture on the basis of crop reporting for the Common Agricultural Policy, as the main source to characterise crop cover in agricultural landscapes.

We merged water surfaces with impervious areas from the CoSIA layer, and considered them non-accessible to pollinators, since most water bodies in our dataset correspond to large rivers (e.g., the Seine river), which offer neither foraging nor nesting resources. We grouped land cover categories into three simplified categories (Semi-natural elements, Artificial elements and Agricultural elements), based on ecological and land-use characteristics of each land cover type, aiming to produce ecologically meaningful and interpretable categories (Figure S3.1). The artificial areas, mainly composed of impervious surfaces and buildings, are used as a proxy for urbanisation.

2.3. Use of strawberry plants as phytometers for pollination

We used strawberries (*Fragaria* × *ananassa*, cv. Charlotte) to evaluate pollination services, as they are insect-pollinated (Klein et al., 2007; Gudowska et al., 2024) and widely cultivated in both commercial and private gardens. Fruit production in *Fragaria* × *ananassa* hybrid varieties depends on pollinators for approximately 19% to 55% of fruit weight (Siopa et al., 2024; Gudowska et al., 2024). The Charlotte variety produces numerous fruits over an extended period (from May to October), making it convenient for field experiments.

We carried out a two-year experiment (2023 and 2024), with efforts made to standardise the cultivars and their provenance. In March 2023, all strawberry plants were purchased from the same plant nursery (SARL Nicolas le Jardinier). However, plants assigned to agricultural sites were three months younger than those used in urban sites and in three suburban sites. In 2024, additional plants were purchased in April for eight new supplementary suburban sites located in private gardens. Throughout the experiment, all plants were grown in 5 L pots filled with standard potting compost, regularly watered to avoid water stress, and received a 10g uniform organic fertiliser input (DCM ECOR4®) between 2023 and 2024. This setup helped minimise confounding effects related to soil type, nutrient availability, and watering regime. In both years, plants were positioned at the experimental sites in mid-spring, prior to the May–June flowering period.

2.4. Pollination treatments

We measured pollination services over two springs (spring 2023 and spring 2024) across all sites, except for eight of the suburban sites, which were monitored only during spring 2024. Four to six strawberry plants were placed at each site: two (or three) were bagged with fine nets (mesh size < 1 mm) to prevent any pollinator visits to the flowers, while the remaining plants were left unbagged, allowing pollinators to interact with the flowers. Additionally, we manually pollinated a quarter of flowers on both bagged and unbagged plants, (1) prioritising newly opened flowers, and (2) allocating approximately 25% of the flowers to this treatment to maintain a balanced protocol. Manual pollination was achieved by cross pollinating flowers using the same type of standardised paintbrush for all experimenters. Pollen was collected from at least two donor flowers using the same paintbrush and then transferred to the flowers of experimental plants. Thus, we measured pollination under four different treatments, following guidelines from the FAO Protocol to Detect And Assess Pollination Deficits In Crops (Vaissière et al., 2011): Open pollination (O): flowers were exposed to natural pollinators without supplementary manual pollination; Open and hand pollination (O+H): flowers were exposed to natural pollinators and received supplementary manual pollination; Pollinator exclusion (E): flowers were bagged to exclude pollinators, without supplementary manual

pollination; Pollinator exclusion and hand pollination (E+H): flowers were bagged to exclude pollinators but received supplementary manual pollination.

2.5. Fruit measurements

Once flowering was over, all plants were transported to a common site to standardise environmental conditions (e.g. light, watering) within each year, to ensure consistent fruiting conditions and limit potential biases. Strawberries were harvested when ripe, and two response variables were assessed to evaluate fruit quality and pollination services. Fruits that did not reach maturity were excluded from the dataset, whereas those that had turned at least partly red were retained for analysis. First, we weighed the fresh mass of each individual fruit using high-precision scales (± 0.01 g), following (Gudowska et al., 2024). Mass is an indicator of the number of successfully pollinated achenes (Blareau et al., 2023) and thus a proxy for successful pollination. Second, we assessed strawberry morphology by measuring fruit length and width using electronic calipers with a precision of 0.1 mm. Based on these measurements, we estimated fruit deformation to reflect morphological irregularities. Deformation was calculated with the following equation (1):

$$\text{(Equation 1) } D = \left| \frac{\text{length}}{\text{width}} - 1 \right|$$

with *length* representing the strawberry length and measured from the apex of the fruit to the point of petiole insertion, and *width* representing the strawberry width and measured as the maximum diameter. *D* values closer to 1 indicate more deformed fruits, while *D* values closer to 0 reflecting more regular shapes (Figure S3.2). This index reflects the fact that fruits with a regular shape tend to have equal length and width, while fruits with malformations tend to have large differences between width and length. Malformation is a criterion for strawberry marketability (OECD, 2021), highlighting the need to understand how this measure responds to pollination and land-use.

2.6. Statistical analyses

Statistical analyses were performed in R version 4.3.2 (R Core Team, 2025). Sites belonging to the same broad discrete landscape category tended to be geographically closer to each other—for example, agricultural sites were generally located further from urban areas and thus clustered together. To account for this spatial structure, we adopted two complementary statistical approaches. First, we analysed the variation of strawberry mass across the three discrete landscape categories based on the geographic location of the sites: agricultural,

suburban and urban. Then, we aimed to estimate the underlying mechanisms more precisely. To this end, we fitted Linear Mixed Models (LMM) incorporating land-use gradients in the surrounding landscape (calculated within 100, 200, 500 and 1000m radius around each site), as continuous predictors.

2.6.1. Assessing the effectiveness of hand pollination

To assess the effectiveness of the hand-pollination treatment, we used a LMM coupled with the Estimated Marginal Means (*emmeans*) (Lenth, 2024) approach to test whether this manual intervention led to a significant increase in fruit set (Table S3.1). The LMM was built with the following equation:

$$\text{(Equation 2)} \quad Mass_{ijkl} = mean + T_i + SP_{kl} + \varepsilon_{ijkl}$$

where $Mass_{ijkl}$ is the strawberry mass in treatment i at site k , on plant l and for fruit m . Mean is the overall intercept, T is the fixed categorical effect of pollination treatment, with four levels (O, OH, E and EH). SP is a random effect for each unique combination of factors *plant number* and *site*, allowing for group-level variability at the level of plant within site; it is assumed to follow a normal distribution with mean 0 and variance σ_g^2 . Finally, ε is an error term assumed to follow a normal distribution with mean 0 and variance σ_e^2 .

No significant increase was observed with hand pollination for E+H compared to E, serving as a test of the effectiveness of this method and also for O+H vs. O (Table S3.2). Hand pollination even reduced fruit mass significantly in the E treatment. We therefore focused on the E and O treatments only, excluding the hand-pollination treatments from further analysis, although its lack of effectiveness is discussed later on. In total, 1181 strawberries with treatment E and O were harvested and measured as part of the experiment.

2.6.2. Strawberries as phytometers to assess pollination services across the three discrete landscape categories: agricultural, suburban and urban

We assessed the potential effect of the three discrete landscape categories (i.e. agricultural, suburban, and urban) on fruit mass and deformation by comparing the two treatments (E) and (O), in order to evaluate the contribution of insect pollinators to strawberry yield. We fitted a LMM including the pollination treatment, landscape type and their interaction. We included a random intercept for plants nested within sites (1|Site ID:Plant ID). We also tested the inclusion of an additional site-level intercept, which did not change the results. We then performed pairwise comparisons using estimated marginal means (*emmeans*) to test the effect of pollination treatment on strawberry mass within each landscape type, using the *glmmTMB* R

packages (Brooks et al., 2017) and *emmeans*. This approach allowed us to test whether open pollination significantly increased fruit mass and deformation index compared to pollinator exclusion, within each discrete landscape category, while accounting for potential variation in sample size and variance structure. The model was built with the following equation:

$$(Equation\ 3)\ Var_{ijklm} = mean + Y_i + TL_{jk} + SP_{kl} + \varepsilon_{ijklm}$$

where Var_{ijklm} is either the strawberry mass or the deformation index, measured in year i for treatment j at site k , on plant l and for fruit m . Mean is the overall intercept, Y is a fixed categorical effect accounting for year-specific variation (2023-2024), TL is the interaction between the fixed effect of pollination treatments (Open or Exclusion) with the fixed effect of discrete landscape categories (agricultural, suburban, or urban). SP is a random effect for each unique combination of factors *plant ID* and *site ID*, allowing for group-level variability at the level of plant within site; it is assumed to follow a normal distribution with mean 0 and variance σ_g^2 . Finally, ε is an error term assumed to follow a normal distribution with mean 0 and variance σ_e^2 .

c. Effect of landscape composition on pollination services along continuous land-use gradients

We performed a Principal Component Analysis (PCA) to investigate how pollination services varied along continuous land-use gradients. We calculated the landscape composition at 100, 200, 500 and 1000m radius for each site, using the ecological groups defined in Table S3.1 and the *ade4* (Dray and Dufour, 2007) and *factoextra* (Kassambara and Mundt, 2020) R-packages. This allowed to reduce correlated land cover variables into two main uncorrelated axes: Dimension 1 captured a gradient ranging from predominantly agricultural sites to mixed urban and semi-natural environments, while Dimension 2 reflected a contrast between semi-natural and urban (artificial) habitats (see Figure S3.1).

These two PCA axes were then used as continuous predictors in spatially explicit LMMs using the *spaMM* package (Rousset et al., 2025), which allows the inclusion of spatial *Matérn* correlation function of *spaMM* was used based on site coordinates to account for spatial autocorrelation. Equivalent analyses were conducted using the *glmmTMB* package (Brooks et al., 2017) and correcting models with site coordinates to check the consistency between methods. Results from both models were used for graphical display using the *ggeffects* R package (Lüdtke, 2018). Fruit mass and deformation were modeled as proxies for pollination services, with treatment (O vs. E) and its interaction with each PCA axis included as fixed effects. This interaction reflects the influence of land-use on pollination services, as it compares differences in fruit mass and deformation between open and exclusion treatments along the

land-use gradients. As in previous models, we specified (1|*site ID:plant ID*) as a random factor. Adding site-level intercept removed the significance of the semi-natural to urban gradient on strawberry mass at 100m (Table S3.3). Separate models were built for each buffer size to capture potential scale-dependent effects. The model was built with the following equation:

$$\text{(Equation 4) } Var_{ijklm} = mean + Y_i + T_j + (a_0 + a_j)Dim1_k + (b_0 + b_j)Dim2_k + SP_{kl} + \varepsilon_{ijklm}$$

where Var_{ijklm} is either the strawberry mass or the deformation index, measured in *year i* for *treatment j* at site *k*, on *plant l* and for fruit *m*. Mean is the overall intercept, *Y* is a fixed categorical effect accounting for year-specific variation (2023-2024), *T* is the fixed effect of pollination treatment (Open or Exclusion), and *Dim1* and *Dim2* are the first two axes of the principal component analysis (PCA) summarising land-use gradients. *SP* is a random effect for each unique combination of factors *plant number* and *site*, allowing for group-level variability at the level of plant within site; it is assumed to follow a normal distribution with mean 0 and variance σ_g^2 . Finally, ε is an error term assumed to follow a normal distribution with mean 0 and variance σ_e^2 . For each equation, we used a spatial correlation structure modeled using a Matérn covariance function based on site coordinates of each site (longitude and latitude).

3.Results

3.1. Strawberries as phytometers to assess pollination services across agricultural, suburban, and urban landscape categories

We found a significant difference in fruit mass between the open (O) and exclusion (E) pollination treatments only in agricultural sites, where fruit mass was lower by 10.2% (LMM, Estimate = -1.33 ± 0.66 ; $p = 0.04$) under pollinator exclusion (Figure 3.2A, Table 3.2). In contrast, we found no significant difference in fruit mass between pollination treatments at suburban or urban sites ($p > 0.1$, see Figure 3.2 and Table 3.2). Deformation never differed between treatments across all site categories ($p > 0.1$, Figure 3.2B and Table 3.2).

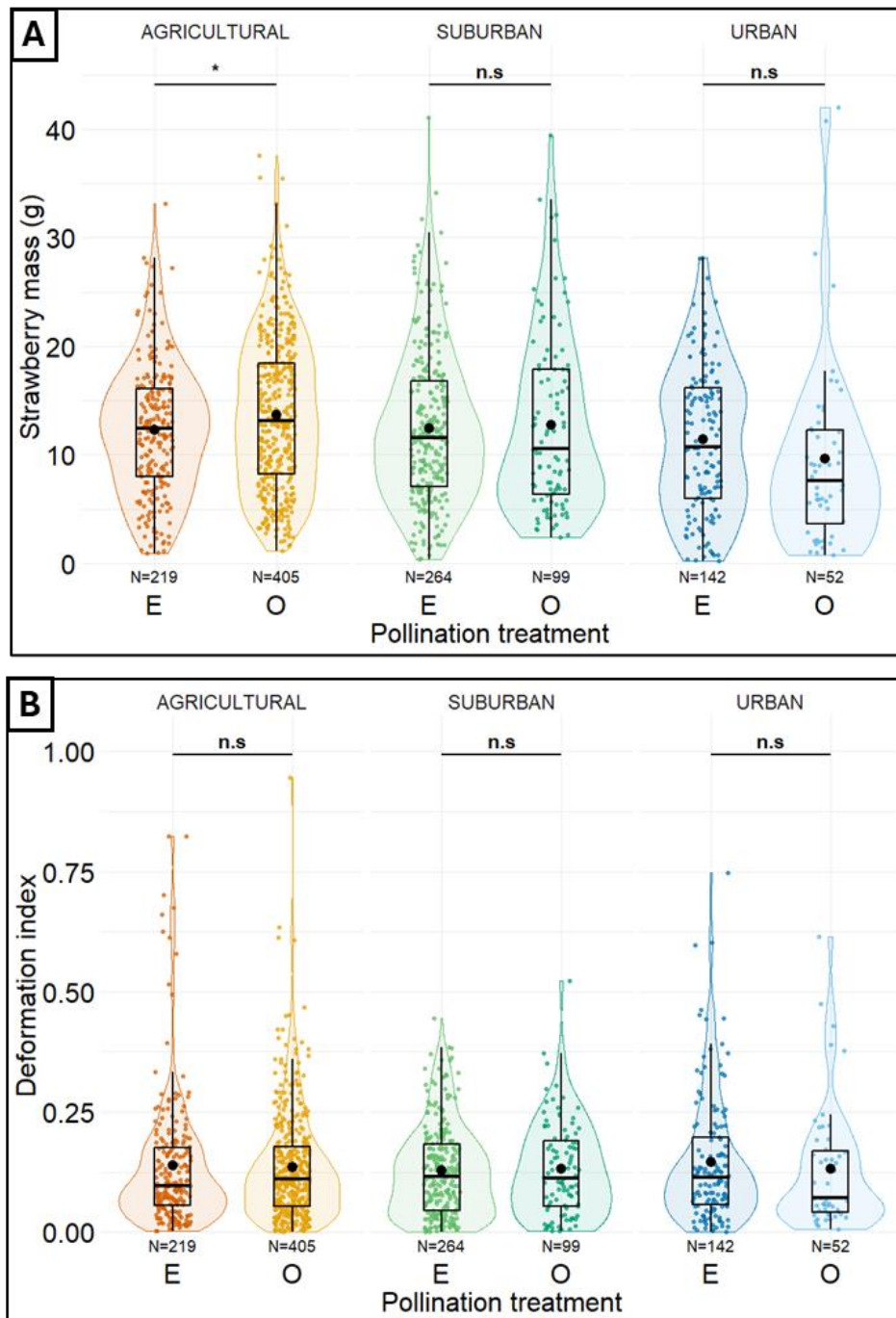


Figure 3.2. Violin plots of strawberry fruit mass (A) and fruit deformation (B) under open pollination ("O") and pollinator exclusion ("E") treatments across agricultural (n = 51), suburban (n = 11), and urban (n = 3) sites. Boxes show the interquartile range (IQR), medians (horizontal line), whiskers (1.5 × IQR), and means (black dots). Sample size (N) indicates the number of fruits per category. Statistical comparisons were performed with Estimated Marginal Means after LMMs (n.s. = not significant; * = $p < 0.05$).

Table 3.2. Estimated Marginal Means of fruit mass and deformation from LMMs described in Equation 3, across agricultural ($n = 51$), suburban ($n = 11$), and urban ($n = 3$) sites. “O” = open pollination; “E” = pollinator exclusion; Significant effects ($p < 0.05$) are shown in **bold**.

Fruit mass	Landscape category	Estimate	SE	<i>t</i> ratio	<i>p</i>
E - O	Agricultural	-1.33	0.66	-2.01	0.04
E - O	Suburban	-0.39	1.04	-0.38	0.71
E - O	Urban	1.93	1.48	1.30	0.19
Deformation					
E - O	Agricultural	1.54e-3	0.01	0.12	0.90
E - O	Suburban	-1.52e-3	0.02	-0.07	0.94
E - O	Urban	-0.01	0.03	-0.42	0.68

3.2. Effects of continuous land-use gradients on strawberry pollination

Across all spatial scales, we found a consistent positive effect of the open pollination treatment compared to the exclusion treatment on fruit mass. Dimension 1 of the PCA, representing the gradient from high to low agricultural cover, had no significant effect on fruit mass at any scale, either on its own or in interaction with pollination treatment (Fig. 3.3A, Table 3.3). In contrast, fruit mass decreased along the semi-natural to urban gradient (Dimension 2) in the exclusion treatment at 100 m ($p = 0.008$, Table 3.3). However, this effect was no longer significant when adding the *site ID* as a random factor (see Table S3.3). We also detected a marginally significant interaction between pollination treatment and Dimension 2 at the 100 m scale ($p = 0.078$, Table 3.3), such that fruit mass in the open pollination treatment (O) tended to be relatively constant along this gradient, whereas it decreased along this gradient in the exclusion treatment. As a result, the contribution of pollinators to fruit mass, as estimated from the difference between the open and exclusion treatments, tended to be larger in landscapes with more urban areas vs. more semi-natural landscapes, but only at 100 m radius (Fig. 3.3B, Table 3.3). Finally, year had a significant effect on fruit mass and deformation at all spatial scales, with fruits harvested in 2024 being consistently lighter and more deformed than those from 2023 ($p < 0.05$ for all radii, Table 3.3, Table S3.4).

Table 3.3. Effect of landscape gradients and pollination treatment on strawberry mass. LMMs with correction of spatial autocorrelation were fitted separately for four spatial scales (buffers of 100, 200, 500, and 1000m) using the first two axes of a Principal Component Analysis (PCA) on landscape composition as continuous land-use predictors. Fixed effects included year (2023–2024), treatment (open vs. exclusion), PCA axis as landscape composition gradients, and their interactions with treatment. Spatial autocorrelation was accounted for using a Matern covariance structure based on site coordinates, with site as a random effect. Significant effects ($p < 0.05$) are shown in **bold**; marginal trends ($0.05 \leq p < 0.1$) are shown in **bold italics**. When similar models were fitted using fruit deformation instead of fruit mass as the response variable, no significant effect of pollination treatment, land-use gradients and their interaction was detected (see Table S3.4).

Independent variables	Radius	Estimate	SE	<i>t</i> value	p
Treatment O (vs E)	100m	0.908	0.531	1.710	0.087
	200m	1.193	0.526	2.268	0.023
	500m	1.280	0.526	2.432	0.015
	1000m	1.202	0.524	2.293	0.022
Dimension 1 = High to low agricultural cover gradient	100m	-0.349	0.390	-0.896	0.37
	200m	-0.256	0.361	-0.71	0.478
	500m	-0.319	0.364	-0.876	0.381
	1000m	-0.442	0.392	-1.129	0.259
Dimension 2 = Semi-natural to Urban cover gradient	100m	-1.312	0.497	-2.641	0.008
	200m	-0.812	0.906	-0.896	0.370
	500m	-0.015	0.347	-0.017	0.986
	1000m	-0.020	0.730	-0.028	0.978
Year 2024 (vs 2023)	100m	-1.732	0.0554	-3.128	0.002
	200m	-3.258	0.627	-5.199	< 10⁻⁴
	500m	-3.514	0.633	-5.553	< 10⁻⁴
	1000m	-3.350	0.625	-5.363	< 10⁻⁴
Open pollination × Dimension 1	100m	-0.170	0.341	-0.499	0.618
	200m	-0.166	0.334	-0.498	0.618
	500m	-0.136	0.347	-0.393	0.694
	1000m	-0.214	0.361	-0.593	0.553
Open pollination × Dimension 2	100m	1.390	0.789	1.762	0.078
	200m	0.960	0.789	1.217	0.224
	500m	-0.554	0.724	-0.765	0.444
	1000m	-0.699	0.639	-1.093	0.274

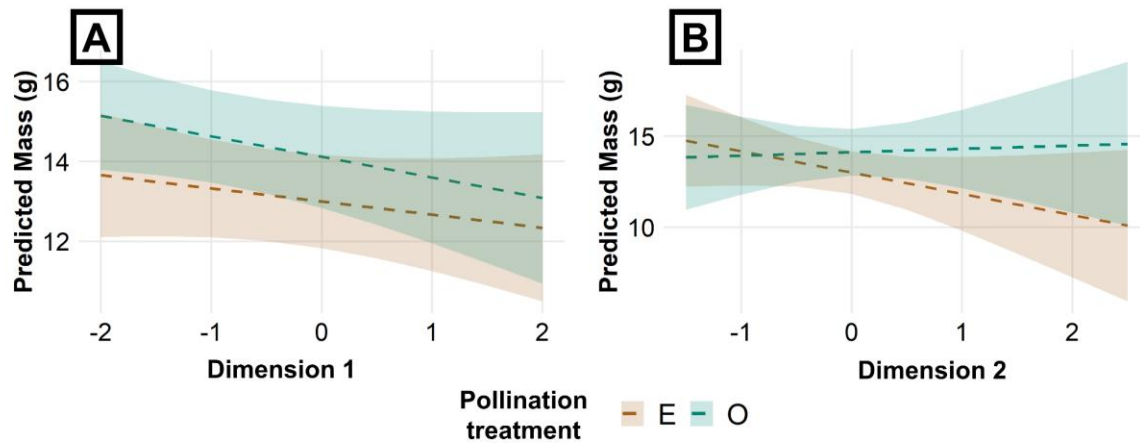


Figure 3.3. Predicted strawberry mass (g) across the two land-use dimensions based on LMM outputs for 100m radius. Solid areas represent 95% confidence intervals around the predicted values. Colours indicate treatment type: E = pollinator exclusion, O = open pollination.

4. Discussion

The present multi landscape approach is one of the few studies that have explored the relative impacts of agriculture, suburban and urban landscapes on pollination services (but see Renaud et al. 2022), thereby allowing us to compare the impacts of these broad landscapes on pollination within a single standardised experimental design. We tested two methods to describe the landscapes, either at a coarse scale using discrete landscape categories, or considering a more refined view of landscapes using gradients based on land-use and calculated within different radii, which, to our knowledge, has never been done to investigate pollination services. In this study, these two methods provide complementary results, since we detect different subtleties of pollination and landscape effects with each method. We observed animal pollination benefits on fruit mass only in agricultural sites using the discrete categorical method. In contrast, when considering land-use as a continuous gradient, we detected a marginal landscape effect only at the 100 m scale: fruit mass in the exclusion treatment (E) decreased with increasing urbanised landscape, while pollination services increased along the same gradient. Fruit deformation did not vary with pollination treatment or landscape type, whether using the discrete categorical or land-use gradient approach. In the following, we discuss the consistency of the results obtained by these two complementary approaches and conclude on the limitations of the use of strawberry plants as phytometers.

4.1. Complementary results between categorical and land-use gradient methods

4.1.1. Benefits of animal pollination only within agricultural sites

Overall, our results suggest that the difference in strawberry mass between open pollination and pollinator exclusion treatments tended to be higher in agricultural landscapes in the discrete categorical approach, which may indicate higher pollination services there. However, this interpretation should be considered within the broader ecological and temporal context of the current set of experiments. In agricultural sites, strawberry flowering occurred just after the flowering peak of oilseed rape (*Brassica napus*), a mass-flowering crop known to strongly attract pollinators (Stanley and Stout, 2014; Westphal et al., 2003b). As the strawberry plants were placed near oilseed rape fields, they potentially benefited from a residual pollinator presence. Additionally, the strawberry flowering period coincided with the mowing of field and roads margins, which are important floral habitats hosting plants (Nicholls and Altieri, 2013) such as speedwells (*Veronica* spp.), dandelions (*Taraxacum* spp.), and cranesbills (*Geranium* spp.). This may have created a temporary scarcity of floral resources in the landscape, leading pollinators to concentrate on the available strawberry flowers via the “honeypot effect”, which can be stronger than landscape effects (Nunes et al., 2024). In contrast, urban and suburban environments likely provided a more diverse and continuous supply of alternative floral resources (Timberlake et al., 2024). This could result in a dilution effect, with pollinators being distributed among a wider array of floral options (Cohen et al., 2021), some of which may be more attractive than strawberry flowers.

4.1.2. Benefits of animal pollination are independent of landscape gradients

Our results show that fruit weight was higher in open pollination than in pollinator exclusion for all buffer sizes (with however a marginally significant effect only at 100m). This confirms that insects contribute to the pollination of strawberries (Klatt et al., 2014; Wietzke et al., 2018; Bänisch et al., 2021; Blareau et al., 2023), especially within agricultural sites, which represent the majority of sites in this study, and consistently with the abovementioned results. We also found that the semi-natural to urban gradient had a negative effect on strawberry weight in the exclusion pollination treatment, for the 100 m buffer. This suggests that independently of pollination, urbanised landscapes (here characterised by artificial land cover) impacted strawberry fruit growth negatively, possibly due to air pollution (Fitriana et al., 2024). There was also a marginal positive effect of this same land-use gradient in interaction with pollination treatment on fruit mass, whereby strawberry mass remained constant with increasing urbanisation for the open pollination treatment, while it decreased for the pollinator exclusion treatment. This seems to indicate that, at a local scale, in increasingly urbanised landscapes, pollination services may compensate for adverse effects of these environments on fruit

development. This could be due to a local concentration effect of pollinators (Nunes et al., 2024), whereby a scarcity of floral resources in less favorable environments, such as dense urban areas, attracts more pollinators to the phytometer strawberry plants (Dietzel et al., 2023). These findings may seem contradictory to our previous results based on discrete categorical landscape classification, where only agricultural sites showed pollination benefits. Categorical classification, however, does not directly capture land-use variation, particularly at small scales. For example, within a 100 m radius, sites within urban green spaces in cities were classified as urban but could contain more semi-natural cover than some suburban sites (see Figure S3.1). As the radius increases, gradients align more closely with categorical classifications. Similarly, we did not detect any difference in pollination along the gradient associated with agriculture, contrary to the results obtained from the categorical classification.

4.1.3. Advantages and drawbacks of a multi landscape approach

The multi landscape approach used here allowed us to go beyond measuring pollination within a landscape type. Although comparing pollination services among different landscapes is a relatively original approach, this method does not allow for specific features of these landscapes to be tested. Indeed, previous studies have used a phytometer approach within a landscape type to test the effects of different configurations or features of the local landscape on pollination, with examples from agricultural habitats, for instance testing the impact of hedgerows on pollination (Castle et al., 2019), and from urban habitats, testing the impacts of impervious surface on pollination of various plants (e.g. Bennett and Lovell 2019; Zink et al. 2024), including strawberry (Dietzel et al., 2023).

Despite this relatively original approach, the two methods of landscape characterisation may not adequately capture the landscape features that most strongly influence pollinators and pollination. First, the discrete category method did not account for composition at a local scale (see Figure S3.1), and the quantitative one failed to capture fine-scale features such as floral resource availability, to which pollinators are known to respond strongly (Timberlake et al., 2024). (Ammann et al., 2024) found that floral resources maps may better predict wild bees than landscape composition in agricultural landscapes. Characterising this type of local landscape feature could allow us to provide more specific recommendations for local land use management strategies to enhance pollination services. Moreover, using landscape data, as discrete categories or gradients, does not truly account for disturbances such as (1) pesticide use, which can vary among fields in agricultural areas, (2) air pollution, which can vary within cities, or management practices such as mowing frequency, which can vary across private gardens. Accounting for these disturbances directly, not via land-use proxies, may improve our understanding of pollinators' response to highly disturbed environments.

4.2. Limitations of strawberry plants as phytometers for evaluating landscape effects on pollination services

Strawberries present several advantages as phytometers for evaluating pollination services. (1) Strawberries are extensively cultivated across both rural and urban landscapes, for commercial as well as personal purposes in private gardens, and (2) each plant produces numerous fruits, with the ability to analyse the quality of the fruit produced, providing a robust dataset for analysis. Nevertheless, the use of strawberries as phytometers is associated with notable limitations.

Firstly, our results suggest that hand-pollination was largely unsuccessful. This is surprising since previous studies using similar methodology report successful results of hand pollination experiments on strawberry plants (Connelly et al., 2015; Wietzke et al., 2018; Miranda et al., 2025). This discrepancy could be due to the choice of cultivar. Indeed, the Charlotte cultivar has, to our knowledge, not been used in previous pollination studies. (MacInnis and Forrest, 2020) used two strawberry cultivars within the same study, and found contrasting results, with one cultivar responding strongly to pollination treatments, including hand pollination, and the other showing no response to these treatments, confirming that pollinator dependence and relevance of a plant species as a phytometer is cultivar dependent. Moreover, this outcome in our study may further be explained by the very short window during which viable pollen could be collected, as highlighted in the FAO protocol “*Protocol to Detect and Assess Pollination Deficits in Crops: A Handbook for its Use*” (FAO, 2018), which emphasizes the importance of synchronizing pollen availability and flower receptivity. Another possible explanation is that the manipulation itself may have damaged the flowers more than it facilitated pollination. In addition, we found no impact of landscape or pollination treatment on fruit deformation. The method used here to estimate deformation, by calculating an index from size measurements, could be less sensitive to changes in landscape and pollination than mass. A more precise evaluation of deformation would be relevant, for example by quantifying the strawberry perimeter through image analysis and comparing it to the expected shape resulting from good pollination. Nonetheless, previous studies have found that pollinators reduce the occurrence of deformation on strawberries (Herrmann et al., 2019; Klatt et al., 2014), although these studies used categorical rather than quantitative measurements of deformations.

Another key concern is the tendency of strawberries toward self-pollination. We observed a high degree of self-fertilization despite careful choice of the cultivar. As a result, the overall dependency of strawberry plants on pollinators remains moderate, limiting the suitability of this species to detect fine variations in pollination services across landscape gradients. This constraint can reduce our ability to detect nuanced mechanisms influencing pollination at a

local scale and pushed us to interpret results primarily in relation to broader land-use categories. Moreover, strawberries are vulnerable to damage from theft and are particularly appetizing for mammals, which can compromise the integrity of experimental setups deployed in the field. For studies aiming to investigate fine-scale drivers of pollination, we therefore recommend the use of phytometers with a higher reliance on insect-mediated pollination and greater resilience to field conditions. Other phytometer species with lower rates of self-pollination are also being tested to improve the sensitivity of pollination service assessments. For instance, buckwheat (*Fagopyrum esculentum*) has been shown to produce virtually no yield without insect pollination, while achieving markedly higher yields when pollinated (Chen et al., 2024). Similarly, *Symphyotrichum* spp. have been used effectively as insect-dependent phytometers (Woodcock et al., 2014). To capture a broader spectrum of pollinator assemblages, mixed phytometer approaches can also be implemented. For example, (Casanelles-Abella et al., 2023) combined species differing in nectar accessibility—*Daucus carota* L. (wild carrot, Apiaceae), *Raphanus sativus* L. (radish, Brassicaceae), *Onobrychis viciifolia* Scop. (common sainfoin, Fabaceae), and *Symphytum officinale* L. (common comfrey, Boraginaceae)—to attract and sample a wider range of pollinator guilds.

Conclusion

Overall, our study suggests that strawberry may not be the most appropriate species to use as a phytometer for pollination, since it does not allow for fine scale changes in pollination, associated with land use change, to be assessed. Nevertheless, our findings suggest that small landscape features may be more relevant to pollination than large landscape types, and we call for future research to explore this in more depth, since it was only a marginally significant result in the present study. Furthermore, further research is needed to select appropriate phytometers based on the research questions, study site, experimental design and associated constraints, and thus to better capture the fine scale responses of pollinators and pollination to land use pressures.

Supplementary materials

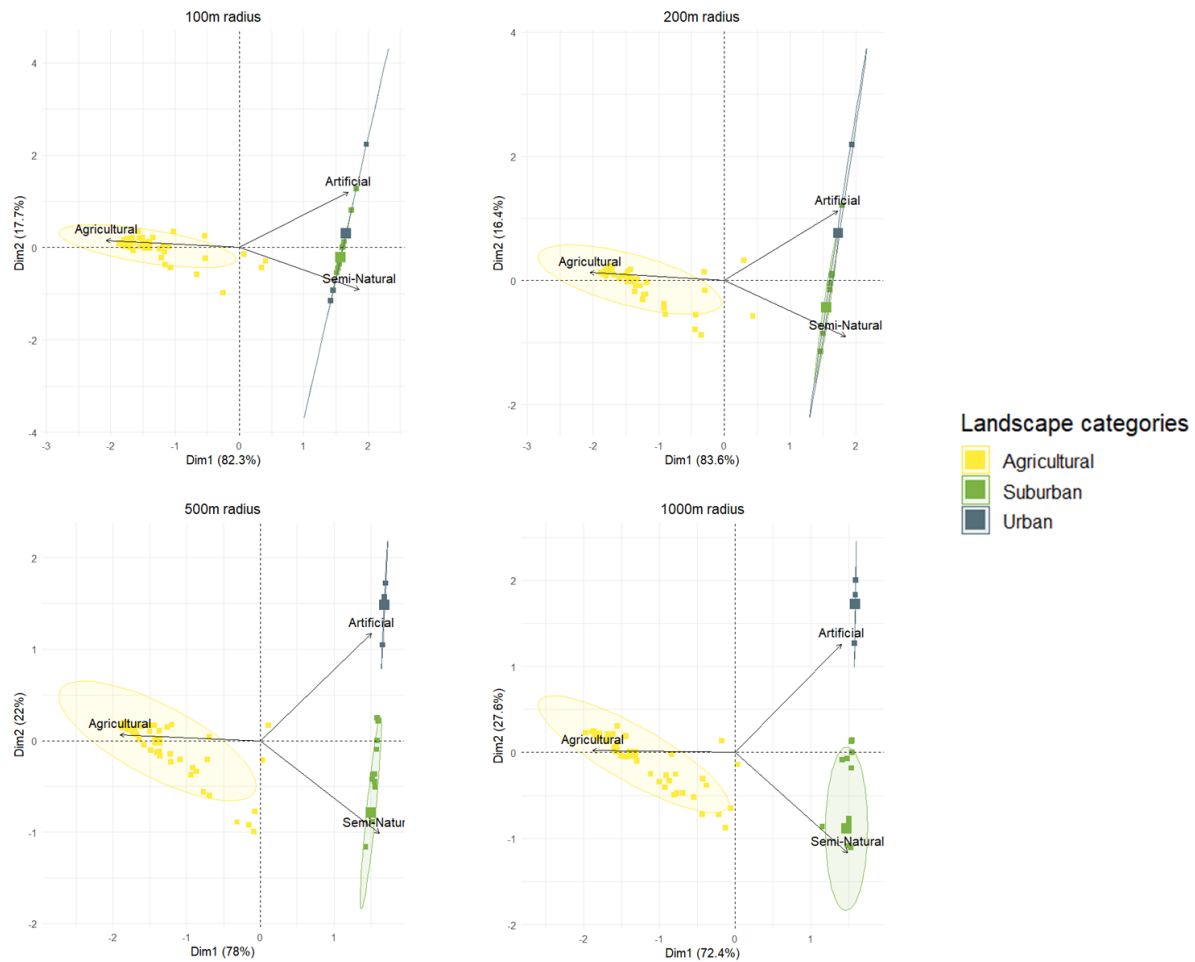


Figure S3.1. Principal component analysis (PCA) of landscape composition within (A) 100m, (B) 200m, (C) 500m, and (D) 1000m radii around sampling sites. Landscape types are defined for each site as agricultural (yellow), suburban (green), or urban (grey). Arrows representing agricultural, semi-natural, and urban land cover indicate the composition of landscapes around sites. Dimension 1 (Dim1) represents a gradient from high to low agricultural areas, and Dimension 2 (Dim2) corresponds to a gradient from semi-natural to artificial areas. This highlights that at small scales (100m), some urban sites include a higher proportion of semi-natural areas than suburban ones. As the radius increases, however, landscape gradients align more closely with discrete categorical classifications.

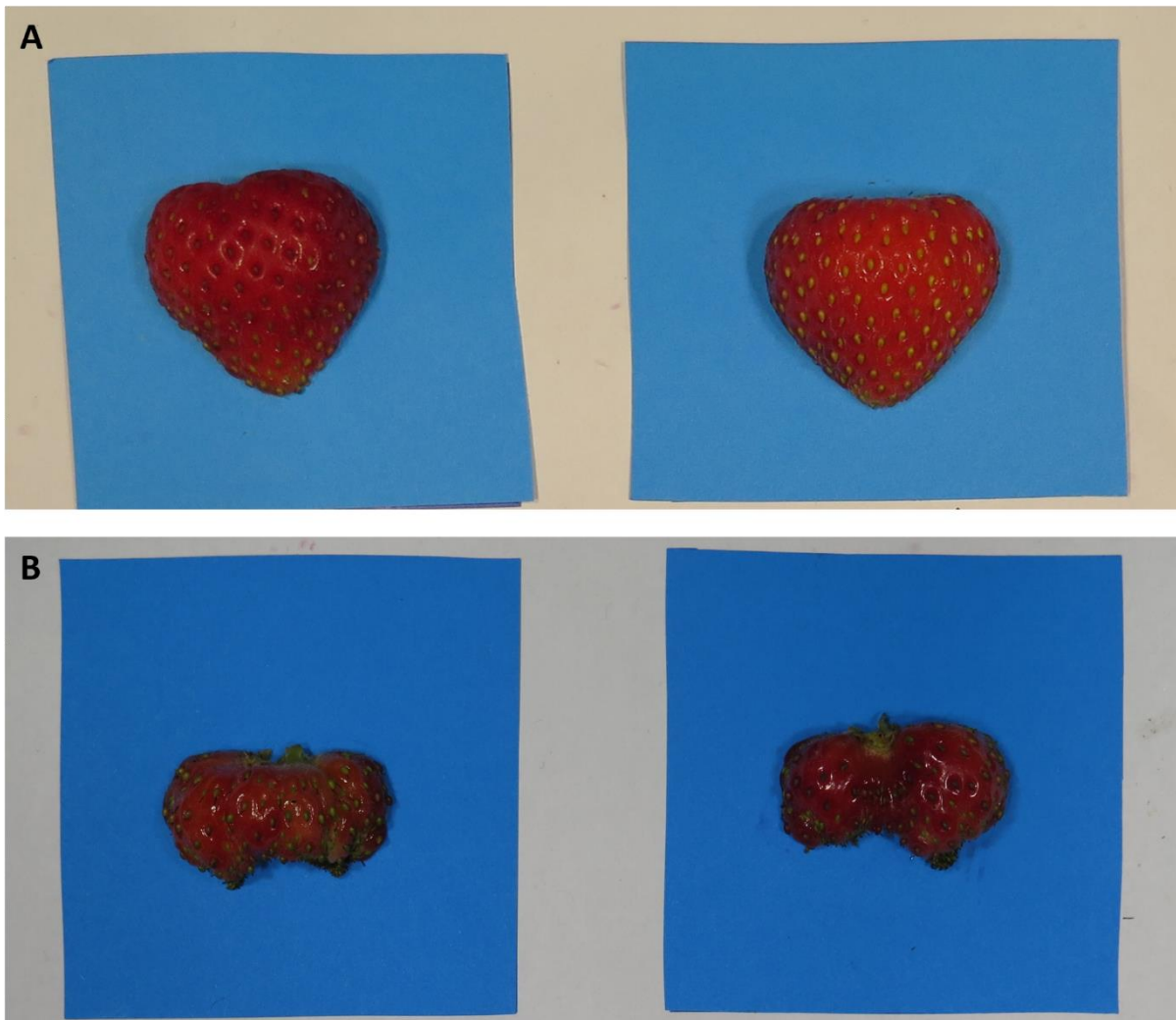


Figure S3.2. Strawberry with a low deformation D value (A) and a strawberry with a high D value (B).

Table S3.1. Land cover groupings based on ecological and land-use characteristics. Note that the “snow” category in Cosia is an AI misclassification and generally corresponds to light-colored ground cover, such as buildings and greenhouses; it was thus included in the artificial areas.

Ecological groups	Land cover type	Source
Semi-natural elements	Shrubland	Cosia
	Coniferous trees	
	Deciduous tree	
	Clear-cuts	
	Lawn	
	Bare soil	
Artificial areas	Anthropogenic pervious areas	Cosia
	Anthropogenic impervious areas	
	Buildings	
	Non accessible (Water surfaces + Swimming pools)	
	Greenhouses	
	Snow	
Agriculture	Declared plots	LPIS
	Arable land	Cosia
	Vineyards	

Table S3.2. Summary table showing fruit mass comparisons among treatments using Tukey post-hoc tests, with the *emmeans* R package (Lenth, 2024). We found an overall negative or null effect of manual pollination. Specifically, we observed an opposite pattern from E to EH (manipulated emasculation and hand-pollination), with lower outcomes compared to the control, while no significant effect was detected from O to OH (open-pollinated to hand-pollinated). This analysis revealed that hand pollination failed to produce fruits with greater mass than no hand pollination, i.e. the mass of fruits from treatments O and O+H were not significantly different (p), nor that of fruits from treatments E and E+H with strawberries being significantly smaller in EH than in E, which probably reflects more damage to the reproductive parts of the flowers by the brush than an actual pollination enhancement. Therefore, we excluded the treatments O+H and E+H from the following analyses. Significant effects ($p < 0.05^*$) are shown in **bold**.

Contrast	Estimate	SE	df	<i>t</i> ratio	<i>p</i>
EH -> E	1.548	0.558	1, 572.800	2.777	0.028
O -> E	-0.697	0.436	1, 493.629	-1.600	0.379
OH -> E	-1.010	0.600	1, 578.984	-1.683	0.333
O -> EH	-2.246	0.571	1, 572.172	-3.932	0.001
OH -> EH	-2.559	0.707	1, 577.353	-3.617	0.002
OH -> O	-0.313	0.603	1, 578.273	-0.519	0.955

Table S3.3. Parameter estimates from spatial LMMs assessing the influence of landscape gradients and treatment on strawberry mass, when using as random effects the interaction of *Site ID* and *Plant ID*, and *Site ID* alone. Models were fitted separately for four spatial scales (buffers of 100, 200, 500, and 1000m) using the first two axes of a Principal Component Analysis (PCA) of landscape composition (Dimension 1 = high to low agricultural cover gradient; Dimension 2 = semi-natural to artificial cover gradient) as continuous predictors. Fixed effects included treatment (open vs. exclusion), with exclusion the reference level, year (2023–2024), and their interactions with PCA axes. Spatial autocorrelation was accounted for using a Matern covariance structure based on site coordinates, with site as a random effect. Significant effects ($p < 0.05$) are shown in **bold**; marginal trends ($0.05 \leq p < 0.1$) are shown in **bold italics**.

Independent variables	Radius	Estimate	SE	<i>t</i> value	<i>p</i>
Treatment O (vs E)	100m	1.172	0.524	2.236	0.025
	200m	1.198	0.527	2.274	0.023
	500m	1.306	0.527	2.476	0.013
	1000m	1.208	0.525	2.299	0.022
Dimension 1 × High to low agricultural cover gradient	100m	-0.259	0.426	-0.608	0.544
	200m	-0.240	0.423	-0.566	0.571
	500m	0.262	0.570	0.459	0.646
	1000m	-0.529	0.510	-1.037	0.300
Dimension 2 × Semi-natural to Artificial cover gradient	100m	-1.185	0.830	-1.427	0.154
	200m	-0.833	0.913	-0.913	0.361
	500m	0.100	0.981	0.101	0.919
	1000m	0.025	0.839	0.030	0.976
Year 2024 (vs 2023)	100m	-0.314	0.632	-4.969	<10-3
	200m	-3.289	0.634	-5.189	<10-3
	500m	-3.524	0.636	-5.541	<10-3
	1000m	-3.385	0.636	-5.321	<10-3
TreatmentO × Dimension 1	100m	-0.175	0.334	-0.523	0.601
	200m	-0.165	0.334	-0.493	0.622
	500m	-0.134	0.347	-0.386	0.700
	1000m	-0.207	0.362	-0.572	0.568
TreatmentO × Dimension 2	100m	1.301	0.764	1.702	0.089
	200m	0.943	0.790	1.194	0.233
	500m	-0.579	0.726	-0.797	0.425
	1000m	-0.738	0.640	-1.152	0.249

Table S3.4. Parameter estimates from spatial LMMs assessing the influence of landscape gradients and pollination treatments on strawberry deformation. LMMs were fitted separately for four spatial scales (buffers of 100, 200, 500, and 1000m) using the first two axes of a Principal Component Analysis (PCA) of landscape composition (Dimension 1 = high to low agricultural cover gradient; Dimension 2 = semi-natural to artificial cover gradient) as continuous predictors. Fixed effects included treatment (open vs. exclusion), with exclusion the reference level, year (2023–2024), and their interactions with PCA axes. Spatial autocorrelation was accounted for using a Matern covariance structure based on site coordinates, with site as a random effect. Significant effects ($p < 0.05$) are shown in **bold**; marginal trends ($0.05 \leq p < 0.1$) are shown in **bold italics**.

Independent variables	Radius	Estimate	SE	<i>t</i> value	<i>p</i>
Treatment O (vs E)	100m	-0.002	0.010	-0.210	0.837
	200m	-0.003	0.010	-0.310	0.757
	500m	-0.003	0.010	-0.240	0.810
	1000m	-0.003	0.010	-0.270	0.787
Dimension 1 × High to low agricultural cover gradient	100m	-0.009	0.007	-1.244	0.214
	200m	-0.002	0.007	-0.280	0.783
	500m	-0.010	0.008	-1.240	0.220
	1000m	-0.018	0.010	-1.830	0.067
Dimension 2 × Semi-natural to Artificial cover gradient	100m	0.008	0.009	0.822	0.411
	200m	0.004	0.012	0.318	0.751
	500m	0.004	0.011	0.342	0.733
	1000m	0.007	0.010	0.717	0.473
Year 2024 (vs 2023)	100m	0.019	0.009	1.980	0.048
	200m	0.019	0.010	1.992	0.046
	500m	0.019	0.009	1.996	0.046
	1000m	0.019	0.009	1.992	0.046
TreatmentO × Dimension 1	100m	-0.004	0.007	-0.670	0.503
	200m	-0.005	0.007	-0.705	0.481
	500m	-0.004	0.007	-0.524	0.600
	1000m	-0.002	0.007	-0.316	0.752
TreatmentO × Dimension 2	100m	-0.018	0.016	-1.139	0.255
	200m	-0.011	0.016	-0.694	0.488
	500m	0.001	0.015	0.092	0.927
	1000m	0.004	0.013	0.274	0.784

4

Application of a crop yield-based pollination index to a small agricultural landscape: comparison with land-use indicators and pesticide use



Pieris rapae, in the Cévennes, 2021, © Thibault Gandara

From field experiments to landscape-scale indicators of pollination

So far, we have explored how pollination services vary through field experiments comparing open and closed pollination treatments. Local plot observations, as implemented in the previous chapters, are time-consuming and cannot be deployed on a large spatial extent. In the following section, we adopt a complementary approach: rather than measuring pollination services at experimental sites, we use crop yield data to estimate the former at a broader spatial scale. Specifically, we adapt an indicator based on farmers declared crop yields, initially developed at the national scale, to the scale of a small agricultural landscape. This indicator, called the *Realized Pollination Index*, infers the contribution of animal pollinators by comparing the standardized yields of pollinator-dependent vs. non-dependent crops. It requires relatively few data, which are generally accessible and can be computed at multiple spatial resolutions and extents — from individual fields (Gandara et al., 2025) to the whole of France (Martin et al., 2019). Such an approach can be widely implemented to identify areas with pollination deficits, assess the influence of agricultural practices on pollination efficiency, and monitor temporal changes in crop pollination success.

The general philosophy behind this indicator is straightforward: all else being equal, in areas with a deficit of pollinators, the standardized yield of pollinator-dependent crops should, on average, be lower than that of non-dependent crops. Other factors influencing crop yield are assumed to have, on average, a comparable effect on both pollinator-dependent and non-dependent crops within a given area. This assumption is acceptable provided that a sufficient number of crop species is included in each pollination-dependence category. Under this framework, relative differences in standardized yields between crop groups can be interpreted as reflecting spatial variation in pollination services and thus allow us to spatialize pollination.

We adapted an indicator originally developed at the national scale to a smaller territorial scale, allowing us to estimate pollination services within a local landscape. This yield-based indicator relies on already available data, making it potentially applicable to other regions beyond our study area. In Fénay, we benefited from a high-quality dataset spanning 2007–2019, including field-level yields and detailed pesticide use, which enables a robust local implementation of the Realized Pollination Index.

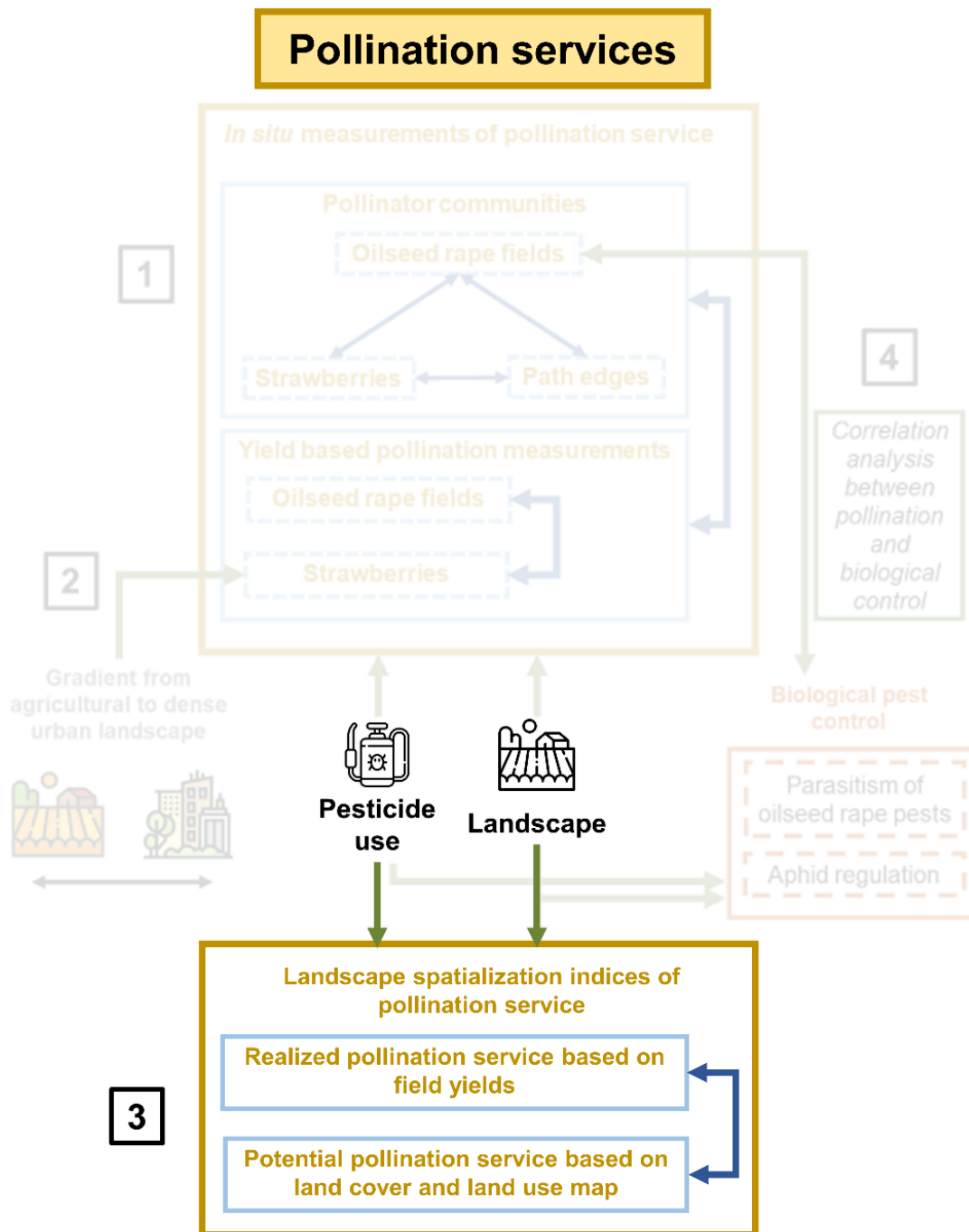


Figure 4.0. Third research axis within the general diagram summarizing the whole thesis.

A crop yield-based pollination index reveals the impacts of land cover and pesticide use on realized pollination at a landscape scale

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Abstract

The current pollinator loss raises numerous concerns, because animal pollination maintains the diversity of wild plant communities and is essential for human food. Yet, its consequences for pollination remain unclear, because there is no simple relationship between pollinator abundance or diversity and pollination efficiency. Large scale indicators based on direct measurements of pollination are therefore essential for an accurate assessment of the consequences of pollinator loss for pollination services. Here, we test whether the “realized pollination index” (RPI), a crop yield-based index, is informative on pollination services in a French agricultural landscape. We calculated the index at different spatial resolutions, down to individual fields, compared it with a “potential pollination index” (PPI) based on land cover/land use, and examined its relationship with pesticide use. At the landscape scale, the RPI was positively related to the land cover-based pollination index, and its temporal variations were strongly correlated with those observed at regional or national scales. At the field scale, the RPI was negatively related to pesticide use. These results suggest that the yield-based RPI captures variation in pollination services across landscapes accurately, with large-scale effects of landscape composition, including the spatial arrangement of semi-natural elements and cultivated fields, and more local effects of pesticide use. It could provide an unprecedented, easy-to-use tool for implementing automated pollination monitoring in farmland, from single fields to large areas, and help stakeholders to design biodiversity-friendly territories that efficiently deliver ecosystem services.

Keywords: Pollination indicator; Crop yield; Ecosystem services; Intensive farming; Land cover and land use

Highlights

Indicators based on direct measurements of pollination services are essential

Yield- and land cover-based pollination indices correlated at landscape scale

Yield-based pollination index correlated negatively with pesticide use at field scale

Spatiotemporal patterns of the index suggest accurate measurement of pollination

The crop yield-based pollination index could be a simple, powerful tool for farmers

1.Introduction

Animal pollination ensures the maintenance of diversity in communities of wild plants (Biesmeijer et al., 2006; Thomann et al., 2013; Ehlers et al., 2021) and contributes significantly to the quantity and quality of human food (Klein et al., 2007; L. A. Garibaldi et al., 2013; Potts et al., 2016). However, human activities, and particularly intensive agriculture, cause a major current and forecasted loss of pollinating insects (Potts et al., 2010; Holzschuh et al., 2016; IPBES 2016), as measured by decreased biomass and diversity (Ghisbain et al., 2024). For example, Powney et al. (2019) reported a 25% decline in spatial occupancy for bees and syrphids in the UK between 1980 and 2013, and Zattara and Aizen (2021) estimated a 17-41% worldwide decline in species richness for wild bees between the 1990^s and the 2010^s, depending on bee families. The main purported drivers are changes in land cover, land use and landscape configuration, as well as pesticide use (Dicks et al., 2021; Nicholson et al., 2024a), especially in intensive farmland, characterized by reduced habitat diversity and availability for insects (Ockermüller et al., 2023) and a strong reliance on pesticides (Bloom et al., 2021).

Whether the loss of pollinators is associated with decreased pollination services, defined here as the reproductive success attributable to the action of pollinating insects at field or farm scale (Bartholomée and Lavorel, 2019) remains unclear, because there is no unequivocal relationship between pollinator abundance or diversity and pollination effectiveness (Steffan-Dewenter and Westphal 2008; Loy et Brosi 2022). Generally, pollination is more effective when pollinator communities are diverse and abundant (Woodcock et al., 2019), as more frequent and diverse interactions lead to better plant reproduction (Vázquez et al. 2005). However, numerous factors contribute to the complexity of pollination beyond a simple cause-and-effect relationship such as the identity of pollinator species (Rader et al., 2016; Celis-Diez et al., 2023) or weather during blooming (Nielsen et al., 2017). Therefore, direct measurements of pollination are essential to accurately assess the consequences of pollinator loss on pollination services. In addition, if these measurements are to be of any use for farmers or local land managers, they need to cover broad areas, such as one or several farms, which is typically a landscape scale for ecologists.

Current methods to measure pollination range from indirect estimates based on land cover and land use data (Sihag, 2018; Bartholomée and Lavorel, 2019; O'Connor et al., 2019) to refined manipulations on individual plants. The most accurate method to assess pollination services directly is the measurement of the effect of pollinators on plant reproduction, by comparing open-pollinated flowers either to flowers where pollinators were excluded or to manually pollen-supplemented flowers (Klein et al., 2007; Siopa et al., 2024). However, this approach is time-consuming and focuses generally on a small number of individual plants; it is therefore

rarely implemented at a landscape scale because it requires substantial expenses and observation time (Vaissière et al., 2011; Bommarco et al., 2013; Blaauw and Isaacs, 2014; Potter and LeBuhn, 2015). A second, but more indirect, approach to assessing pollination is to use netting or trapping to measure the abundance and diversity of insect taxa, which assumes that all captured insects contribute to pollination and a positive relationship between insect abundance or diversity and the rates of transfer of compatible pollen among plants (Popic et al., 2013; Perrot et al., 2018; Shi et al., 2024). However, pollinator identification requires considerable naturalist skills and time, making it difficult to apply on a large scale. Third, pollination can be assessed via spatial models predicting insect abundance and probability of visits to plants (Rouabah et al., 2024), based on estimated nesting and floral resource potentials in each landscape element, as well as on the insect foraging distances and climate preferences (Lonsdorf et al. 2009; Zulian et al. 2013). This type of land cover and land use-based index, hereafter referred to as the 'potential pollination index' (PPI), although applicable at large scale and useful to explore the potential effects of landscape composition and configuration scenarios on presence of pollinators and plant pollination (Kennedy et al. 2013; Desaegher et al. 2021; Zhao et al. 2023), provides only indirect estimates of plant pollination (Desaegher et al. 2022; Cusser et al. 2023). Moreover, the latter index has been applied to wild bees mostly and may not adequately picture the contribution of other insect taxa, including domesticated bees, in the pollination of entomophilous crops.

Recently, Martin et al. (2019) introduced a new approach to measure pollination services directly, on the basis of crop yield data. This approach, hereafter referred to as the realized pollination index (RPI), stands out from the aforementioned methods in that it allows pollination services, i.e. the reproductive success attributable to the action of pollinating insects, to be estimated directly across a broad area. The general logic of this index is to calculate, within a geographical area, the difference in yield between crops that are dependent on pollinators to ensure their yield, and crops that are not dependent. When calculated at coarse spatial resolutions (French administrative departments, NUTS3, average area ca. 5800 km²), the RPI produced results consistent with ecological knowledge on pollinators and pollination. For example, it was correlated with the land-cover based PPI calculated across Europe (Zulian et al. 2013), showing that pollination services are indeed higher where pollinator communities are expected to be more abundant. Yet, the correlation was not perfect, suggesting that the RPI may inform more closely on actual pollination services than the PPI, e.g. because it includes all pollinator types contributing to crop pollination.

Although the RPI offers a promising tool for a rapid but accurate appraisal of pollination services and has produced sensible results at a national scale, it has never been tested at finer spatial resolutions, across landscapes. However, landscape is a relevant spatial scale for farmers

and land use planning to identify areas that require attention for the maintenance or implementation of agroecological structures to sustain or restore pollination services. Here, we test whether this crop yield-based index can be informative of pollination services at the agricultural landscape scale by examining its spatiotemporal variations and checking their consistency through different ways. To this end, (1) we calculated the index from yield data at various spatial resolutions, down to the spatial resolution of single fields, and also across years, (2) we compared (2a) the spatial variation of the RPI with that of the PPI adapted to the landscape scale with the InVEST model (Lonsdorf et al., 2009), as well as (2b) the temporal variation in the RPI in the study area with that at regional and national scales and (3) we examined the relationship between RPI and pesticide use, a well-known driver of pollinator loss (Main et al., 2020; Douglas et al., 2022; Nicholson et al., 2023). For this study, we used data from 12 crop species grown between 2007 and 2019 in a French experimental platform of ca. 950 hectares with detailed monitoring of crops at field level.

In other words, we specifically addressed the following questions:

- How do pollination services, as measured via the spatial variation in RPI, correlate with the potential presence of pollinators (wild bees), as measured by the land cover-based index (PPI)? We expect a positive correlation between the two, as pollination services are generally improved by higher abundances of the main pollinators (Woodcock et al., 2019), but not necessarily a strong correlation, as the RPI is expected to provide a more direct and accurate estimate of pollination.
- How does spatial variation in RPI correlate with pesticide use? This tests whether the expected negative effects of pesticides on pollinators and pollination can be detected with the RPI.
- How do the spatialization method and spatial resolution influence the answer to the abovementioned questions? We expect that altering the resolution will impact the strength of the relationship between indices, as the RPI is estimated more precisely with more data, i.e. with coarser spatial resolution, but coarse spatial resolutions also imply pooling together several fields with contrasting farming practices, therefore blurring the potential impacts of pesticide use.
- Is the temporal variation in RPI calculated in the landscape we chose to test the index related to interannual variation of the same index at a national scale? A positive relationship would suggest that the RPI is not fully site-specific, and that the approach could be transferred to other territories.

2. Materials and methods

2.1. Study site

The study area was the Fénay platform, located in a plain south of Dijon in eastern France (47°13 N, 5°03 E). The landscape is composed mainly of commercial arable farms (ca. 65%), producing mostly cereals, oilseed rape and mustard, and forested areas (ca. 12%). The platform consists of 140 contiguous crop fields managed by 23 farmers, covering a total of 950 ha that have been monitored by INRAE Dijon between 2007 and 2019. Farmers were interviewed annually for comprehensive records of farming operations, including detailed information on pesticide use and yield in each field. A total of 79 different crop species were grown in the area between 2007 and 2019 (Table S4.1 in Supplementary material), among which 26 market garden crops. Cropping practices were variable in terms of intensity and reliance on pesticides (Yvoz et al., 2020). The area was thus characterized by heterogeneous farming management and landscape composition (location and area of semi-natural elements).

Annual crop yields were retrieved for the whole area, and we selected 14 crop species that are harvested for fruits and/or seeds, i.e. for which yield is controlled by pollination, regardless of the pollination vector (insects, wind, self-pollination...). From an initial dataset comprising 2404 yield data (one crop species × one field × one year), a final set of 1069 yield data was selected by discarding missing data on crop species, yields or pesticide use, as well as crops with yield depending on vegetative growth. To characterize farming practices, we retained the total amount of pesticides used, as numerous studies have shown lethal and sub-lethal toxicity of pesticides (insecticides, fungicides and herbicides) on pollinators (C. Brittain et al., 2010), including honeybees (Balbuena et al., 2015), bumblebees (Stanley et al. 2015a; Stanley et al. 2015b; Nicholson et al. 2023) and wild bees (Woodcock et al., 2017), and their visitation rates in crop fields (Bloom et al., 2021). For pesticide use, we calculated the treatment frequency index as the sum of the applied dose of each active substance, over the crop cycle (beginning after the harvest of the previous crop and ending at crop harvest), divided by the highest dose approved by French national regulations. This index informs on the number of treatments on each crop and on the relative amounts of substance used.

2.2. Description and calculation of the two pollination indices

The potential pollination index (PPI) predicts pollinator presence by integrating land cover and land use data with expert insights into pollinator ecology. In contrast, the realized pollination index (RPI) quantifies the contribution of pollinators to yields using crop yield data.

2.2.1. Potential Pollination Index (PPI)

We used the InVEST pollination model (Sharp et al., 2018), primarily based on the equations of Lonsdorf et al. (2009) to assess the probability of pollinator presence and to calculate the PPI. We worked with the pollinator supply metric, which provides the potential presence of wild pollinators (especially wild bees) annually in each cell of a raster, based on estimated available nesting sites in that cell and on floral resources in surrounding cells (Figure S4.1 in Supplementary material). We opted to model an “average” pollinator with a flight distance of 500 m, which is typical of many wild bees (Zurbuchen et al., 2010).

We generated Land Cover and Land Use (LCLU) maps for each year between 2007 and 2019 on the Fénay platform and within a 2 km buffer around the area, combining data (1) from the cropping system survey of the platform by INRAE Dijon and the Land Parcel Identification System sourced from the Common Agricultural Policy (available at <https://geoservices.ign.fr/rpg>) for the crops grown in each field each year; and (2) from the OSO Land Cover Map by Theia (Inglada et al., 2018) for stable semi-natural elements and urban areas between 2007 and 2019. After topological corrections, we merged the three datasets into a single vector layer with the “ALM” package (Allart et al., 2021). We created a map for each year between 2007 and 2019, since the French Land Parcel Identification data were available only since 2007. The resulting maps were composed of 165 LCLU categories, comprising 156 agricultural land use categories (such as wheat, barley, oilseed rape, and mustard) and nine other LCLU categories (including buildings, hedgerows, and water bodies). We then converted the vector layer into a raster with a spatial resolution of 5 m allowing us to maintain reasonably high spatial resolution while managing the data volume effectively during the InVEST simulation processes. For each LCLU category, we used the expert-based dataset of Desaegher et al. (2022) to characterize the availability of nests and the monthly floral resources. Finally, in each raster cell, we averaged pollinator supply over all study years to identify locations where wild bees, or wild pollinators with similar ecology, are expected to be more abundant.

2.2.2. Realised Pollination Index (RPI)

Martin et al. (2019) introduced a pollination service index based on yield data and crop-pollinator dependence, enabling a post-harvest assessment of pollination services. This relative index enables the comparison of pollination services across different sites (or different periods, when relevant), with the following rationale: the relationship between crop yield and crop dependence on pollinators, examined by pooling all crops together, should be informative on pollination, all else assumed equal. Although all information on how to calculate the index can

be found in Martin et al. (2019), we reiterate the key points below so that the current study stands alone.

(Klein et al., 2007) introduced five degrees of dependence of crop plants on pollinators, defined as the percent yield loss in the absence of pollinators: none (0% yield reduction), little ($< 10\%$ yield reduction), modest (10–39% yield reduction), great (40–89% yield reduction), and essential ($\geq 90\%$ yield reduction), which we used to characterize the 14 study crops (Table S4.2 in Supplementary material). For each crop, yields are standardized across the whole study area, allowing a comparison across crop species. Following this transformation, positive (negative) values of standardized yield for a given crop are considered to be yield surplus (respectively deficits) in a field or larger area compared to the average yield of this crop across the entire territory. Besides, the yield of pollinator-independent crops can be used to evaluate whether environmental conditions influencing yield, beyond pollinators, (i.e., weather, farming practices, soil type, biological pest control, etc.) are favourable or not for production in a given location relative to the average in the study area.

The index is calculated on subsets of the study area, which we call “sites”, by linearly regressing standardized crop yields (response variable) on yield dependence on pollinators (independent variable) in each site. The RPI in a given site is the slope of this regression (Figure 4.1). Due to standardization constraining yield values in the same range across all pollinator-dependence levels, any positive slope in one site will be offset by a negative slope in another. Consequently, the RPI provides only a relative, not absolute, indicator of pollination services, ranking sites within a study area from those where pollination is most limiting to those where it is less so, as follows. By definition, in sites with a positive slope, pollinator-dependent crops outperform on average crops that do not depend on pollinators for their yield. In such sites, pollinator-dependent crops also tend to have yields above the average across the study area, while the other environmental conditions affecting yield do not favour particularly high yields for pollinator-independent crops (pollinator-independent crop yield at or below the average, e.g. sites A, B and D on Figure 4.1). On the whole, this suggests that pollination services are likely higher in these vs. other sites, although not necessarily at their maximum (Figure 4.1). On the contrary, in sites with a negative slope, the environmental conditions are favourable for crop yield (pollinator-independent crop yield at or above the average, e.g. sites C, E and F on Figure 4.1), yet the yield of pollinator-dependent crops tends to be lower than the average yield across the study area, which is likely attributable to a pollination deficit.

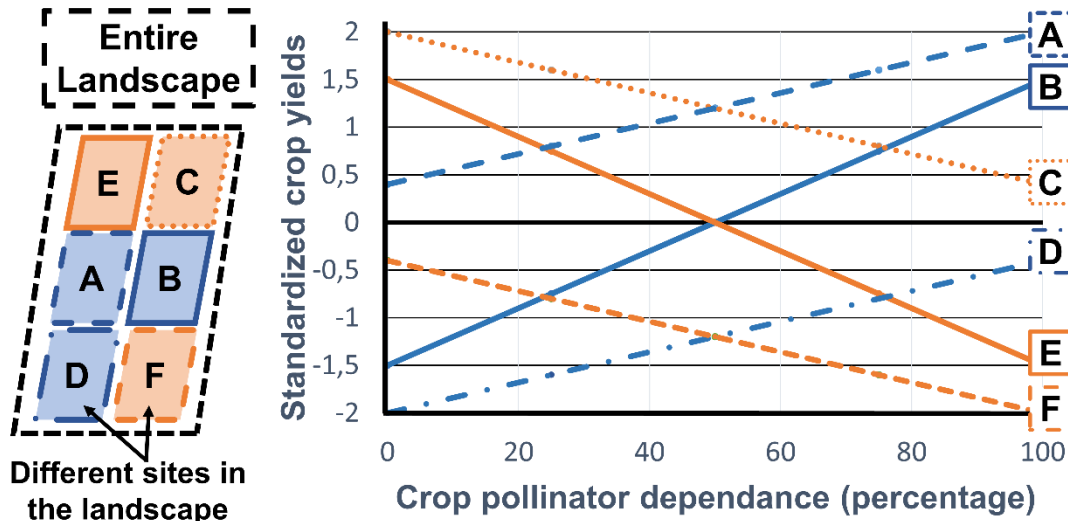


Figure 4.1. Toy example for the calculation of the realized pollination index (RPI) based on hypothetical data. In this example, the study area is partitioned into six sites (left panel). In each of these sites, standardized yields are regressed on crop pollinator dependence (right panel). This approach ranks the sites from those where animal pollination is most limiting (negative slopes, orange) to those where it is less so (positive slopes, blue).

We adapted the RPI calculation from Martin et al. (2019) to the landscape scale. Crop yield data were retrieved for all years between 2007 and 2019. For each crop species, all data (all fields, all years) were standardized across the whole Fénay platform. Standardized yields were then grouped geographically into “sites” (see below), to perform linear regressions of standardized yield against crop dependence on pollinators within subsets of the Fénay platform and obtain the RPI as the slope of this linear regression. For this analysis, we pooled data from all years together to obtain enough data for the linear regressions, and also because yields do not show major temporal trends between 2007 and 2019 for the crops studied (Schauberger et al., 2018).

2.2.3. Spatial resolution of the Realised Pollination Index (RPI)

The RPI is a relative measure of pollination services, i.e. comparing sites, here subsets of the Fénay platform. There are numerous ways to split up a given area, hence we evaluated the influence of three contrasting approaches, with different spatial resolutions, on calculating the RPI. The coarsest resolution was provided by sliding windows, i.e. spatial smoothing across fields. The intermediate resolution was associated with clusters of varying numbers of agricultural fields. Finally, the finest resolution was obtained by considering stable agricultural fields over time.

Sliding window approach

The sliding window is the coarsest spatial resolution method allowing a smoothing of pollination values across fields, within several hundreds of meters, which is close to the potential flight range of pollinators between fields. This approach consists of two steps. First, the landscape was split up into fixed size square windows (dashed squares on Figure 4.2.A), and the RPI of each window was calculated using standardized yield data across all fields and years. Window size was chosen as a trade-off between (1) number of yield data per window, i.e. windows must be large enough to contain several fields x years, for the calculation of the index, and (2) number of windows, i.e. windows must be small enough to produce at least 35 replicates of RPI values across the study site. Second, the output spatial resolution was controlled by the offset between each of the windows at the sliding step. Since the windows were larger than the pixels in the output raster, each of the final pixels was intersected by multiple windows during the "sliding" process (Figure 4.2.A). The RPI for a pixel was therefore the average RPI values computed across all windows that intersect the pixel. Thus, each pixel was not independent of the neighbouring pixels because they shared some windows. For this study, we used a gradient of window sizes and spatial resolutions: from 2000 m × 2000 m (400 ha) to 500 m × 500m (25 ha) windows and from 750 m × 750 m to 250 m × 250 m output pixel sizes. The lower limit for window size (500 m × 500 m) was set to ensure there were enough fields included in each window.

Cluster approach

We clustered fields with the *k*-means method, using the ``res.hcpc`` function from the 'FactoMineR' package in R, which allows spatial resolution to be modulated by the number of clusters defined. A hierarchical clustering on fields coordinates was performed to facilitate the identification of spatially contiguous clusters within the study area (Figure 4.2.B). The number of clusters was chosen by visual assessment of the dendrogram. The RPI was calculated in each cluster, using standardized crop yields in all fields and years within each cluster. The minimum number of clusters was set to 25, with a mean cluster area of 33 ha, so that there was sufficient statistical power to examine the relationships between pesticide use and RPI (one RPI value per cluster; Jenkins and Quintana-Ascencio, 2020). The maximum number was set to 50, with a mean cluster area of 16.5 ha, which ensured at least two fields within each cluster.

Stable field approach

"Stable fields", the finest spatial resolution, correspond to management units that were stable over time and within which crop species and management practices were homogeneous within a year. The mean area of a stable field was 3.9 ha. We used the methodology of successive annual intersections (Yvoz et al., 2022) on the Fénay platform. When a farmer subdivided a single field into two smaller fields in the subsequent year, both resulting fields were retained for analysis. This approach involves performing successive intersections of the crop rotation across years between 2007 and 2019. Each (sub)division of a field results in the creation of new fields, most of which were included in the final analysis. We only discarded polygons below 0.1 ha, which eliminated all market garden fields, in which the methods for measuring yields are anyway highly different from those used in field crops, making them little comparable (Figure 4.2.C). The RPI was then calculated in each stable field, using the time series of standardized crop yields between 2007 and 2019 for this stable field.

For comparison purposes, we converted raster formats (i.e., RPI obtained with sliding windows and PPI) into vector formats, by computing their average value within each stable field. This enabled us to examine the relationship between pollination indices and pesticide use at field level. For each stable field, we computed an area-weighted mean PPI or RPI, by retaining all raster pixels that overlapped partly or entirely with the stable field, and weighting their contribution by the proportion of the field area included in the pixel.

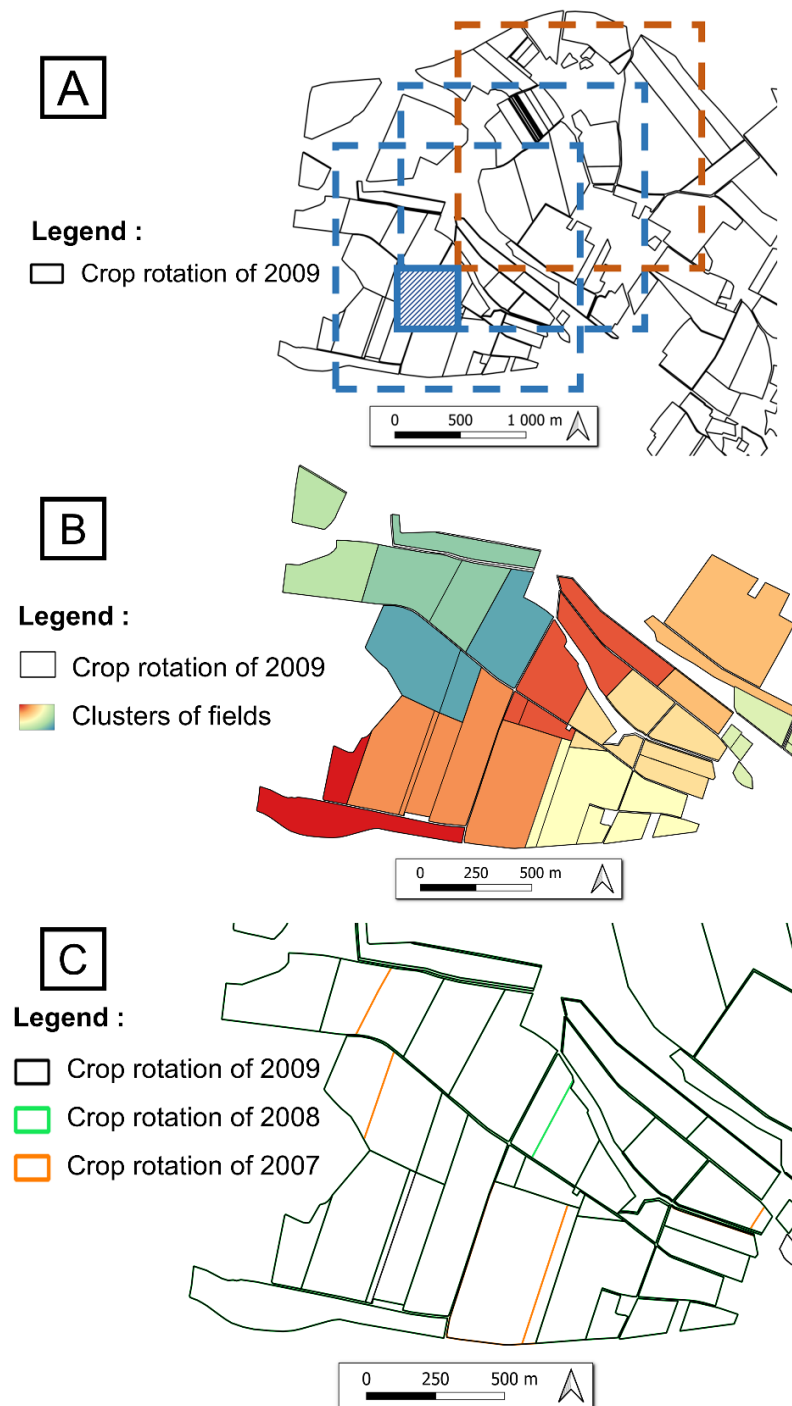


Figure 4.2. Different methods to split up the study area, illustrated over a subset of the Fénay platform. A. Sliding windows return output pixels (solid square hatched in blue) that average the pollination index for all the sliding windows that encompass this pixel. Windows that encompass the output pixel are shown with blue dashed lines, while one that does not pass through the output pixel is shown with orange dashed lines. B. Clusters are groupings of fields based on their proximity to each other. C. Stable fields are the result of the intersection of crop rotation across successive years, shown here in different colours.

2.3. Temporal variation in RPI

To test whether the temporal variation in RPI calculated in the Fény platform was related to interannual variation of the same index at broader spatial scales, we calculated the RPI in the whole Fény platform across years. The range of dates was 2007-2017, because crop yield data were not available in 2018 and 2019 in Côte d'Or (see below). Interannual variation in RPI of the Fény platform was compared with that of Côte d'Or (the French administrative department encompassing the Fény area) and of France as a whole. RPI at the department and national scales was calculated from Agreste data (available at <https://agreste.agriculture.gouv.fr/agreste-web/>), filtered to retain only the crop categories corresponding to the 14 crop species studied in the Fény platform. The methodology mirrors that used for the spatial approach, but the grouping of standardized yield data was temporal (per year) rather than spatial. We used Spearman correlations to study the relationship of the Fény inter-annual variations of RPI with those at departmental and national scale, because the number of replicates was small (11 years).

2.4. Statistical analysis

In all the spatial partitioning methods used to calculate the RPI, the same statistical analyses were performed. We first calculated Pearson's correlation coefficients between RPI and PPI to examine how these two indices correlated at landscape level. To examine jointly the relationship between RPI (dependent variable), scaled PPI and scaled pesticide use, we used an analysis of variance on the following linear model.

$$RPI_i = \alpha + \beta \times PPI_i + \gamma \times Pesticide_i + \varepsilon_i$$

where α is the intercept, RPI_i , PPI_i , and $Pesticide_i$ are the RPI, and time-averaged PPI and pesticide use, respectively, in stable field i , and ε_i is an error term, following a Gaussian distribution with mean 0 and variance σ^2 . The distribution of model residuals (normality, homoscedasticity, outliers) was checked visually by examining diagnostic plots. Given that semi-natural elements were integrated into the InVEST model, we did not introduce a specific variable for semi-natural elements in the linear models. These analyses were performed across all spatial resolutions.

All analyses were performed using R version 4.3.3. Indices were calculated and mapped using R packages ggplot2 (Wickham, 2016) version 3.5.1, RColorBrewer version 1.1.2 (Neuwirth, 2022), sf version 1.0-16 (Pebesma and Bivand, 2023) and tidyverse version 2.0.0 (Wickham et al., 2019).

3. Results

The predominant crops in the study area, used to calculate the RPI, ranged from non-dependent – 0% (cereals) to modestly dependent – 25 % (brown mustard, oilseed rape and sunflower) crops. Even such limited variation in pollinator dependence enabled us to obtain a relative, yield-based pollination index, and to compare it with the PPI, an indirect index estimating the potential presence and activity of pollinators. The range of RPI values varied across spatial resolution methods (see below). Our analysis also accounts for pesticides, a factor known to influence pollinators and not included in the PPI calculation. Pesticide use (treatment frequency index) varied from 0.05 to 8.5. It was generally high for some crops such as mustard (mean TFI = 6.4 ± 0.3) or oilseed rape (mean = 6.0 ± 0.1) and lower for e.g. sunflower (mean = 3.0 ± 0.4). Herbicides, fungicides and insecticides represented 25%, 33% and 37% of the treatment frequency index, respectively.

3.1. Comparison of RPI, PPI and relationship with pesticide use at coarse spatial resolution: sliding window approach

The spatial patterns of RPI obtained with the sliding window approach and of PPI were generally consistent. The PPI exhibited a north-west/south-east gradient, which was most obvious with the projection on stable fields (Figure 4.3.A), with higher PPI values in the north-eastern side of the Fénay platform (see also Figure S4.2 in Supplementary material for the raster gradient). A similar, albeit not completely identical, gradient was observed for the RPI projected onto stable fields, for example with the 2000 m $\times$ 2000 m windows and an output resolution of 500 m $\times$ 500 m (Figure 4.3.B). As a consequence, the relationship between the RPI calculated with the sliding window method and the PPI was positive and strong, regardless of the statistical analysis (Pearson's ρ up to 0.60; coefficient of the linear model up to 0.61; Table 4.1 and Figure 4.4). The relationship was significantly positive for all sliding window resolutions (Table 4.1), but was weaker with smaller windows or larger pixels (from $\rho = 0.6$ for the largest windows with a resolution of 500 m $\times$ 500 m to $\rho = 0.32$ for 1000 m $\times$ 1000 m windows with the same resolution; Table 1). In contrast, no significant relationship between RPI and pesticide use was found for the sliding windows approach in the linear model, although the estimates were negative across all spatial resolutions ($P > 0.05$, Table 4.1).

Table 4.1. Relationship between RPI calculated with the sliding window approach, PPI and pesticide use, across different spatial resolutions. Summary of results of linear models testing the relationship between the Realised Pollination Index (RPI, dependent variable) and the Potential Pollination Index (PPI) and pesticide use (explanatory variables). For each independent variable, the table shows the estimates and their associated standard error, P-values ($P < 0.05$ in bold), as well as R^2 of the model. Person correlation coefficients between RPI and PPI are shown in the last column.

Sliding window size / output pixel size	Linear model					RPI-PPI Pearson's ρ
	Variable	Estimate	Standard error	P-value	R^2	
2000 / 750	PPI	0.51	0.064	<0.001	0.28	0.53
	Pesticide use	-0.074	0.059	0.91		
2000 / 500	PPI	0.61	0.059	<0.001	0.35	0.60
	Pesticide use	-0.0077	0.066	0.21		
1500 / 500	PPI	0.50	0.065	<0.001	0.23	0.48
	Pesticide use	-0.080	0.066	0.23		
1000 / 500	PPI	0.34	0.082	<0.001	0.11	0.32
	Pesticide use	-0.064	0.091	0.49		
500 / 250	PPI	0.42	0.080	<0.001	0.17	0.41
	Pesticide use	-0.089	0.094	0.35		

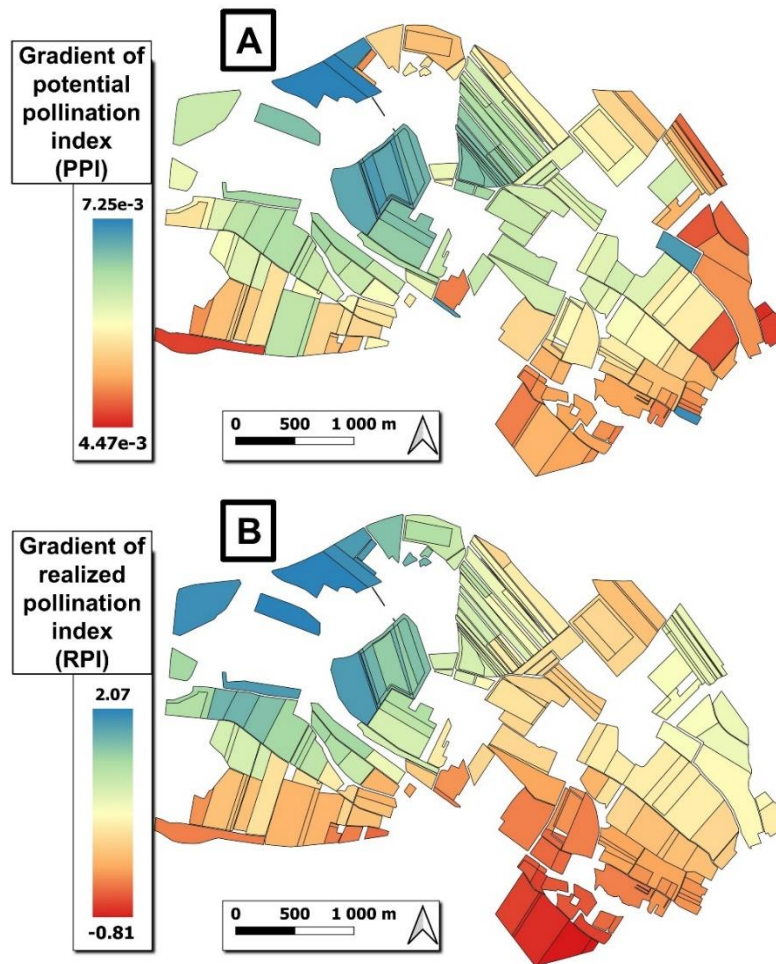


Figure 4.3. Visual comparison between the Realized Pollination Index (RPI) and the Potential Pollination Index (PPI) projected on stable fields. A. Potential Pollination Index, calculated from the 2007-2019 land cover/ land use data. B. Realized pollination Index, calculated from 2007-2019 crop yield data, with 2000 m x 2000 m sliding windows and 500 m x 500m output pixels.

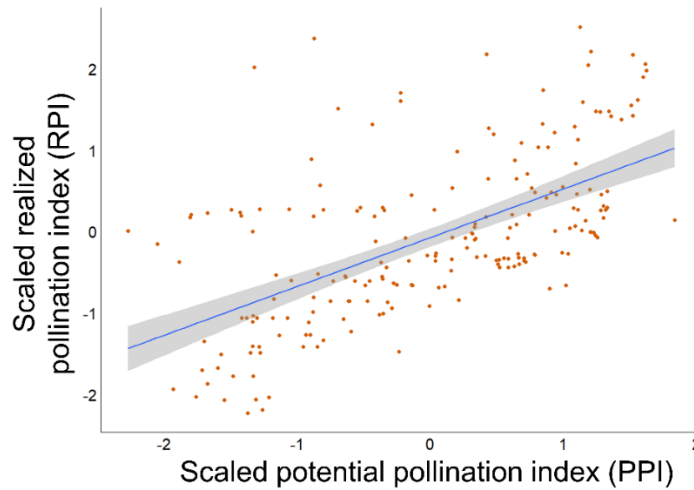


Figure 4.4. Regression of the scaled Realized Pollination Index (RPI) calculated with the 2000 m x 2000 m sliding window approach and 500 m x 500m output pixels against the scaled Potential Pollination Index (PPI). Each point corresponds to one stable field on Figure 4.3. $R^2 = 0.36$ and P -value < 0.001 .

3.2. Comparison of RPI, PPI and pesticide use at intermediate to fine spatial resolution: cluster and stable field approaches

The correlates of RPI calculated with a cluster approach depended on cluster size, hence spatial resolution. With a small number of larger clusters (25 or 30), representing the coarsest resolution, the relationships between RPI and (1) PPI (positive estimates) or (2) pesticide use (negative estimates) were marginally significant, with P -values < 0.10 for both variables (Table 2). With more, but smaller clusters (≥ 35), thereby at finer spatial resolution, RPI was negatively related to pesticide use ($P < 0.01$; Table 4.2). At such finer spatial resolution, the relationship with PPI was not significant in the cluster approach (Figure 4.5.A and Figure 4.5.B), although all estimates were positive ($P > 0.1$).

When the RPI was calculated at the finest spatial resolution, i.e. within each of the 87 stable fields, the patterns were similar to those observed with fine-resolution clusters, i.e. a negative relationship between RPI and pesticide use, but no relationship with PPI (Table 4.3).

Table 4.2. Relationship between the RPI calculated with the cluster approach, the PPI and pesticide use, across different spatial resolutions. Summary of results of linear models testing the relationship between the Realised Pollination Index (RPI, dependent variable) and the Potential Pollination Index (PPI) and pesticide use (explanatory variables) across different numbers of clusters. For each independent variable, the table shows estimates and their associated standard error, P-values, ($P < 0.05$ in bold; $0.05 \leq P < 0.10$ in italics), as well as the R^2 of the model. Identical standard errors are related to the design of the dataset and to the scaling of the explanatory variables.

Number of clusters	Variable	Estimate	Standard error	P-value	R^2	Model P-value
25	<i>PPI</i>	0.47	0.26	0.064	0.26	0.01
	<i>Pesticide use</i>	-0.52	0.26	0.059		
30	<i>PPI</i>	0.44	0.26	0.093	0.20	0.02
	<i>Pesticide use</i>	-0.50	0.26	0.059		
35	PPI	0.21	0.29	0.47	0.32	< 0.001
	Pesticide use	-1.08	0.29	< 0.001		
40	PPI	0.21	0.35	0.55	0.16	0.014
	Pesticide use	-0.90	0.35	0.013		
45	PPI	0.27	0.31	0.38	0.18	0.0054
	Pesticide use	-0.88	0.31	0.0064		
50	PPI	0.13	0.29	0.67	0.18	0.0037
	Pesticide use	-0.96	0.29	0.0021		

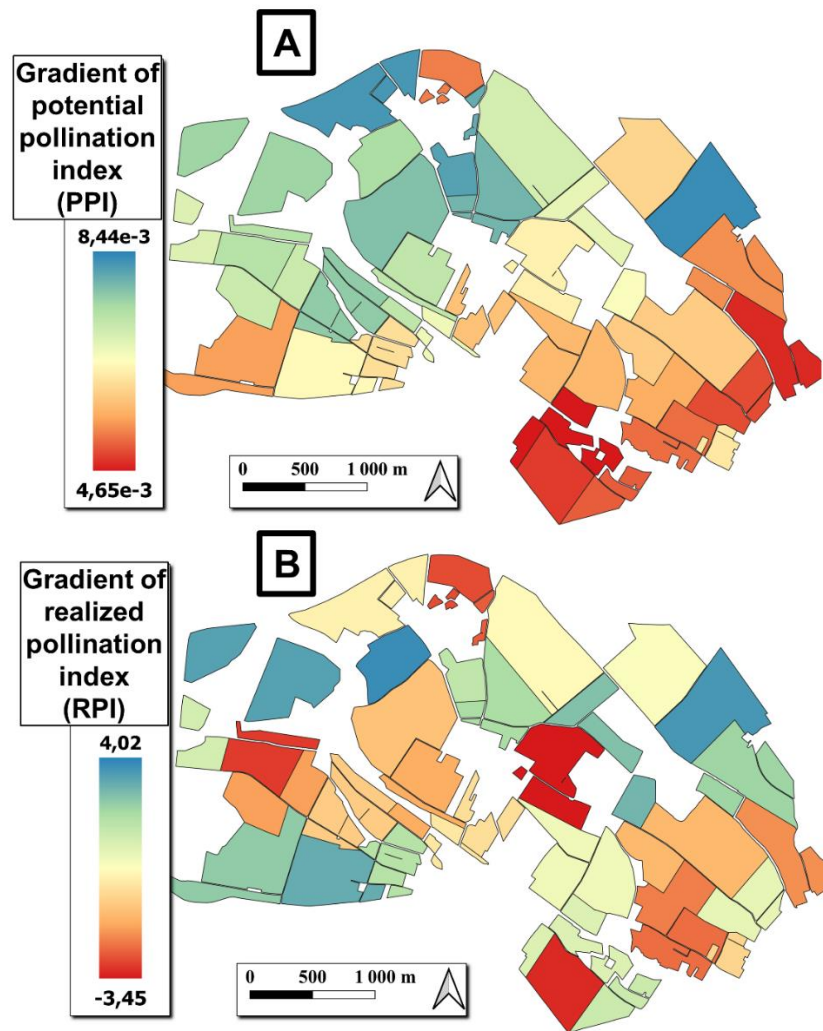


Figure 4.5. Spatial variation in pollination indices across 35 clusters. A. Weighted mean Potential Pollination Index (PPI). B. Realized Pollination Index (RPI) calculated directly from yield data for each cluster.

Table 4.3. Relationship between the RPI calculated with the stable plot approach, the PPI and pesticide use. Summary of results of linear models testing the relationship between the Realised Pollination Index (RPI, dependent variable) and the Potential Pollination Index (PPI) and pesticide use (explanatory variables). For each independent variable, the table shows the estimates and their associated standard error, P-values, ($P < 0.05$ in bold), as well as the R^2 of the model.

Variable	Estimate	Standard error	P-value	R^2
PPI	0.224	0.30	0.46	0.14
Pesticide use	-1.09	0.31	<0.001	

3.3 Interannual variations and comparison with the rest of France

The interannual variations in RPI were highly consistent across spatial extents (Figure 4.6). Interannual variations across the whole Fénay platform were strongly correlated with the interannual variations in RPI calculated at national scale (Spearman's rank correlation coefficient $r_s = 0.86$; $P = 0.0012$) and marginally significant across the administrative department encompassing the platform, with a smaller correlation coefficient ($r_s = 0.57$; $P = 0.07$).

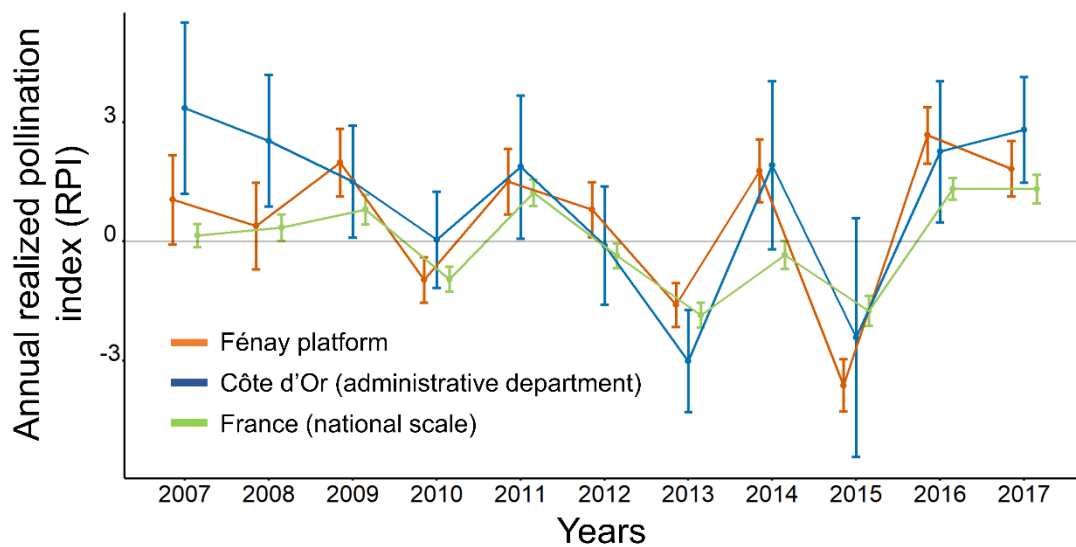


Figure 4.6. Interannual variation in the temporal Realized Pollination Index (RPI) calculated across different spatial extents. Côte d'Or is an intermediate administrative scale encompassing the local Fénay area. Error bars indicate standard errors.

4. Discussion

To our knowledge, this is the first study aiming to assess the relevance of RPI, a crop yield-based index, to provide a direct measurement of pollination services at a landscape scale. Our main results, namely positive correlations with the land cover-based PPI and interannual variations across larger spatial extents, as well as a negative correlation with pesticide use at field scale, suggest that the RPI does depict variation in pollination services at the landscape scale. In the following, we discuss the conditions required for RPI to provide an accurate and low-cost map of variation in pollination services at the landscape scale. We emphasize that the message delivered by RPI values strongly depends on the calculation method, particularly on spatial resolution, and provide recommendations to tailor calculations to the question addressed. Finally, we list future research perspectives to improve our understanding of the determinants of pollination services in farmland.

4.1. Spatiotemporal patterns in the Realized Pollination Index, and its relationships with environmental variables, suggest accurate assessment of pollination services, from field to landscape scale

We observed a significant positive correlation between the PPI (Lonsdorf et al., 2009) and RPI (Martin et al., 2019) downscaled to the Fénay platform, i.e., a landscape scale, but only when the latter was calculated using yield data from numerous fields pooled together (i.e. sliding window approach). Previous research at the national scale (Martin et al., 2019) showed a similar significant positive correlation between the RPI calculated with a spatial resolution of an administrative department and another land-cover based pollination index (Zulian et al., 2013). Regardless of spatial extent, both indices therefore tend to mutually validate each other by yielding consistent information from independent, contrasting, and apparently unrelated datasets: land cover and land use (PPI) vs. crop yields (RPI). Such positive correlations between pollinator abundance predicted on the basis of nesting and foraging resources and the reproductive success attributable to the action of pollinating insects (Klein et al., 2007; Bartholomée and Lavorel, 2019) can be interpreted causally. Environmental determinants such as the area of semi-natural elements influence potential pollinator supply positively in the InVEST model, but also contribute to actual pollinator abundance in the field (Raderschall et al., 2021; Maurer et al., 2022; Rivers-Moore et al., 2023) and more efficient pollen delivery to crops (Eeraerts, 2023), hence a positive relationship with the yields of pollinator-dependent crops.

However, the positive correlation between RPI and PPI varied depending on the method or spatial resolution for the calculation (see also below), suggesting that the RPI carries

information complementary to the PPI. In particular, at the finer spatial resolutions of clusters and stable fields, we observed significant negative relationships between the RPI and pesticide use. This effect of pesticides was not incorporated into the InVEST model, and can be caused by a decrease in nesting and/or food resources for pollinators (e.g., due to lower weed abundance or diversity; Crochard et al., 2022), or by a direct effect on insect survival in the fields. To examine the relationship between RPI and pesticides, we considered a cumulative impact by summing insecticides, fungicides, and herbicides. The direct effects of insecticides and fungicides on pollinator health and behaviour are extensively documented, with consequences for pollination services (Stanley et al., 2015a). Herbicides, on the other hand, may also directly affect pollinator behaviour (Farina et al., 2019; Godara et al., 2023), but have an additional direct impact on plant communities, which provide important floral resources throughout the year for pollinators to complete their life cycles. Many studies point to pesticides as a major factor in the decline of pollinator populations, particularly bees, in increasingly intensive agricultural landscapes (Abati et al. 2021; Yordanova et al. 2022). Our study goes one step further and demonstrates an impact on crop pollination, consistently with the work of e.g. Stanley et al. (2015a), Perrot et al. (2024) or Scheper et al. (2023). In contrast to earlier studies however, data required to demonstrate the consequences of pesticide use on pollination are much easier to gather (see below). Note that the negative relationship between the RPI and pesticide use was observed only when all fields were considered, including those with low pesticide use, which could be considered as outliers. Yet, these fields represent important reference values to properly assess the impacts of pesticides.

Finally, consistent interannual variations across spatial extents, from the Fénay platform to France as a whole, suggest that the RPI can be generalized (see below), but also reveals a strong impact of weather conditions, the environmental factor most likely to exhibit large year-to-year variation, on pollination. Pollinator activity is known to depend heavily on weather, with e.g. warm and dry conditions favouring bees (Sanderson et al. 2015), but this major influence is unlikely to affect the spatial version of the index, as interannual variations in weather are averaged out by the multi-year approach. Examining the weather determinants of the interannual variation in RPI is a natural perspective of this work. We note that no obvious temporal trend in pollination services jumps out, regardless of spatial extent, but a time frame of ca. 10 years may be too short to detect such trend.

4.2. The spatial resolution used to assess pollination services impacts their measurement

The calculated RPI values varied depending on the spatial partitioning method and associated spatial resolution used. The sliding window method, with the coarsest spatial resolution, incorporates a smoothing aspect that may reflect the flight distance between nests and floral resources and better picture the impacts of landscape structure and composition on pollination, similar to the InVEST model for PPI. Thus, this could account for the observed positive correlation between RPI and PPI with this approach only, given that pollinators are mobile and not restricted to a single field. Consistent with this interpretation, the strength of the correlation between RPI and PPI decreased with decreasing window size, suggesting that too fine spatial resolutions do not properly incorporate the impacts of landscape. Finally, no significant relationship was observed between RPI and pesticide use with this method, regardless of window size. This absence of a signal for a negative impact of pesticide use on pollinators and pollination is likely due to the combination of (1) a relatively homogeneous spatial distribution of pesticide use across the Fénay platform, with intermingled low- and high-pesticide fields and (2) a method that combines yields from neighbouring, here contrasting, fields within a window to produce a single estimate of pollination services. The sliding window approach could be able to produce estimates of pollination services that are impacted by pesticide use in an area with more spatially structured pesticide use, such as contiguous organic farms interspersed in conventional farms.

The cluster and stable field approaches yielded pollination patterns that were partly inconsistent with the sliding windows approach, namely no correlation between RPI and landscape composition (PPI), although the correlation was marginally significant in the low-resolution cluster approach but a negative correlation with pesticide use. In other words, local effects seem to outweigh the overall landscape effects progressively with finer resolution. The absence of significant correlation between the RPI and PPI in the cluster and stable field approaches may be due to several mechanisms. First, pesticides may have a stronger impact than landscape on pollinators at the field level, so that, even with semi-natural elements adjacent to a crop field, high pesticide pressure eliminates most pollinators, with consequences for pollination services (C. Brittain et al., 2010; Main et al., 2020; Bloom et al., 2021). Alternatively, the model we used for PPI essentially considers wild bees and wild pollinators with similar ecologies, while other pollinator types, such as domestic bees or flies are not considered in the calculation of the PPI. For example, a lack of data on location of beehives could explain the discrepancy between the PPI and RPI, whereas this effect could be smoothed out with sliding windows. Finally, our approach may have lacked statistical power, due to the limited number of stable

fields, and particularly of clusters: the relationship between the RPI and the PPI was always positive, as expected, but never significantly so.

4.3. Recommendations for the application of the RPI to assess pollination services for practical purposes

The RPI could prove a useful tool for the implementation of simplified and automated pollination monitoring in agricultural areas, provided several requirements are met. First, the index obviously requires yield data, for as many crops as possible, covering a gradient of pollinator-dependence, at a spatial resolution as fine as possible and for as many years as possible. The potential user should be aware that with only one or two crops per pollinator-dependence level, the index becomes highly sensitive to the effects of other environmental variables (farming practices, weather, soil type, biological pest control...) on specific crops. For example, with two crops only, a dry year may be beneficial for the yield of crop A but detrimental for that of crop B, regardless of their pollinator-dependency. If crop B is highly pollinator-dependent, but not crop A, the RPI would be negative, suggesting pollination deficits when there are only weather effects. The strength of the RPI relies in the use of multiple pollinator-dependent crop species, with different relationships with environmental variables influencing yield, such that the effects of the latter are evened out. From this respect, the RPI appears well-suited to the agricultural context of Fénay, monitored since 2007 and characterized by large fields with cereal crops in rotation with oilseed rape, sunflower, and occasionally mustard. The positive correlation of our index, calculated at the Fénay scale, with interannual variations at broader geographic extents also supports the potential for generalization to other areas. Indeed, similar rotation practices are prevalent across France (47% of farmland in France is cultivated with large-scale crops) and western Europe. However, the RPI cannot readily be transferred to farmland with a large fraction of grasslands or crops cultivated for vegetative parts, for which yields do not depend primarily on pollination, or a large fraction of crops for which the measurement of yields is not standardized, such as market garden crops.

Second, an important step in calculating the index is the choice of the spatial resolution, which depends on the aim or questions asked. The sliding window approach appears most suitable for large-scale implementation to measure pollination services across whole landscapes. Note, however, that this relatively coarse spatial scale still requires fine-resolution yield data, ideally within each field, as these are used as replicates within a given window. With systematic, fine spatial resolution monitoring of large agricultural areas, the yield-based index could be used as a guide for land-use planning thanks to the assessment of pollination services across a whole landscape. On the one hand, areas identified as already conducive to pollinators could be

prioritized for the cultivation of pollinator-dependent crops to maximize yields. On the other hand, landscape managers could encourage measures to improve the suitability of areas where pollination is deficient, and domestic bees do not seem to compensate for the lack of wild pollinators in terms of yields.

At a finer resolution, studying clusters of fields or single stable fields provides insights into the effects of farming practices on pollination services, provided that farming practices are sufficiently diversified across the territory and that yield data is available for each type of farm. Note that sufficiently long time series of yield data in each field (ideally >10 years) are a necessary requirement to calculate the RPI at the field level. At this resolution, the yield-based index could be used to advise farmers on practices that are less harmful to pollinators, e.g. when a negative effect of pesticides is observed. More diversified crop rotations with an increased presence of nectar-producing plants (Raderschall et al., 2021) or a reduction in pesticide use could enhance pollination services. These results could also be used to parameterize InVEST more precisely, for instance, by adding data on practices to the Land Cover and Land Use raster and creating new categories such as crops with low vs. high pesticide inputs.

4.4. Limitations and perspectives for improving the assessment of pollination services

This work opens up new perspectives for future research to enhance the measurement and understanding of pollination services. First, the crop yield-based index is only applicable to areas with a diversity of field crops. In regions dominated e.g. by extensive grasslands, a composite indicator that considers both yields, land use, and the quantity and diversity of floral resources in grasslands could subsequently be developed to appraise pollination services more accurately. This extension of the approach could also be complemented by indicators based on the floral traits of the main species observed in each grassland (Ansquer et al., 2009; Ricou et al., 2014; Goulnik et al., 2020).

Furthermore, RPI values depend on accurate estimates of pollinator dependence. We used the assessment of pollinator dependence by (Klein et al., 2007), a useful resource but that provides a single value per species and is now almost 20-years old. The varieties currently bred for rapeseed and sunflower have sometimes been selected to be less dependent on pollinators (Hudewenz et al., 2014), which may encourage farmers to grow these varieties in areas of pollination deficit. Therefore, the use of larger and more recent studies (Siopa et al., 2024), along with more accurate information on the varieties cultivated in a given area and their respective dependence on pollinators, could be a further step in refining the index. To optimize the assessment of pollination services using sliding windows, the window size and raster resolution could be adapted based on the average field size in the area and the extent over which

yield data are available. Additional test sites would be required to calibrate this method. In the long term, it may also be possible to incorporate GIS data on the presence of beehives to attempt to partition pollination between wild vs. managed pollinators.

Conclusion

Our results indicate a dual influence on pollination services: a large-scale effect of landscape composition, including the spatial arrangement of semi-natural elements and cultivated fields, and a more local effect of pesticide use. These findings underscore the importance of a synergistic approach in intensive agricultural settings, combining land-sharing and land-sparing strategies. Land-sharing, by integrating conservation within productive areas, maintains habitat connectivity, while land-sparing targets specific zones solely for conservation, preserving critical pollinator habitats. This dual strategy acknowledges the need for biodiversity conservation in the face of intensive agriculture, ensuring sustainable pollination services by striking a balance between productivity and ecological preservation (Grass et al. 2021) and enhancing yields of pollinator-dependent crops (Deguines et al., 2014; Eeraerts et al., 2019; Perrot et al., 2024). The crop yield-based index presented here could help identify areas where changes in practices and agro-environmental measures need to be prioritized, such as blackcurrant cultivation in Burgundy, where pollinator populations have declined by 99% (Anstett et al. 2022). In the current context of environmental crisis, such landscape-scale direct indicators can support stakeholders in designing whole territories that are favourable for biodiversity and the resulting ecosystem services.

Acknowledgements

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Author contribution

Thibault Gandara: Conceptualization, data curation, data analysis, investigation, methodology, visualization, writing – original draft; Antoine Gardarin: conceptualization, funding acquisition, supervision, writing and revision of the manuscript; Sandrine Petit: contribution to conceptualization, revision of the manuscript; James Desaegher: contribution to conceptualization and data analysis, revision of the manuscript ; Emmanuelle Porcher: conceptualization, funding acquisition, supervision, writing and revision of the manuscript; Alice Michelot-Antalik: conceptualization, funding acquisition, supervision, writing and revision of the manuscript

Data availability

The data is available within the framework of collaborative projects on the Fénay platform:
<https://umr-agroecologie.dijon.hub.inrae.fr/plateformes-et-infrastructures/infrastructures/plateforme-d-observation-paysagere-de-fenay>

Chapter 4. Supplementary materials**Table S4.1.** List of crops present in the territory of Fénay. Among the 79 crops, some have been grouped together, such as wheat or mustard, to simplify reading.

Alfalfa	Flageolet beans	Nursery wheat	Spelt
Barley (including Winter barley, Spring barley)	Forage 1	Oats	Strawberry
Beans (including Green beans)	Garlic	Onions (including Spring transplanted onion, Spring sown onion)	Sugar beet
Beet trials	Grass fallow	Other	Sunflower
Bell pepper-Chili pepper	Grass strips	Other ornamentals	Triticale
Blackcurrant	Industrial winter rapeseed	Parsley	Turnip
Carrots (including Large carrot)	Legume and grass fallow	Peas (including Winter protein peas, Spring protein peas)	Unseeded fallow
Cabbages	Lentil	Poppy	Vegetables
Celery	Lettuce	Potatoes (including Consumption potatoes, Seed potatoes, Early potatoes)	Tomato
Chia	Lemon balm	Pumpkin	Zucchini
Corn (including Silage corn, Grain corn)	Maize	Rapeseed (including Winter rapeseed)	
Cucumbers	Mallow	Red beet	
Eggplant	Melliferous fallow	Shallot	
Fava bean (Winter)	Miscanthus	Soft wheat	
Flax (including Oilseed flax)	Mustard (including Brown mustard, Winter mustard, Spring mustard)	Soybean	

Table S4.2. Dependency of the 14 selected crop species on pollinators

Crop name	Taxonomic group	Level of pollinator dependence	Positive impact of animal pollination on production
Rapeseed	Brassica napus	25	modest
Winter rapeseed	Brassica napus	25	modest
Brown Mustard	Brassica juncea	25	modest
Winter Mustard	Brassica rapa	25	modest
Mustard	Brassica rapa	25	modest
Sunflower seeds	Helianthus annuus	25	modest
6-row barley	Hordeum vulgare	0	no increase
Winter barley	Hordeum vulgare	0	no increase
Spring barley	Hordeum vulgare	0	no increase
Total bread wheat	Triticum aestivum	0	no increase
Total bread wheat	Triticum aestivum	0	no increase
Triticale	Triticosecale	0	no increase
Maize (grain and seed)	Zea mays	0	no increase
Maize (sweetcorn)	Zea mays	0	no increase

Table of association between LCLU categories, nesting and food resources

The table of associations of Land Cover and Land Use (LCLU) with floral resources and nest availability is available in the supplementary materials of the article by Desaeher et al. (2022b). For our study, the number of LCLU categories is higher due to the duplication of land use between the INRAE database and the RPG, which covers parcels neighbouring the Fénay area.

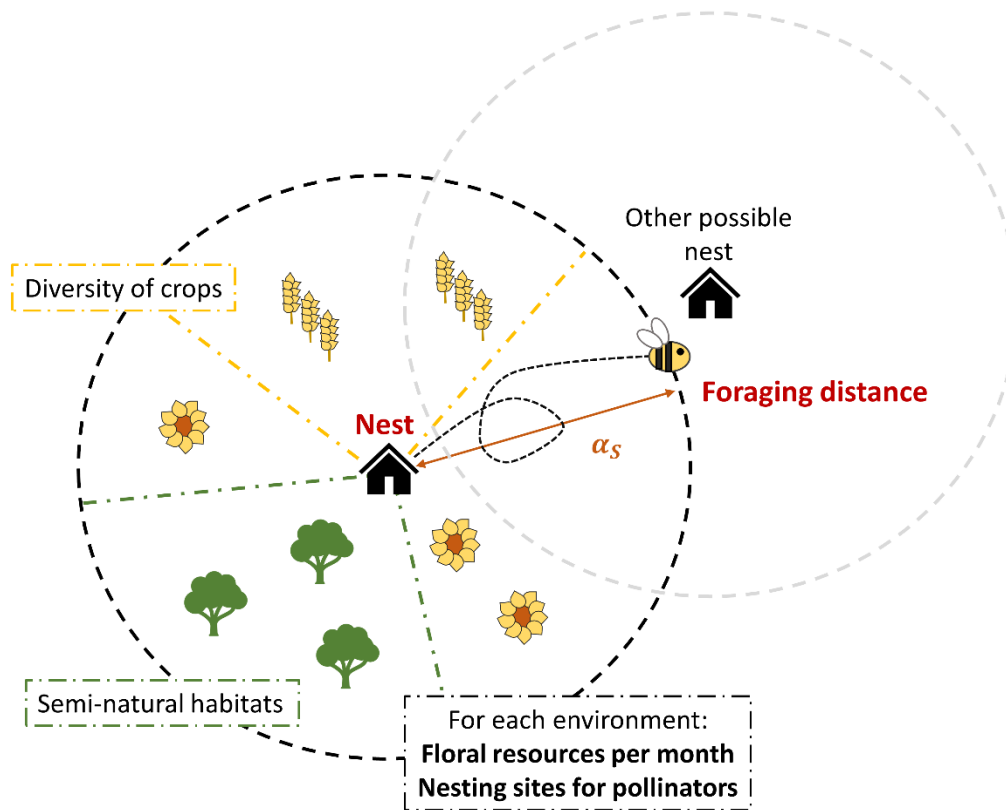


Figure S4.1. Schematic representation of the InVEST model used to produce the Potential Pollination Index (PPI), on the basis of the average flight distance of the modelled pollinator (α_s). Bees are assumed to locate their nests in sites surrounded by floral resources within their foraging range (dotted line circle). *All illustrations are personal and created using PowerPoint software.*

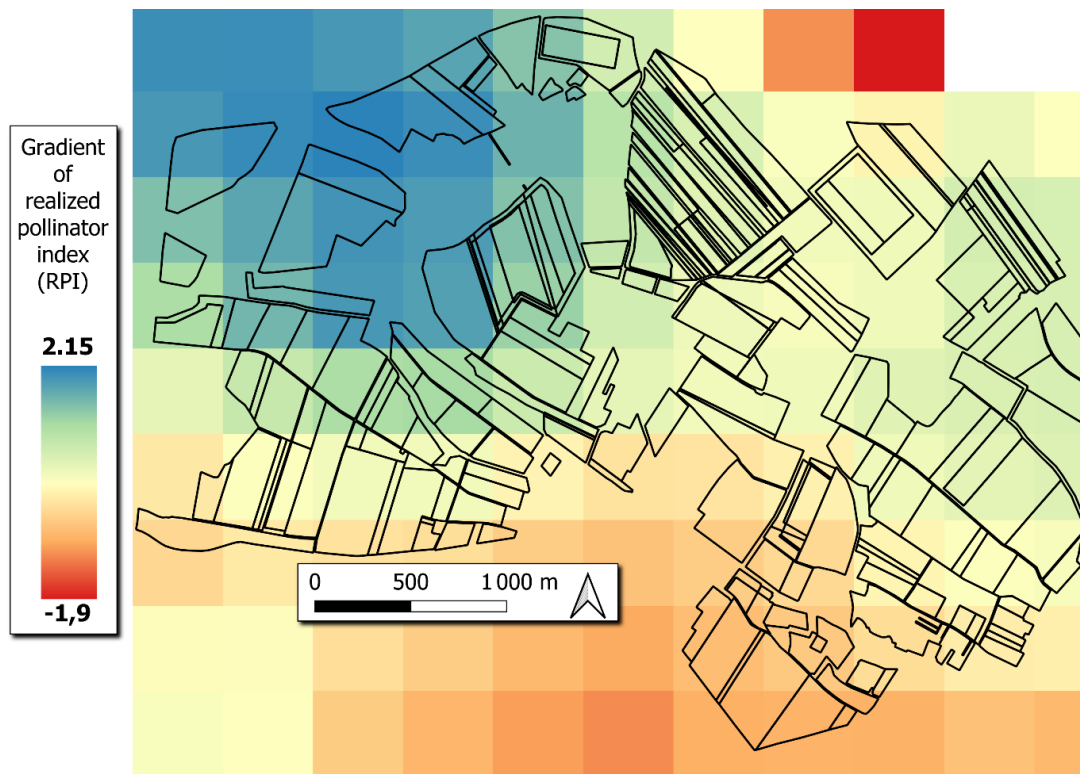


Figure S4.2. Raw map of a raster output produced using the moving window method with a resolution calculated with the 2000 m x 2000 m sliding window approach and 500 m x 500m output pixels before projection done with the weighted averages on stable plots.

5

Complementarity between pollination and biological control



Chrysura sp., © Mathieu Lachaise

Linking pollination to biological pest control: toward the assessment of multiple ecosystem services

After presenting different approaches to spatialize and estimate pollination services, we now turn to the potential relationships with biological pest control — another key ecosystem service in agricultural landscapes, which also relies on numerous insect auxiliaries. Chapter 5 focuses on the empirical assessment of both pollination and natural pest control services in oilseed rape fields (Figure 5.0). A unique aspect of our study design lies in the simultaneous implementation of two complementary field protocols, allowing us to evaluate these two ecosystem services in parallel. Over two consecutive years, we monitored plant–pollinator interactions and measured parasitism rates of key pest species, including flea beetles and pollen beetles. In addition, during one of these years, we assessed crop yield components and measured aphid colony lengths on oilseed rape plants to estimate the strength of biological pest control. This integrated approach provides a rare opportunity to explore the potential connections between pollination and pest control processes, as well as their determinants, within the same agricultural landscapes.

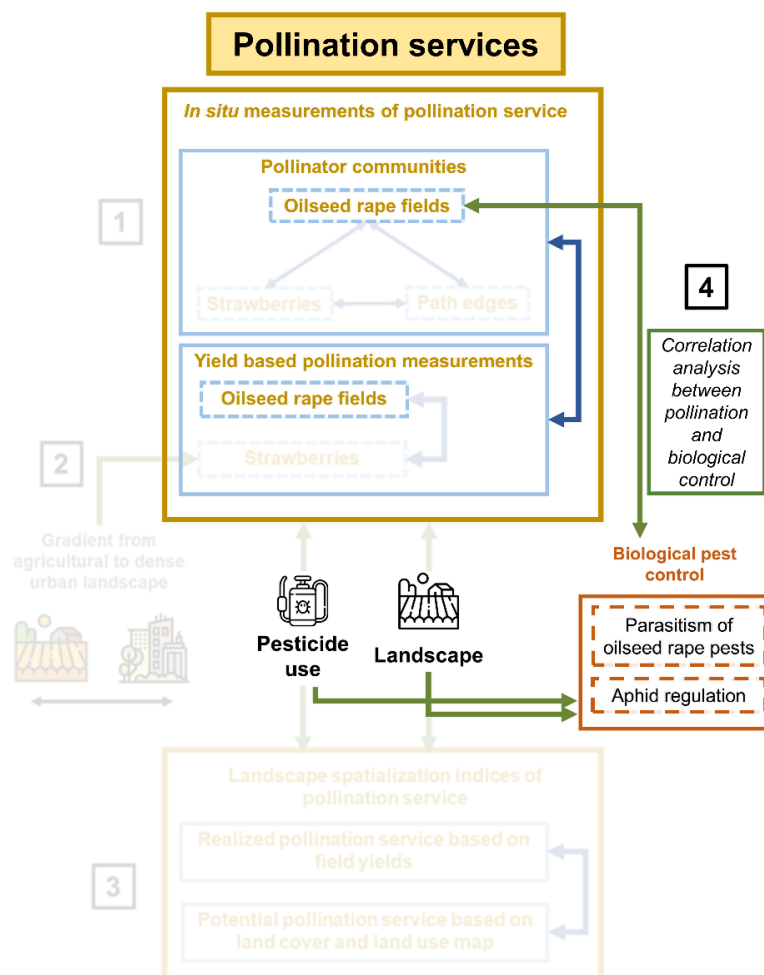


Figure 5.0. Fourth research axis within the general diagram summarizing the whole thesis.

Pollination and conservation biological control are positively correlated but driven by contrasting landscape composition and agricultural practices

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Keywords: oilseed rape; ecosystem service; pesticide; multifunctionality; parasitism; flower

Abstract

Agroecosystem sustainability relies on multiple ecosystem services, notably pollination and biological control. While these services are known to be affected by landscape composition and farming practices, how they co-vary and whether they respond to shared drivers remains unclear. In this study, we explored the landscape- and practice-related determinants of pollination and biological control services in oilseed rape fields across gradients of pesticide use and area of semi-natural elements in the Paris Basin, France. Over two years, we observed that pollination and biological control tended to co-occur, suggesting a degree of functional synergy in these intensively managed landscapes. However, these services did not respond uniformly to the different landscape and agricultural practices drivers examined in this study. Pesticide use had negative impacts, notably at the field scale, on both pollinators and natural enemies or their functions, except for aphid regulation at field scale. Landscape features were also related to pollination and biological pest control, but with contrasting effects across services: while semi-natural elements generally benefited pollinators, their influence on biological control was less consistent and sometimes even negative. The year-to-year variation in oilseed rape area across the landscape further shaped ecosystem services, but its effects differed depending on the ecosystem service considered. Altogether, our findings illustrate how different services can broadly align in outcome while responding to distinct, and sometimes

opposite, environmental drivers, underscoring the importance of context-adapted strategies, considering both synergies and trade-offs, as well as the landscape level, to support multiple ecosystem functions and promote sustainable agriculture in farmlands.

1. Introduction

In the face of the dramatic decline in biodiversity, particularly insects, in farmland (Outhwaite et al., 2022) and of the need to reduce the use of synthetic inputs in agriculture (Rani et al., 2021), agroecology offers a promising framework by integrating biodiversity-based strategies into the management of agricultural systems (Lundin et al., 2021). Agroecology encourages the design and multi-criteria management of agroecosystems (Tichit et al., 2010). This means taking greater account of the multifunctionality of agroecosystems, understood here as the ability to simultaneously provide multiple ecosystem services to agriculture and society (food production, biological control, pollination, etc.), based on interdependent processes (Manning et al., 2018; Hölting et al., 2019). Understanding the determinants of multifunctionality in ecosystem services, and promoting it, is a major scientific challenge because of the complexity of ecological interactions, trade-offs between services and dependence on common agricultural levers and landscape factors. In particular, both pollination and biological control rely heavily on biodiversity, involving groups of arthropods that likely share common drivers. For example, heterogeneous landscapes with high plant diversity in arable fields or along their borders can enhance natural enemy diversity and support pest control in oilseed crops (Schipanski et al., 2014; Morandin et al., 2016; Redlich et al., 2018; Serée et al., 2023). Preserving and improving semi-natural elements, especially those rich in flower resources is also essential for pollinators (Holland et al., 2017), thereby ensuring continuous pollination services to pollinator-dependent crops such as oilseed rape (Stanley et al., 2013). Additionally, reducing pesticide use helps maintain populations of insects providing ecosystem services (Vanbergen and Initiative, 2013; Meunier et al., 2024). Studies at the European scale showed that three service-providing taxa (birds, carabid beetles, and plants) were distinctly negatively affected by pesticide use, with reductions in species richness, abundance, and functional diversity (Emmerson et al., 2016). Pesticide use can enhance yields, particularly in cereals (Gagic et al., 2017), but reducing pesticide use and enhancing semi-natural elements can help achieve a balance that maximizes ecosystem services and farmers' incomes (Catarino et al., 2019).

Yet, although pollination and biological control often involve overlapping taxa with shared drivers, their combined effects can be additive, synergistic, or even antagonistic (Garibaldi et al., 2018). Under controlled conditions, (Gagic et al., 2019) demonstrated that negative interactions between these two ecosystem services can lead to compensatory effects, where the reduction in one is offset by the other. Although integrated pest and pollinator management plans are more and more common (Egan et al., 2020; Lundin et al., 2021; Merle et al., 2022),

we still lack knowledge to manage these services, notably on which practices and landscape configurations can simultaneously enhance both, raising the question of whether management should prioritise field-level interventions (e.g. plant cover, reduced inputs) or landscape-scale strategies (e.g. habitat connectivity) to maximise multifunctionality. It is not currently possible to answer these questions on the basis of existing knowledge, because the two services are generally measured separately from each other, or even estimated on the basis of indirect proxies, which underestimates the effects of interactions (Holland et al., 2017). This gap is particularly striking in large-scale arable systems under crop rotation, including oilseed rape, where such interactions remain poorly understood (Bartomeus et al., 2015; Garibaldi et al., 2018).

In this study, we investigated how pollination and conservation biological control, along with the abundance and diversity of the insect groups involved, are correlated and influenced by local farming practices and landscape features across an agricultural mosaic in the Paris Basin, France. In contrast to studies based on proxies or controlled experiments, we assessed both services directly in the field under real farming conditions, to better understand how they interact and what influences them. We focused on winter oilseed rape, a crop of high economic and agronomic value that is grown on 8.5 % of all European arable land (FAO 2016, in Ruser et al. 2017) and that depends on both biological control and pollination. Oilseed rape is subject to high pest pressure from insects such as pollen beetle (*Brassicogethes aeneus*, Coleoptera: Nitidulidae, Fabricius, 1775) and cabbage stem flea beetle (*Psylliodes chrysocephala*, Coleoptera: Chrysomelidae, Linnaeus, 1758). The chemical management of these pests has become more difficult since they are increasingly resistant to insecticides (Bruce, 2010; Hervé, 2018), but they can be down-regulated by specialist parasitoids (Williams, 2010; Gagnon et al., 2017; Riggi et al., 2017) and by generalist predators (Ekbom, 2010). The latter are sufficiently widespread and abundant across Europe to be of potential importance for the conservation biological control of these target pests (Ulber et al., 2010). In addition, oilseed rape is a mass-flowering crop highly attractive to pollinators, with a pollinator dependence estimated at 27% on average, but varying across varieties (Siopa et al., 2024). However, insecticide applications—particularly those targeting inflorescence herbivores such as pollen beetles during the flowering period—can have deleterious effects on pollinators (Mänd et al., 2010). Understanding the joint provision of services such as pollination and biological control is key to developing effective, biodiversity-friendly management strategies that support both yield optimization and input reduction, contributing to more sustainable and resilient oilseed rape production.

As described above, despite increasing efforts to promote integrated pest and pollinator management, a clear understanding of how multiple services interact is still lacking. To determine whether pollination and biological control services share common ecological drivers

or respond independently to landscape and practices variability within a single intensive farming context, we addressed the following questions: (i) To what extent are pollination and biological control services correlated? We hypothesized a positive correlation between pollination and pest control, as both services depend on floral resources and on suitable habitats to complete the life cycles of their providers; (ii) Which landscape variables and farming practices influence their provision in intensively managed croplands? We expected reduced pesticide use and increased area of semi-natural elements to enhance all ecosystem services provision, particularly for pollination, as widely supported in the literature. (iii) How do these services covary with oilseed rape yields at the field scale? We predicted that promoting ecosystem services through less input-intensive practices could partly offset potential yield losses.

2. Material and methods

2.1 Selection of study fields

The study was conducted in 2023 and 2024 in the south-western part of the Paris Basin (Yvelines, Essonne, and Eure-et-Loir administrative departments). The landscape is characterized by a large-scale mosaic of arable crops with a few scattered semi-natural elements. A total of 41 oilseed rape fields, distributed in four distinct areas, were selected across two uncorrelated gradients of (1) percent semi-natural elements in the surrounding landscape within 1000 m of the focal fields and (2) pesticide use in the field, obtained from farmer interviews (Figure 5.1). These gradients were chosen on the basis of the known influence of landscape and pesticide use on the dynamics of pollinator and natural enemy populations. Among the 41 fields monitored for pollinators (20 in the first year and 21 in the second), 39 were also surveyed for pollen beetles (20 in the first year and 19 in the second), 37 for flea beetles (20 in the first year and 17 in the second), and 20 fields in the first year were additionally monitored for aphid colonies and yield components. Note that the oilseed rape fields were not the same across the two years due to crop rotation.

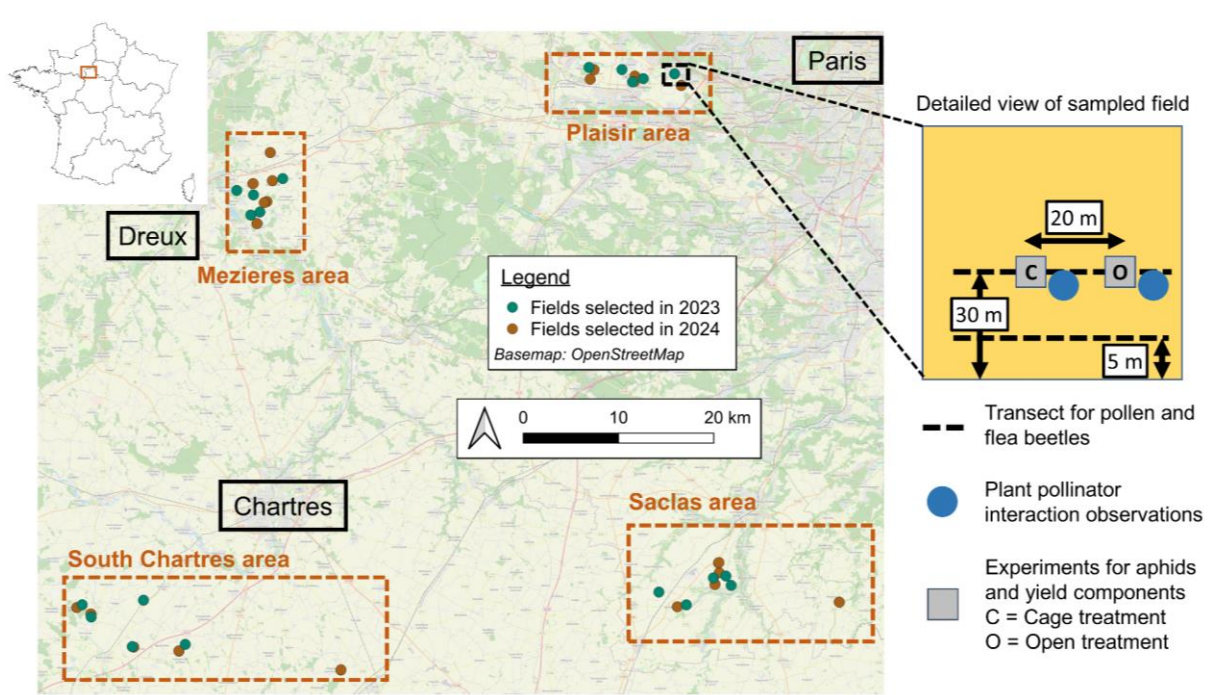


Figure 5.1. Location of study sites clustered into four main areas, and detailed view of the within-field sampling design for 2023. Field measurements include insect-proof cages, observations of plant-pollinator interactions, and flea beetle and pollen beetle larval sampling along transects placed at 5 m and 30 m from the field edge.

2.2 Measurement of pollination services

2.2.1 Pollination assessed through plant–pollinator interactions

Pollination services were evaluated by assessing the ecosystem capacity to support pollination (Bartholomée and Lavorel, 2019). The pollination service supply capacity was defined based on the organisms responsible for the pollination function, focusing on both the diversity of pollinator groups and their interactions with plant reproductive structures. Pollinator observations were carried out within oilseed rape fields, 30 meters from the field edge. At each location, two 2 m × 2 m quadrats were placed, spaced twenty meters apart, in areas representative of the overall floral density.

In each quadrat, each observation lasted 5 minutes and was conducted under standardized weather conditions during the oilseed rape flowering period (March to May): sunny conditions with temperature above 12°C, and average wind speed ≤ 20 km/h. In 2023, data were collected over three sessions between April 5th and May 5th, totalling 120 observations (20 fields × 2 quadrats × 3 sessions). In 2024, due to weather constraints, only two sessions were conducted between March 20th and April 29th, resulting in 80 observations (20 fields × 2 quadrats × 2 sessions).

During observations, all interactions between a pollinator (*sensu lato*, i.e. all flower visitors, including parasitoids), visually identified and assigned to a morphogroup, and the reproductive parts of a flower were recorded. The 13 morphogroups were: small wild bees (less than 1 mm), large wild bees, honey bees, bumblebees, wasps, parasitoid Hymenoptera (individuals akin to *Tersilochus spp.* targeting oilseed rape pests), other Hymenoptera, hoverflies, bee-flies, other Diptera, beetles, butterflies, and other pollinators, excluding interactions with pollen beetles. We calculated the total floral area for each quadrat as the product of the number of floral units and the average floral unit area, measured directly in the field. To obtain the average floral unit area, we measured the diameter of 20 oilseed rape flowers using a digital calliper and approximated each flower as a circle to calculate their floral area.

2.2.2 Pollination and aphid regulation assessed through direct measurement of oilseed rape yields components

The effect of ecosystem service providers (pollinators and natural enemies of aphids) on oilseed rape yields was estimated in each field using exclusion cages in 2023. Two cages covering 2.25 m² (1.5×1.5 m) were set up in each field at the beginning of oilseed rape flowering. One cage was fully closed with a mesh excluding all insects (0.3 mm PVC mesh); the other served as a control, with the mesh only on top of the cage to ensure the same shading conditions as in the insect exclusion treatment, while allowing free pollinator and natural enemy visits on the sides. As with the quadrats, cages were placed 10 ± 5 m apart and 30 ± 5 m from the field edge (Figure 5.1), depending on farmers' requirements for tractor passage. The cages were removed at the end of flowering early May, and their locations were marked. All oilseed rape plants within cages were harvested at the end of their cycle, i.e. mid-June. Yield components were measured on oilseed rape plants sampled within 1 m² plots from 20 fields, under two treatments: insect exclusion cages and open control zones (40 samples in total). Each sampled plant was classified into one of three size categories: small, medium, or large based on overall plant size (stem diameter and number of ramifications). In cases where the number of plants within the 1 m² plot was too high to allow for complete measurement within the allocated time, a total subsample of 10 to 15 plants selected proportionally to their relative abundance in the plot was retained. Subsequently, for each branch and sub-branch of the selected plants, yield-related traits were recorded, including the number of full siliques, short and long pedicels, aborted siliques (with no or underdeveloped seeds), as well as the siliques shattered during transportation. The yield components were used to estimate flower abundance for each branch by summing all structures associated with a flower, namely all siliques and pedicels regardless of their reproductive success. The length of aphid colonies was also measured for each branch. Plants were then oven-dried for 48 hours at 80 °C to measure overall yield components for each treatment on each field: total dry biomass, number of seeds per silique, thousand-grain weight

—collected just before harvest to ensure full seed filling—. We then compared the yield components in the modalities 'with' vs. 'without' insect exclusion (see “Statistical analyses”).

2.3 Measurement of pest biological control

Conservation biological control was assessed for three major pests of oilseed rape: cabbage stem flea beetles (*Psylliodes chrysocephala*), pollen beetles (*Brassicogethes aeneus*), and cabbage aphids (*Brevicoryne brassicae*).

2.3.1 Parasitism of cabbage stem flea beetle larvae

In early April, late-stage flea beetle larvae were collected from the leaf petioles at the base of oilseed rape plants, at 5 and 30 m from the field edge, along a transect until 100 larvae at least were collected, when possible. The 30-m-transects overlapped with the pollinator observation points, allowing for spatial correspondence between herbivore and pollinator data. A total of 20 fields were monitored in 2023 and 17 in 2024 due to differences in workforce between the two years. The larvae were placed in one rearing box per field and per distance, where they spontaneously burrowed for pupation; those remaining on the surface after five days were removed from the boxes. The boxes were incubated at room temperature (20-25°C). After about three weeks, non-parasitized flea beetles emerged and were counted. Rearing boxes were stored at room temperature until autumn, then placed in a cold room (5°C) for four months to simulate winter conditions. The boxes were then re-incubated at room temperature. After five days and over the next two months, parasitoid emergence was monitored daily. To stimulate parasitoid emergence, boxes were re-cooled for a month and then monitored again. The parasitism rate per transect was calculated as the number of emerged adult parasitoids divided by the total number of emerged adult flea beetles plus parasitoids recovered.

2.3.2 Parasitism of pollen beetle larvae

At the end of the oilseed rape flowering period in each field (late April), at least 100 larvae at their final development stage (> 4 mm) were collected whenever possible, within oilseed rape flowers along two transects at the same location as flea beetle larvae collection, i.e. at 5 and 30 m from the edge. A total of 20 fields were monitored in 2023 and 19 in 2024 different fields sampled for each protocol. Collected larvae were preserved in 70% ethanol for later analysis in the laboratory. To assess parasitism, larvae were examined under a binocular microscope to detect the presence of one or more parasitoid eggs, which are visible through the larvae body (eggs of *Tersilochus heterocerus*, the dominant parasitoid in the area). Parasitism rate within each transect was calculated as the number of pollen beetle larvae containing at least one parasitoid egg divided by the total number of larvae examined. Priority was given to examining

large larvae (4 mm), but medium-sized (3 mm) larvae were also examined when the number of large larvae was insufficient.

2.3.3 Regulation of cabbage aphid populations

To assess the role of insect predators and parasitoids in aphid regulation, we compared the length of aphid colonies on oilseed rape plants grown under exclusion vs. open cages. Colony length was measured on each branch of the selected plants as explained in section 2.2.2. Exclusion cages prevented access by natural enemies, allowing us to estimate the impact of biological control on aphids by comparing treatments. For statistical analyses, the total colony length per plant was calculated by summing the lengths measured on all individual branches, providing an integrative measure of aphid pressure at the whole-plant level. In our analyses, we focused on within-field comparisons, using the closed cage treatment as a reference representing the potential maximum aphid pressure, and the open cage treatment to assess the reduction in aphid pressure potentially attributable to biological control by natural enemies.

2.4 Description of landscape and farming practices

We selected landscape and farming practices variables known from the literature to influence pollination and biological control services. To quantify landscape composition, we defined three buffer sizes (500 m, 1000 m, and 2000 m) around the observation points in the studied fields. The percent cover of semi-natural elements was derived from two complementary sources: BD TOPO® (available at <https://geoservices.ign.fr/bdtopo>) was used to extract woody semi-natural elements such as forests, shrublands, and hedgerows, while herbaceous elements, including fallows and grasslands, were obtained from the Land Parcel Identification System (LPIS, available at <https://geoservices.ign.fr/rpg>). By merging these layers, we calculated the total area of semi-natural elements. Oilseed rape cover from the previous year was included, as it is known to influence both the emergence of parasitoid wasps (by providing overwintering hosts) and wild pollinator activity and reproduction (Beyer et al., 2021; Van der Meersch et al., 2022). The previous year area of other mass-flowering crops (see Table S5.1) was also extracted from the LPIS, as they may provide important resources that benefit pollinator populations (Beyer et al., 2021). This information was extracted from the LPIS. We also retrieved data on oilseed rape cover for the sampling year: in 2023 from the LPIS, and in 2024 by analysing aerial imagery from the Sentinel program (available at <https://apps.sentinel-hub.com/eo-browser/>), because the LPIS data was not available yet. Pesticide input for each studied field was quantified from application data obtained through surveys conducted with each farmer overseeing the study fields. Pesticide use was quantified using the treatment frequency index, computed as the cumulative dose of each active substance applied throughout the crop cycle (from the previous to the current crop harvest), divided by the maximum

authorized dose under French national guidelines. In addition, landscape-level pesticide use was estimated at the municipality scale using data provided by Solagro (available at <https://solagro.org>), with the same unit (treatment frequency index) as for field-level pesticide use. A weighted average based on the area of each municipality within the three buffer sizes was calculated to obtain an overall estimate of pesticide use in the landscape.

2.5 Statistical analyses

2.5.1. Correlation among pairs of services

As a preliminary step, we estimated the overall value of each ecosystem service in each field, accounting for repeated measurements under varying observation conditions and controlling for relevant covariates. Differences in sampling protocols among services were also taken into account. To this end, each service proxy was modelled using (generalized) linear mixed-effects models fitted with the “lme4” package (Bates et al., 2015), including appropriate covariates and a random intercept for field identity. Within this generic procedure, each proxy of services was modelled with a different approach and covariates, as described below. We then extracted the random effects of each field, together with their standard errors, using the “ranef” function and Best Linear Unbiased Predictors (BLUPs). These corrected estimates of field-level services were used to compute pairwise Spearman’s rank correlations between services on the different fields we studied, weighted by the inverse of their associated standard errors to account for differences in precision.

For the rates of parasitism of flea beetles and pollen beetles a binomial error distribution was used as in (Serée et al., 2023), with the number of parasitized and non-parasitized larvae treated as "successes" and "failures". For flea beetle parasitism, the model was the following:

$$(1) \text{logit}(p_{ijk}) = \text{mean} + Y_i + D_j + a \times \text{Sampling date}_{ijk} + F_k$$

where p_{ijk} is the proportion of parasitized flea beetle larvae in year i at distance j for field k , mean is the intercept, Y is a fixed categorical year effect (2023 and 2024), D a fixed categorical distance effect considered (5m and 30m), Sampling Date corresponds to the date of larval collection, expressed in scaled Julian days starting from January 1st. F_k is a random intercept accounting for unmeasured variation specific to field k , assumed to follow a normal distribution with zero mean and variance σ_F^2 across all fields.

For pollen beetles, the following model was used:

$$(2) \text{logit}(p_{ijkl}) = \text{mean} + Y_i + D_j + S_l + c \times \text{Sampling date}_{ijkl} + F_k$$

where p_{ijkl} is the proportion of parasitized pollen beetles larvae in *year i*, at *distance j*, collected at *stage l*, in field *k* *mean* is the intercept, *Y* is a fixed categorical year effect (2023 and 2024), *D* a fixed categorical distance effect (5m and 30m), *S* is a fixed effect of larval stage (L2 and L3), *Sampling date* corresponds to the date of larval collection, expressed in scaled Julian days starting from January 1st. F_k is a random intercept accounting for unmeasured variation specific to field *k*, assumed to follow a normal distribution with zero mean and variance σ_F^2 across all fields.

For aphids, models included a fixed cage effect, and a random effect of field on this cage effect; the latter was used to estimate the regulation services occurring between the exclusion-cage and open treatments within each field. We also controlled for plant size, estimated from the number of flowers, based on the total count of siliques and pedicels. We assumed a Poisson distribution of aphid colony length, which provided the best fit according to diagnostic plots. Although aphid regulation was measured via the length of aphid colonies rather than direct counts of individual aphids, colony length serves as a proxy for the number of aphids, reflecting count-based data through the presence and estimated abundance of aphids.

$$(3) \log(\text{Aphid}_{ijk}) = \text{mean} + a \times \text{Flower per plant}_{ijk} + b \times \text{Sampling date}_{ijk} + CF_{jk}$$

where Aphid_{ijk} is the mean rounded length of aphid colonies on each plant *i* for cage treatment *j* in field *k*, *mean* is the intercept, *flower per plant* is an estimation of plant size via the total number of flowers, including those that aborted, *sampling date* corresponds to the scaled date of larval collection, expressed in Julian days starting from January 1st 2023. CF_{jk} is a random effect of field *k* on the cage treatment effect, estimating one difference in aphid colony size between the open and caged treatments in each field; it is assumed to follow a normal distribution with zero mean and variance σ_{CF}^2 .

For pollination, we computed two indices of visitation of oilseed rape flowers, defined as the total number of insect-flower interactions observed within 10 minutes: one including all observed floral visitors (hence incorporating honeybees), and another restricted to wild pollinators. For statistical analyses, the sampling unit was the observation session. Observations from the two quadrats surveyed in parallel were pooled to form a single sampling event, corresponding to a 10-minute observation over 8 m². Total floral area and pollinator-flower interactions were both summed across quadrats to avoid spatiotemporal autocorrelation and reflect total activity per session.

Pollinator indices were modelled using generalized linear mixed-effects models with a Poisson distribution. Control variables included weather conditions (temperature, wind), Julian day, and total floral area, as follows:

$$(4) \log(\text{Pollinator}_{ijk}) = \text{mean} + Y_i + a \times \text{Sampling date}_{ijk} + b \times \text{Floral area}_{ik} \\ + c \times \text{Wind}_{ijk} + d \times \text{Temperature}_{ijk} + e \times \text{Hour}_{ijk} + F_k$$

where Pollinator_{ijk} is the mean number of pollinator visits recorded at year i and sampling date j in field k , associated with a given floral area, wind speed, temperature and hour; mean is the model intercept, Y is a fixed categorical year effect accounting for interannual variation in pollinator activity (2023 and 2024), sampling date is the scaled Julian day of sampling starting from January 1st, Floral area is the floral area measured during the observation session, Wind is the wind speed during the observation session, Temperature is the temperature during the observation session, Hour is the decimal hour of the observation session. F_k is a random intercept accounting for unmeasured variability associated with each field, assumed to follow a normal distribution with zero mean and variance σ_F^2 .

2.5.2. Landscape and practices effects on ecosystem services

To examine the second question about which landscape and practices variables influence ecosystem services, we tested the relationships between landscape variables or agricultural practices on one hand, and biological control and pollination on the other hand. Here, we focused exclusively on wild pollinators, as data on the location of managed honeybee hives were unavailable and we assumed that the presence of honeybees in fields was primarily driven by hive placement decisions rather than by landscape composition variables. Starting from the raw data collected for each ecosystem service, we fitted generalized linear mixed-effects models that included the full set of explanatory variables described above in section 2.5.1 plus one additional variable related to in-field practices, namely treatment frequency index, as well as five variables describing landscape characteristics : mean treatment frequency index in the landscape, total area of semi-natural elements, oilseed rape cover in the year of sampling, oilseed rape cover in the previous year, and total area of other mass-flowering crops in the previous year.

All these numerical variables were scaled in the models. Landscape composition was assessed at multiple spatial scales (500 m, 1000 m, and 2000 m buffers), and all models were adjusted for relevant control variables, such as sampling date and meteorological conditions, as detailed previously. In contrast to previous models, we chose to use the “glmmTMB” package (Brooks et al., 2025) to fit the models examining relationships with practices and landscape variables. Compared to “lme4”, “glmmTMB” provided better model fit when using negative binomial distribution to incorporate landscape and practices variables. For wild pollinator visitation and aphid abundance, we used a negative binomial model with “nbinom1” variance structure, based on dispersion diagnostics and model comparisons. We used a negative binomial GLMM to

account for overdispersion and improve model fit. Marginal and conditional R-squares were estimated using the *r2* function of the package “*performance*”.

2.5.3. Effect of aphid regulation and pollination on yields

To assess the effect of aphid regulation and of pollinators on crop yield, while correcting yield by the estimated initial flower abundance, we used a partial regression approach. We first calculated the difference in yield (Y , g m^{-2}) between open and caged treatments, using the formula:

$$Y = N \times S \times P$$

where N is the number of filled siliques per square meter, S is the mean number of seeds per silique and P is the thousand seed weight (g). We then extracted the residuals from a linear model in which the difference in yields was explained by the initial difference in flower abundance between open and caged treatments, with the following equation: $DY_i = \text{mean} + a \times DF_i + \varepsilon_{DY_i}$

where DY_i is the difference in yields, and DF_i the difference in flower abundance, between the open and caged treatments for a *field i* and ε_{DY_i} is a residual variation in yield. Residuals ε_{DY_i} were then used as a corrected measure of yield variation and regressed against the total pollination visitation index and aphid regulation (see 2.5.1) using the following linear regression:

$$\varepsilon_{DY_i} = \text{mean} + a \times \text{Aphid Effect}_i + b \times \text{Pollinator Effect}_i + \eta_i$$

where Aphid Effect_j is the effect of aphids regulation and $\text{Pollinator Effect}_j$ the effect of pollinators in *field i* and η_i are the residuals of the model, assumed to follow a Gaussian distribution with mean 0 and variance σ_F^2 .

2.5.4. Model diagnostics

Model diagnostics were conducted using the “DHARMA” package (Hartig et al., 2024) to evaluate residual patterns. The “performance” package (Lüdtke et al., 2025) was used to detect potential overdispersion with the function “check_overdispersion”, and multicollinearity among explanatory variables was examined using variance inflation factors (VIFs) calculated with the “check_collinearity” function. All VIF values were below 5, except in the aphid model, with VIF values up to 7.5, which likely results from the inclusion of interaction terms, inherently inducing collinearity with main effects. Nonetheless, these values remain within acceptable thresholds and do not compromise model validity. In addition, spatial

autocorrelation of residuals was tested using Mantel test using the “vegan” package (Oksanen et al., 2025), and no significant residual spatial structure was detected ($P > 0.05$ in all models).

The interpretation of significance levels will follow ranges that approximately translate the P-value into the language of evidence (Muff et al., 2022)

3. Results

3.1 Correlations among ecosystem services

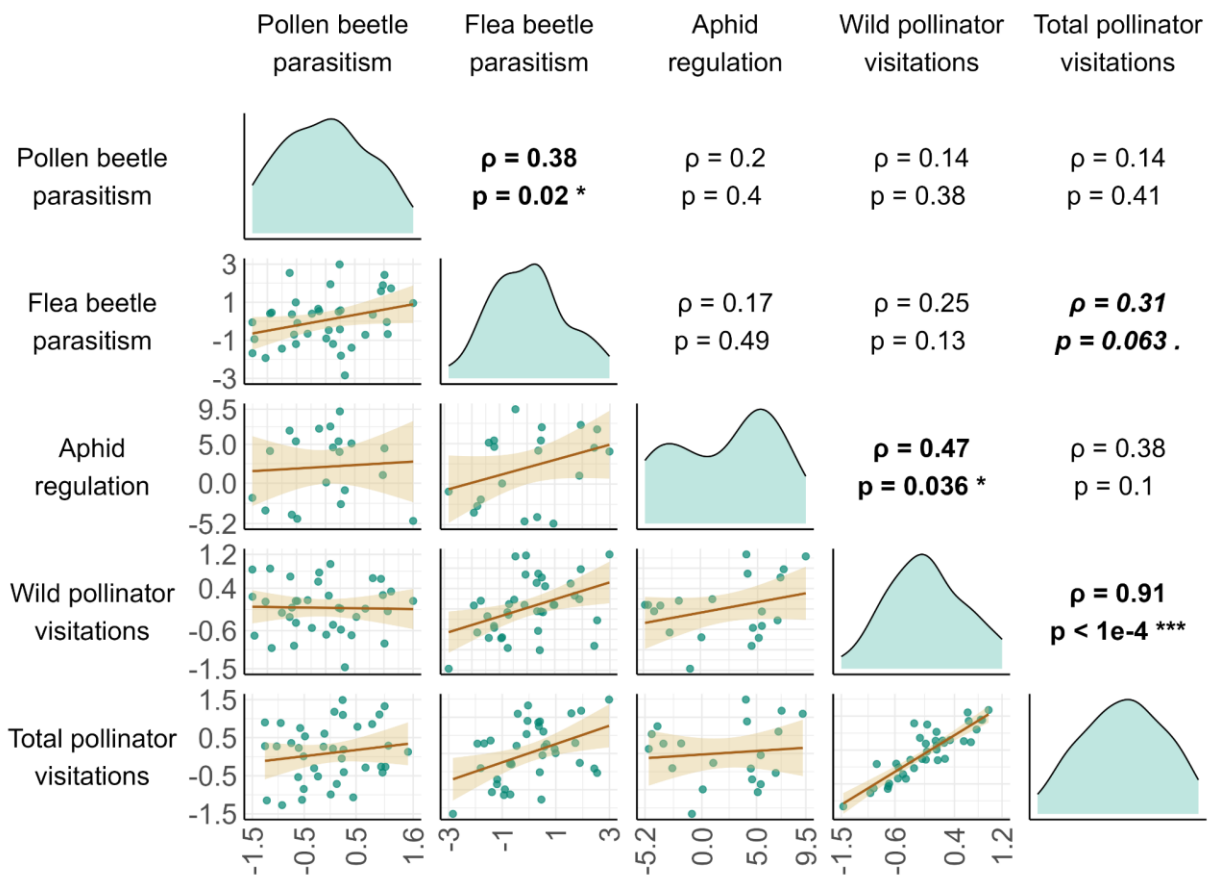


Figure 5.2. Pairwise correlations between ecosystem service indicators at the field level, corrected for control variables. Each variable (flea beetle parasitism, pollen beetle parasitism, aphid regulation, wild pollinator abundance, and total pollinator abundance) was adjusted for control variables to obtain standardized field-level indices. Pairwise Spearman correlations (ρ), weighted by the standard error of each service estimate, are shown in the upper triangle, with p-values. The lower triangle displays unweighted linear regressions to visualize general trends. Each circle represents one field. Diagonal panels show density histograms for each service indicator.

Pairwise correlations among variables related to ecosystem services—flea beetle parasitism, pollen beetle parasitism, aphid regulation, wild pollinator abundance, and total pollinator abundance—were all positive (Figure 5.2), suggesting that environments supporting natural enemies may also support pollinators, albeit with varying from little to moderate evidence. Notably, aphid regulation was positively associated with pollinator visits (measured as wild or total pollinator abundance), with correlation coefficients exceeding 0.38 and a significant correlation between aphid regulation and wild pollinator interaction abundance with moderate evidence ($\rho = 0.47$, $p = 0.036$). The positive correlation between flea beetle parasitism and total pollination interactions on oilseed rape exhibited weak evidence ($\rho = 0.31$, $p = 0.063$). Furthermore, biological control services were positively interrelated: flea beetle and pollen beetle parasitism were significantly correlated, with moderate evidence ($p = 0.02$) supporting their association.

3.2. Influence of agricultural practices and landscape components on ecosystem services

Pollination and biological control services were related to farming practices, as well as to landscape variables regardless of buffer size, but the identity of environmental correlates and the direction of correlations varied across services (Table 5.1 for a summary of the effects of landscape and field-level variables on multiple ecosystem services for a 1000 m buffer radius). At field scale, we found strong evidence that both wild pollinator interactions ($\beta = -0.32 \pm 0.01$, $p = 0.0012$) and that parasitism rate of flea beetles ($\beta = -0.62 \pm 0.24$, $p = 0.01$) were negatively associated with pesticide use. In contrast, pesticide use had no significant effect on pollen beetle parasitism ($p = 0.79$), but was positively associated with aphid regulation with moderate evidence ($\beta = 0.71 \pm 0.29$, $p = 0.014$).

At landscape scale, mean pesticide use within a 1-km radius was moderately negatively related to wild pollinator interactions ($\beta = -0.29 \pm 0.12$, $p = 0.019$) and aphid regulation ($\beta = -1.02 \pm 0.41$, $p = 0.012$), but did not show any significant association with parasitism rates of either flea beetles ($p = 0.39$) or pollen beetles ($p = 0.19$). Regarding semi-natural elements (SNE), we found a strong positive relationship between total SNE cover (woody and herbaceous) and wild pollinator interactions ($\beta = 0.29 \pm 0.10$, $p = 0.0033$). Pollen beetle parasitism was negatively associated with SNE ($\beta = -0.39 \pm 0.13$, $p = 0.002$), particularly with woody areas (Table S5.10), an association that received little evidence for flea beetles (-0.453 ± 0.26 , $p = 0.075$, mostly driven by grassland area, Table S5.13) and that was not significant for aphid regulation ($p = 0.45$). Finally, area of oilseed rape in the current year was strongly positively associated with aphid regulation ($\beta = 1.91 \pm 0.41$, $p < 0.001$), but not with other services. Oilseed rape area in the previous year had a moderate positive effect on flea beetle parasitism ($\beta = 0.57 \pm 0.25$, $p = 0.022$), but no clear effect on wild pollinator interactions or

other services. No significant effects of the area of other mass flowering crops in the previous year were detected. Results for the other tested buffer distances (500 m and 2000 m) showed similar patterns and are provided with full model outputs for 500, 1000, and 2000 m buffers in supplementary tables S5.2 to S5.16.

Table 5.1. Summary of the relationships between pollination or biological control services and environmental variables, namely pesticide use and landscape composition. The estimates and P-values were extracted for comparative purposes from full models that differed across services; their complete outputs are provided in supplementary Tables S5.2 to S5.16. Values are presented as estimates $\pm$ standard error. R_C^2 and R_M^2 represent marginal and conditional R-squared values, respectively.

Explanatory variables (1000m radius)	Wild pollinator interactions	Flea beetle parasitism	Pollen beetle parasitism	Aphid regulation
Treatment frequency index (field level)	-0.32 $\pm$ 0.01 p=0.0012	-0.62 $\pm$ 0.24 p=0.01	-0.03 $\pm$ 0.1 p=0.79	0.71 $\pm$ 0.29 p=0.014
Treatment frequency index in the landscape	-0.29 $\pm$ 0.12 p=0.019	-0.27 $\pm$ 0.31 p=0.39	0.2 $\pm$ 0.15 p=0.19	-1.02 $\pm$ 0.41 p=0.012
Total SNE area (woody and herbaceous)	0.292 $\pm$ 0.1 p=0.0033	-0.453 $\pm$ 0.26 p=0.075	-0.39 $\pm$ 0.12 p = 0.002	0.18 $\pm$ 0.24 p=0.45
Oilseed rape area of the current year	0.04 $\pm$ 0.1 p = 0.7	-0.3 $\pm$ 0.26 p=0.25	0.09 $\pm$ 0.13 p=0.46	1.91 $\pm$ 0.41 p< 10⁻³
Oilseed rape area of the previous year	0.15 $\pm$ 0.1 p = 0.14	0.565 $\pm$ 0.25 p=0.022	-0.04 $\pm$ 0.12 p=0.76	-0.37 $\pm$ 0.23 p=0.11
Flower crop area of the previous year (excluding oilseed rape)	0.03 $\pm$ 0.1 p = 0.75	0.057 $\pm$ 0.23 p=0.81	-0.13 $\pm$ 0.11 p=0.36	0.351 $\pm$ 0.31 p=0.26
R ²	R_C^2 : 0.62	R_C^2 : 0.987	R_C^2 : 0.963	R_C^2 : 0.999
	R_M^2 : 0.61	R_M^2 : 0.669	R_M^2 : 0.563	R_M^2 : 0.675

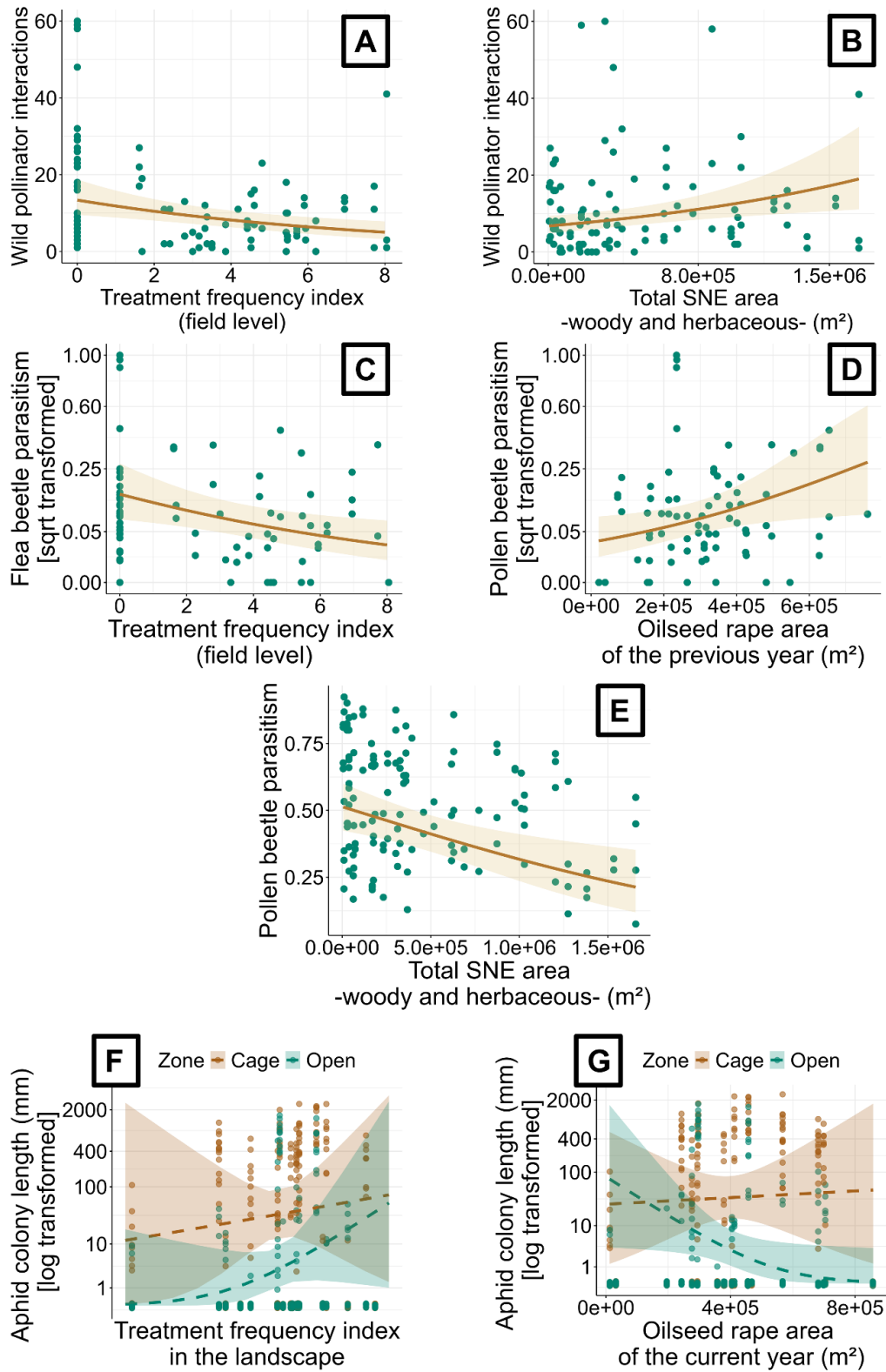


Figure 5.3. Modelled effects of farming practices and landscape variables on ecosystem services proxies.

Predicted marginal effects (solid lines) and 95% confidence intervals (shaded areas) derived from GLMM, illustrating the influence of landscape variables and farming practices on ecosystem services. Observed values (proportions or counts) are overlaid to model regressions. Aphid regulation is estimated as the difference in aphid colony length responses to environmental variables between the open and cage treatments. Panels F and G illustrate how environmental variables differentially affect aphid colony length under the two treatments, with significant regulation effects emerging from this difference.

3.3. Pollination and aphid regulation impacts on yield

Neither aphid regulation nor total pollinator visitations were significantly associated with plant size-corrected yields (Table 5.2, Figure 5.4).

Table 5.2. Summary of partial regressions linear models of the relationship between aphid and pollinator abundance and yield residuals after plant size correction.

Predictor	Estimate	SE	t	p-value
Aphid regulation	-1.458	5.571	-0.262	0.799
Total pollinator abundance	33.340	29.603	1.126	0.276

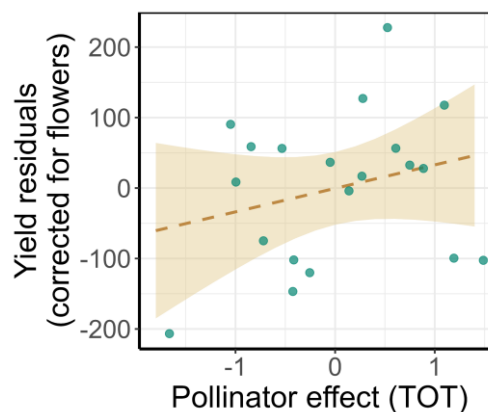


Figure 5.4. Partial regression showing the relationship between plant size-corrected yield and the number of interactions between pollinators and oilseed rape flowers. Predictions were obtained from the linear model fitted on yield residuals (corrected for flower abundance). Dots represent original observation points.

4. Discussion

Overall, we found positive correlations between pollination services and biological control, suggesting that ecological contexts favouring one service often support the other as well, but

these correlations were not always significant. The moderate strength of these associations indicates that the relationships were not systematic and may vary depending on landscape composition and on farming practices. Notably, while pesticide use was a shared driver weakening several services (Table 5.1), landscape variables had more contrasting effects. Taken together, these results highlight the complexity of managing multiple ecosystem services in agroecosystems, but also point to the potential of agroecological solutions to foster both pollination and conservation biological control through integrated landscape design at different scales (Gonthier et al., 2014).

4.1. Farming practices and landscape drivers and their contrasting effects on ecosystem services

4.1.1. A consistent negative effect of pesticide use

Across all ecosystem services except aphid regulation, field-level pesticide use emerged as a negative driver. Pollinator activity seemed to be strongly reduced when pesticide use increased, a pattern consistent with previous findings (Guzman et al., 2024). Similarly, there was moderate evidence that flea beetle parasitism declined with increasing pesticide pressure, supporting the starting point of Integrated Pest Management, which acknowledges the detrimental effects of agricultural intensification on natural pest control (Ortega-Ramos et al., 2022; Li et al., 2024). These assessments are consistent with larger concerns over the impact of chemical inputs on a large panel of non-target organisms (Wan et al., 2025). In particular, pesticide use can drastically reduce pollinator abundance and diversity (Bloom et al., 2021), and similarly affect parasitoids (Brandes et al., 2018), both through direct lethal toxicity (Banks et al., 2020) and through sub-lethal effects that alter insect behaviour (Stanley et al., 2015a; Balbuena et al., 2015). The results were more nuanced for aphid regulation: field-level pesticide use has a positive impact on regulation, which could be due to a lower penetration of pesticides, especially insecticides, in cages than in open pollination treatments.

At a landscape scale, pesticide use was negatively associated with wild pollination and aphid regulation. This negative impact emphasizes the outcomes of chemical control at the landscape scale on pollinators (C. A. Brittain et al., 2010a; Nicholson et al., 2024b) and on natural enemies such as hoverflies which can be both pollinators and aphid predators (Ricci et al., 2019). Therefore, agricultural techniques allowing reduced pesticide use at different spatial scales such as intercropping (Verret et al., 2017) and the implementation of flower strips (Serée et al., 2023) should improve ecosystem services delivered by biodiversity (Kovács-Hostyánszki et al., 2017; Lundin et al., 2021; Perrot et al., 2025). Furthermore, developing more accurate metrics of pesticide use at landscape scale, including the identification of active substances,

would provide a finer understanding of how pesticides can shape biodiversity at the field scale and influence community dynamics across landscapes (Carozzi et al., 2024).

4.1.2. Semi-natural elements have more contrasting effects on pollination vs. biological control services

Semi-natural elements are expected to provide valuable resources for insects delivering ecosystem services in agricultural landscapes, even if these benefits can be hampered by pesticide use (Ricci et al., 2019). Semi-natural elements had a strong positive influence on wild pollinator activity in the fields, in line with previous research highlighting their role in providing key nesting and foraging habitats (Steffan-Dewenter et al., 2002; Hevia et al., 2021; Eeraerts, 2023; Rivers-Moore et al., 2023). The response of biological control services to landscape elements was more complex. Flea beetle parasitism showed no clear pattern, while pollen beetle parasitism rates were negatively associated with semi-natural elements area—an effect largely driven by a few fields surrounded by horse-grazed meadows providing few floral resources (personal observations, Figure S5.1). Another explanation would be that meadows can act as overwintering sites for pollen beetles without enhancing parasitoids (Sutter et al., 2018b).

These apparent divergent responses between pollination and biological control services may reflect basic ecological differences. Pollinators directly benefit from the resources provided by semi-natural elements, whereas parasitism may be indirectly diminished by the positive effects of the same elements on pest populations themselves. Flea beetles can use semi-natural elements for estivation, and pollen beetles overwinter there, which can lead to higher local pest densities and thus potentially reduce parasitism rates near these habitats (Berger et al., 2018; Seree, 2022; Pigot et al., 2024). Here, only parasitism rates were measured, without accounting for pest pressure, which is itself often enhanced by semi-natural elements. While many studies report overall positive effects of semi-natural elements on the parasitism of oilseed rape pests (Rusch et al., 2011; Sutter et al., 2018b) via the provision of trophic resources (Gardarin et al., 2021), these effects seem not to be universal (see Ratsimba et al., 2022) and may depend on the dynamics of pest and parasitoid populations. Nevertheless, a weak (though non-significant) positive relationship between pollination and pollen beetle parasitism was observed at the field scale, suggesting complementarity between the two services despite different responses to semi-natural elements (Lundin et al., 2021).

4.1.2. Limited role of oilseed rape and other mass flowering crops in inter-annual continuity

Across the different ecosystem services measured, their relationship with the area of oilseed rape and other mass flowering crops in the landscape, in previous vs. current year varied in

both direction and magnitude, revealing contrasting underlying ecological processes. Flea beetle parasitism increased in landscapes where oilseed rape had been grown the previous year, suggesting that interannual continuity in crop distribution can support their natural enemies. In contrast, we found no significant effect of previous-year oilseed rape on pollinators, aphid regulation, or pollen beetle parasitism. However, previous studies suggested that such continuity may still enhance pollinator resources (Riedinger et al., 2015; Van der Meersch et al., 2022) or support the overwintering of natural enemies (Rusch et al., 2012), pointing to a potentially broader role of interannual dynamics depending on the species and context. Interestingly, aphid regulation was strongly positively associated with the current-year oilseed rape cover. This pattern may possibly reflect a dilution effect of aphids across larger host plant areas or due to an attraction of aphid enemies to high-density resource patches (e.g. as with flower resources in apple orchards (Gontijo et al., 2013)). Meanwhile, the cover of other mass-flowering crops from the previous year did not influence any of the measured services, likely due to phenological mismatches with the life-cycle of ecosystem service providers and oilseed rape.

4.2. Limitations of the available data for assessing agricultural impacts on biodiversity and yield responses to ecosystem services

Although our analyses included pesticide use as a proxy for agricultural intensification, this variable may also reflect other unmeasured factors such as intensive soil tillage (Frøslev et al., 2022) or high nitrogen input levels (Penuelas et al., 2023), both of which can negatively affect biodiversity. Unfortunately, we lacked access to detailed data on these additional practices at landscape level. In particular, soil management from the previous year—known to influence the emergence of pollen beetles and flea beetle parasitoids (Rusch et al., 2011; Hanson et al., 2015)—cannot not be recorded at a wide spatial scale. Similarly, the absence of an inventory of managed honeybee hives in the landscape limited our ability to assess the potential influence of domestic bee abundance on plant-pollinator interactions. Such data could have helped disentangle local effects of managed bees on both honeybee and wild pollinator communities (Ropars et al., 2019; Bartholomée et al., 2020).

Regarding crop yield responses, we detected no significant effect of either pollination or aphid regulation, with only a very weak positive trend for pollinators. Detecting such effects likely requires larger datasets, both spatially and temporally, such as those used by (Perrot et al., 2018), which reported yield increases associated with wild pollinator activity when assessed across broader spatial and temporal scales. Moreover, the economic margin, rather than yield alone, ultimately determines the relevance of ecosystem services to farmers (Mouratiadou et al., 2024). Future work should therefore assess how multifunctionality responds to pesticide use, not only in terms of ecological outcomes but also in terms of farm profitability.

Conclusion

Our findings highlight that pollination and conservation biological control are generally synergistic and that landscape and agricultural practices mediate these ecosystem services. While lower pesticide use consistently tended to benefit most of the services we examined, the spatial and temporal configuration of the landscape shaped service provision in more complex ways. In the study area—dominated by large-scale cereal farming and where biodiversity-supporting schemes remain scarce—these results underscore that the design of multifunctional landscapes must be coordinated at the regional level, involving all relevant stakeholders. In particular, reducing pesticide use at a territorial scale involves numerous socio-technical barriers (Meynard et al., 2018) and is only possible by involving all upstream and downstream stakeholders, notably by linking production, processing and food supply. Phasing out synthetic pesticides represents a great challenge for achieving agricultural landscapes that deliver multiple ecosystem services. Beyond the benefits we quantified here, previous studies suggest that pesticide-free agricultural systems can promote biodiversity and ecological resilience from the field to the landscape scale (Rey Benayas and Bullock, 2012; Stein-Bachinger et al., 2022), amplifying positive feedback between biodiversity and ecosystem functioning, highlighting the need for their coherent deployment at broader spatial scales.

Acknowledgements

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Supplementary materials

Table S5.1. Selected flowering crops from the French Land Parcel Identification System (RPG), including both mass-flowering crops and less-intensively flowering species.

Pseudo-cereals	Vegetables
SRS – Buckwheat CAG – Other secondary spring cereals or pseudo-cereals (e.g. canary grass, quinoa, chia) Oilseeds CML – Camelina LIH – Winter flax (non-textile) LIP – Spring flax (non-textile) MOT – Winter mustard OEI – Opium poppy TRN – Sunflower OAG – Other spring/summer oilseeds or oilseed mixtures OHR – Other winter oilseeds or oilseed mixtures Legumes ARA – Peanut FEV – Fava bean FNU – Fenugreek FVL – Winter faba bean FVP – Spring faba bean GES – Cowpea, dolichos (incl. lablab), grass pea LEC – Lentil LDH – Winter sweet lupin LDP – Spring sweet lupin LOT – Bird's-foot trefoil, Minette PCH – Chickpea PHI – Winter protein pea (for animal feed) PPR – Spring protein pea (for animal feed) PHS – Dry peas and beans (for human consumption) PHF – Fresh peas and beans (for human consumption) LUZ – Alfalfa (lucerne) SAI – Sainfoin SOJ – Soybean TRE – Clover VES – Vetch, melilot, tare, serradella PAG – Other grain or forage legumes MLF – Pure mixtures of grain or forage legumes Fruits AGR – Citrus fruits CBT – Cherries OLI – Olive grove PVT – Peaches (incl. nectarines, flat peaches) PWT – Pears PRU – Plums (e.g. mirabelle, damson, greengage) VRG – Other orchards (incl. DOM) PFR – Small berries (excluding strawberries)	ART – Artichoke CEL – Celery CCN – Cucumber, gherkin, zucchini FRA – Strawberry (open field) MLO – Melon and watermelon RDI – Radish PVP – Pepper, chili, eggplant POT – Pumpkin, squash, and other gourds TOM – Tomato (open field) FLA – Other annual vegetables or fruits FLP – Other perennial vegetables or fruits Aromatic and Medicinal Plants PPP – Perennial medicinal plants (trees or shrubs, excl. blackcurrant) ARP – Perennial aromatic plants (non-woody) AAR – Annual herbaceous aromatic plants (< 5 years), excl. parsley PRF – Perennial fragrance plants (excluding lavender and lavandin) LAV – Lavender and lavandin AME – Non-perennial medicinal or fragrance plants (< 5 years) PME – Perennial medicinal plants (non-tree species) Other Flowering Plants CHV – Hemp LIF – Fibre flax

Summary of model outputs for ecosystem service indicators

To explore how different environmental variables influence ecosystem service indicators, we provide a series of tables reporting the outputs of generalized linear mixed models for each service. We present the model results for the different ecosystem services, decomposing the contribution of semi-natural elements in the landscape using several complementary approaches. In the first three tables, all semi-natural elements (SNE) are considered together, combining both woody and herbaceous components. We then separate these effects by distinguishing woody from herbaceous elements. Finally, herbaceous elements are further divided into fallow land and mown grasslands to refine our understanding of their respective contributions.

Pollination service

Table S5.2. Results of generalized linear mixed models testing the effects of local and landscape variables on wild pollinator visitation rates to oilseed rape flowers at three spatial scales with all semi-natural elements classified into a single category.

Each model was fitted using a negative binomial distribution (*nbinom1*) to account for overdispersion in pollinator visitation counts. Separate models were run at 500 m, 1000 m, and 2000 m landscape buffer scales. Estimates, standard errors, Chi-squared statistics (type II Wald χ^2 tests), and associated p-values are reported for each explanatory variable. Bold text indicates significant effects ($p < 0.05$), while italic text highlights marginally significant effects ($0.05 < p < 0.10$).

Variable	Estimate	Std. Error	Chi ² (Anova)	Anova p-value
500m				
Treatment frequency index (field level)	-0.333	0.109	9.292	p = 0.0023
<i>Treatment frequency index in the landscape</i>	-0.215	0.113	3.608	<i>p = 0.057</i>
Total SNE area (woody and herbaceous)	0.231	0.094	5.985	p = 0.014
Oilseed rape area in the current year	0.079	0.099	0.638	p = 0.42
Oilseed rape area in the previous year	0.041	0.106	0.151	p = 0.7
Area of other flowering crop area in the previous year	-0.001	0.099	0.000	p = 0.99
Year (ref=2023)	0.248	0.207	1.438	p = 0.23
Flower area on the quadrat	0.219	0.093	5.570	p = 0.018
Wind speed during observation	-0.245	0.095	6.690	p = 0.0097
Temperature during observation	-0.229	0.088	6.727	p = 0.0095
Julian date (observation)	0.235	0.115	4.212	p = 0.04
Decimal hour	0.072	0.088	0.668	p = 0.41
1000m				
Treatment frequency index (field level)	-0.321	0.099	10.503	p = 0.0012
Treatment frequency index in the landscape	-0.286	0.122	5.490	p = 0.019
Total SNE area (woody and herbaceous)	0.292	0.100	8.619	p = 0.0033
Oilseed rape area in the current year	0.040	0.103	0.151	p = 0.7
Oilseed rape area in the previous year	0.150	0.101	2.187	p = 0.14
Area of other flowering crop area in the previous year	0.030	0.096	0.099	p = 0.75
Year (ref=2023)	0.187	0.207	0.815	p = 0.37
Flower area on the quadrat	0.260	0.093	7.741	p = 0.0054**
Wind speed during observation	-0.250	0.086	8.430	p = 0.0037**
Temperature during observation	-0.216	0.087	6.233	p = 0.013*
<i>Julian date (observation)</i>	0.216	0.112	3.730	<i>p = 0.053</i>
Decimal hour	0.048	0.082	0.336	p = 0.56
2000m				
Treatment frequency index (field level)	-0.293	0.099	8.720	p = 0.0031**
Treatment frequency index in the landscape	-0.123	0.139	0.787	p = 0.38
Total SNE area (woody and herbaceous)	0.175	0.107	2.703	p = 0.1
Oilseed rape area in the current year	-0.033	0.149	0.048	p = 0.83
Oilseed rape area in the previous year	0.012	0.149	0.007	p = 0.93
Area of other flowering crop area in the previous year	0.071	0.120	0.356	p = 0.55
Year (ref=2023)	0.198	0.241	0.674	p = 0.41
Flower area on the quadrat	0.246	0.102	5.815	p = 0.016*
Wind speed during observation	-0.210	0.095	4.879	p = 0.027*
Temperature during observation	-0.204	0.091	5.022	p = 0.025*
<i>Julian date (observation)</i>	0.225	0.118	3.652	<i>p = 0.056</i>
Decimal hour	0.057	0.087	0.428	p = 0.51

Table S5.3. Results of generalized linear mixed models testing the effects of local and landscape variables on total pollinators visitation rates to oilseed rape flowers at three spatial scales with all semi-natural elements classified into a single category.

Each model was fitted using a negative binomial distribution (*nbinom1*) to account for overdispersion in pollinator visitation counts. Separate models were run at 500 m, 1000 m, and 2000 m landscape buffer scales. Estimates, standard errors, Chi-squared statistics (type II Wald χ^2 tests), and associated *p*-values are reported for each explanatory variable. Bold text indicates significant effects ($p < 0.05$), while italic text highlights marginally significant effects ($0.05 < p < 0.10$).

Variable	Estimate	Std. Error	Chi ² (Anova)	Anova p-value
500m				
(Intercept)	2.613	0.123	NA	p = NA***
Treatment frequency index (field level)	-0.221	0.094	5.478	p = 0.019*
Treatment frequency index in the landscape	-0.303	0.095	10.135	p = 0.0015**
Total SNE area (woody and herbaceous)	0.140	0.093	2.276	p = 0.13
Oilseed rape area in the current year	-0.018	0.094	0.036	p = 0.85
Oilseed rape area in the previous year	0.114	0.096	1.396	p = 0.24
Area of other flowering crop area in the previous year	-0.119	0.097	1.517	p = 0.22
Year (ref=2023)	0.101	0.207	0.240	p = 0.62
Flower area on the quadrat	0.142	0.092	2.398	p = 0.12
Wind speed during observation	-0.084	0.089	0.877	p = 0.35
Temperature during observation	-0.067	0.086	0.612	p = 0.43
Julian date (observation)	0.217	0.109	3.922	p = 0.048*
Decimal hour	-0.077	0.082	0.889	p = 0.35
1000m				
(Intercept)	2.597	0.125	NA	p = NA***
Treatment frequency index (field level)	-0.225	0.094	5.756	p = 0.016*
Treatment frequency index in the landscape	-0.314	0.116	7.347	p = 0.0067**
<i>Total SNE area (woody and herbaceous)</i>	<i>0.183</i>	<i>0.098</i>	<i>3.459</i>	<i>p = 0.063.</i>
Oilseed rape area in the current year	-0.069	0.103	0.451	p = 0.5
Oilseed rape area in the previous year	0.151	0.101	2.246	p = 0.13
Area of other flowering crop area in the previous year	-0.063	0.095	0.440	p = 0.51
Year (ref=2023)	0.108	0.213	0.258	p = 0.61
<i>Flower area on the quadrat</i>	<i>0.171</i>	<i>0.091</i>	<i>3.485</i>	<i>p = 0.062.</i>
Wind speed during observation	-0.107	0.085	1.595	p = 0.21
Temperature during observation	-0.068	0.083	0.676	p = 0.41
<i>Julian date (observation)</i>	<i>0.213</i>	<i>0.110</i>	<i>3.780</i>	<i>p = 0.052.</i>
Decimal hour	-0.088	0.080	1.221	p = 0.27
2000m				
(Intercept)	2.592	0.133	NA	p = NA***
Treatment frequency index (field level)	-0.215	0.084	6.516	p = 0.011*
Treatment frequency index in the landscape	-0.126	0.126	0.992	p = 0.32
Total SNE area (woody and herbaceous)	0.126	0.094	1.793	p = 0.18
Oilseed rape area in the current year	-0.170	0.141	1.469	p = 0.23
Oilseed rape area in the previous year	-0.050	0.135	0.139	p = 0.71
Area of other flowering crop area in the previous year	-0.010	0.100	0.010	p = 0.92
Year (ref=2023)	0.141	0.231	0.370	p = 0.54
Flower area on the quadrat	0.224	0.095	5.575	p = 0.018*
Wind speed during observation	-0.067	0.088	0.583	p = 0.45
Temperature during observation	-0.082	0.088	0.866	p = 0.35
<i>Julian date (observation)</i>	<i>0.184</i>	<i>0.110</i>	<i>2.811</i>	<i>p = 0.094.</i>
Decimal hour	-0.082	0.081	1.008	p = 0.32

Table S5.4. Results of generalized linear mixed models testing the effects of local and landscape variables on wild pollinators visitation rates to oilseed rape flowers at three spatial scales with semi-natural elements classified into two categories: woody and herbaceous.

Each model was fitted using a negative binomial distribution (*nbinom1*) to account for overdispersion in pollinator visitation counts. Separate models were run at 500 m, 1000 m, and 2000 m landscape buffer scales. Estimates, standard errors, Chi-squared statistics (type II Wald χ^2 tests), and associated *p*-values are reported for each explanatory variable. Bold text indicates significant effects ($p < 0.05$), while italic text highlights marginally significant effects ($0.05 < p < 0.10$).

Variable	Estimate	Std. Error	Chi ² (Anova)	Anova p-value
500m				
Treatment frequency index (field level)	-0.449	0.110	16.685	p < 10^{-3***}
Treatment frequency index in the landscape	-0.149	0.098	2.314	p = 0.13
<i>Woody SNE area</i>	<i>0.156</i>	<i>0.090</i>	<i>3.033</i>	<i>p = 0.082.</i>
Herbaceous SNE area	0.274	0.094	8.536	p = 0.0035**
Oilseed rape area in the current year	0.054	0.090	0.361	p = 0.55
Oilseed rape area in the previous year	0.005	0.106	0.002	p = 0.97
Area of other flowering crop area in the previous year	-0.011	0.098	0.012	p = 0.91
Year (ref=2023)	0.004	0.184	0.000	p = 0.98
Flower area on the quadrat	0.322	0.078	16.908	p < 10^{-3***}
Wind speed during observation	-0.268	0.090	8.883	p = 0.0029**
Temperature during observation	-0.216	0.089	5.822	p = 0.016*
Decimal hour	0.054	0.082	0.432	p = 0.51
1000m				
Treatment frequency index (field level)	-0.360	0.100	12.912	p < 10^{-3***}
Treatment frequency index in the landscape	-0.271	0.128	4.504	p = 0.034*
Woody SNE area	0.232	0.107	4.665	p = 0.031*
<i>Herbaceous SNE area</i>	<i>0.162</i>	<i>0.087</i>	<i>3.483</i>	<i>p = 0.062.</i>
Oilseed rape area in the current year	0.071	0.105	0.453	p = 0.5
Oilseed rape area in the previous year	0.144	0.105	1.890	p = 0.17
Area of other flowering crop area in the previous year	0.015	0.101	0.022	p = 0.88
Year (ref=2023)	-0.023	0.182	0.016	p = 0.9
Flower area on the quadrat	0.341	0.078	19.110	p < 10^{-3***}
Wind speed during observation	-0.251	0.090	7.811	p = 0.0052**
Temperature during observation	-0.192	0.089	4.673	p = 0.031*
Decimal hour	0.045	0.083	0.288	p = 0.59
2000m				
Treatment frequency index (field level)	-0.387	0.101	14.619	p < 10^{-3***}
Treatment frequency index in the landscape	-0.039	0.135	0.085	p = 0.77
Woody SNE area	0.213	0.093	5.291	p = 0.021*
Herbaceous SNE area	0.238	0.103	5.308	p = 0.021*
Oilseed rape area in the current year	0.024	0.147	0.027	p = 0.87
Oilseed rape area in the previous year	-0.034	0.137	0.061	p = 0.81
Area of other flowering crop area in the previous year	0.183	0.125	2.129	p = 0.14
Year (ref=2023)	-0.103	0.219	0.221	p = 0.64
Flower area on the quadrat	0.363	0.084	18.553	p < 10^{-3***}
Wind speed during observation	-0.198	0.088	5.120	p = 0.024*
Temperature during observation	-0.191	0.093	4.234	p = 0.04*
Decimal hour	0.037	0.083	0.193	p = 0.66

Table S5.5. Results of generalized linear mixed models testing the effects of local and landscape variables on total pollinators visitation rates to oilseed rape flowers at three spatial scales with semi-natural elements classified into two categories: woody and herbaceous.

Each model was fitted using a negative binomial distribution (*nbinom1*) to account for overdispersion in pollinator visitation counts. Separate models were run at 500 m, 1000 m, and 2000 m landscape buffer scales. Estimates, standard errors, Chi-squared statistics (type II Wald χ^2 tests), and associated p-values are reported for each explanatory variable. Bold text indicates significant effects ($p < 0.05$), while italic text highlights marginally significant effects ($0.05 < p < 0.10$).

Variable	Estimate	Std. Error	Chi ² (Anova)	Anova p-value
500m				
Treatment frequency index (field level)	-0.290	0.102	8.118	p = 0.0044**
Treatment frequency index in the landscape	-0.265	0.095	7.727	p = 0.0054**
Woody SNE area	0.112	0.091	1.494	p = 0.22
Herbaceous SNE area	0.131	0.096	1.890	p = 0.17
Oilseed rape area in the current year	-0.034	0.094	0.128	p = 0.72
Oilseed rape area in the previous year	0.099	0.101	0.967	p = 0.33
Area of other flowering crop area in the previous year	-0.106	0.097	1.199	p = 0.27
Year (ref=2023)	-0.151	0.188	0.646	p = 0.42
Flower area on the quadrat	0.233	0.078	8.973	p = 0.0027**
Wind speed during observation	-0.080	0.093	0.724	p = 0.39
Temperature during observation	-0.037	0.088	0.177	p = 0.67
Decimal hour	-0.083	0.083	1.017	p = 0.31
1000m				
Treatment frequency index (field level)	-0.258	0.095	7.320	p = 0.0068**
Treatment frequency index in the landscape	-0.321	0.120	7.153	p = 0.0075**
Woody SNE area	0.164	0.106	2.407	p = 0.12
Herbaceous SNE area	0.097	0.089	1.186	p = 0.28
Oilseed rape area in the current year	-0.034	0.105	0.107	p = 0.74
Oilseed rape area in the previous year	0.159	0.103	2.365	p = 0.12
Area of other flowering crop area in the previous year	-0.056	0.096	0.337	p = 0.56
Year (ref=2023)	-0.136	0.183	0.553	p = 0.46
Flower area on the quadrat	0.253	0.077	10.762	p = 0.001**
Wind speed during observation	-0.101	0.093	1.169	p = 0.28
Temperature during observation	-0.030	0.084	0.128	p = 0.72
Decimal hour	-0.091	0.081	1.253	p = 0.26
2000m				
Treatment frequency index (field level)	-0.280	0.094	8.965	p = 0.0028**
Treatment frequency index in the landscape	-0.079	0.130	0.373	p = 0.54
Woody SNE area	0.145	0.089	2.690	p = 0.1
Herbaceous SNE area	0.139	0.100	1.958	p = 0.16
Oilseed rape area in the current year	-0.147	0.146	1.009	p = 0.32
Oilseed rape area in the previous year	-0.065	0.134	0.237	p = 0.63
Area of other flowering crop area in the previous year	0.049	0.112	0.196	p = 0.66
Year (ref=2023)	-0.097	0.209	0.217	p = 0.64
Flower area on the quadrat	0.307	0.082	13.957	p < 10⁻³***

Table S5.6. Results of generalized linear mixed models testing the effects of local and landscape variables on wild pollinators visitation rates to oilseed rape flowers at three spatial scales with semi-natural elements classified into three categories: woody, fallows and grasslands. Each model was fitted using a negative binomial distribution (*nbinom1*) to account for overdispersion in pollinator visitation counts. Separate models were run at 500 m, 1000 m, and 2000 m landscape buffer scales. Estimates, standard errors, Chi-squared statistics (type II Wald χ^2 tests), and associated p-values are reported for each explanatory variable. Bold text indicates significant effects ($p < 0.05$), while italic text highlights marginally significant effects ($0.05 < p < 0.10$).

Variable	Estimate	Std. Error	Chi ² (Anova)	Anova p-value
500m				
Treatment frequency index (field level)	-0.396	0.108	13.343	p < 10^{-3***}
<i>Treatment frequency index in the landscape</i>	-0.195	0.102	3.637	<i>p = 0.057.</i>
Woody SNE area	0.134	0.089	2.235	p = 0.13
Grassland area	0.257	0.087	8.785	p = 0.003**
Fallow area	0.143	0.089	2.609	p = 0.11
Oilseed rape area in the current year	0.080	0.089	0.804	p = 0.37
Oilseed rape area in the previous year	0.050	0.101	0.245	p = 0.62
Area of other flowering crop area in the previous year	-0.025	0.098	0.066	p = 0.8
Year (ref=2023)	0.225	0.200	1.262	p = 0.26
Julian date (observation)	0.244	0.111	4.810	p = 0.028*
Flower area on the quadrat	0.230	0.092	6.295	p = 0.012*
Wind speed during observation	-0.307	0.091	11.402	p < 10^{-3***}
Temperature during observation	-0.252	0.089	8.098	p = 0.0044**
Decimal hour	0.065	0.083	0.612	p = 0.43
1000m				
Treatment frequency index (field level)	-0.334	0.099	11.454	p < 10^{-3***}
Treatment frequency index in the landscape	-0.260	0.125	4.327	p = 0.038*
<i>Woody SNE area</i>	0.205	0.111	3.389	<i>p = 0.066.</i>
Grassland area	0.199	0.082	5.983	p = 0.014*
Fallow area	0.029	0.097	0.092	p = 0.76
Oilseed rape area in the current year	0.030	0.104	0.085	p = 0.77
Oilseed rape area in the previous year	0.173	0.108	2.543	p = 0.11
Area of other flowering crop area in the previous year	-0.034	0.102	0.111	p = 0.74
Year (ref=2023)	0.248	0.208	1.416	p = 0.23
Julian date (observation)	0.241	0.112	4.608	p = 0.032*
Flower area on the quadrat	0.254	0.092	7.669	p = 0.0056**
Wind speed during observation	-0.282	0.090	9.880	p = 0.0017**
Temperature during observation	-0.240	0.087	7.508	p = 0.0061**
Decimal hour	0.064	0.082	0.608	p = 0.44
2000m				
Treatment frequency index (field level)	-0.357	0.101	12.589	p < 10^{-3***}
<i>Treatment frequency index in the landscape</i>	-0.092	0.134	0.474	<i>p = 0.49</i>
Woody SNE area	0.221	0.100	4.823	p = 0.028*
Grassland area	0.258	0.109	5.640	p = 0.018*
Fallow area	0.085	0.088	0.937	p = 0.33
Oilseed rape area in the current year	0.034	0.143	0.057	p = 0.81
Oilseed rape area in the previous year	0.072	0.146	0.245	p = 0.62
Area of other flowering crop area in the previous year	0.187	0.122	2.337	p = 0.13
Year (ref=2023)	0.090	0.234	0.149	p = 0.7
<i>Julian date (observation)</i>	0.200	0.113	3.148	<i>p = 0.076.</i>
Flower area on the quadrat	0.276	0.100	7.588	p = 0.0059**
Wind speed during observation	-0.237	0.088	7.155	p = 0.0075**
Temperature during observation	-0.221	0.092	5.771	p = 0.016*
Decimal hour	0.055	0.083	0.432	p = 0.51

Table S5.7. Results of generalized linear mixed models testing the effects of local and landscape variables on total pollinators visitation rates to oilseed rape flowers at three spatial scales with semi-natural elements classified into three categories: woody, fallows and grasslands.

Each model was fitted using a negative binomial distribution (*nbinom1*) to account for overdispersion in pollinator visitation counts. Separate models were run at 500 m, 1000 m, and 2000 m landscape buffer scales. Estimates, standard errors, Chi-squared statistics (type II Wald χ^2 tests), and associated *p*-values are reported for each explanatory variable. Bold text indicates significant effects ($p < 0.05$), while italic text highlights marginally significant effects ($0.05 < p < 0.10$).

Variable	Estimate	Std. Error	Chi ² (Anova)	Anova p-value
500m				
Treatment frequency index (field level)	-0.256	0.100	6.531	p = 0.011*
Treatment frequency index in the landscape	-0.293	0.097	9.121	p = 0.0025**
Woody SNE area	0.081	0.092	0.773	p = 0.38
Grassland area	0.138	0.089	2.388	p = 0.12
Fallow area	0.064	0.088	0.529	p = 0.47
Oilseed rape area in the current year	-0.002	0.094	0.001	p = 0.98
Oilseed rape area in the previous year	0.120	0.096	1.565	p = 0.21
Area of other flowering crop area in the previous year	-0.118	0.097	1.486	p = 0.22
Year (ref=2023)	0.077	0.208	0.136	p = 0.71
Julian date (observation)	0.227	0.109	4.334	p = 0.037*
Flower area on the quadrat	0.143	0.091	2.453	p = 0.12
Wind speed during observation	-0.123	0.096	1.665	p = 0.2
Temperature during observation	-0.083	0.088	0.877	p = 0.35
Decimal hour	-0.073	0.084	0.761	p = 0.38
1000m				
Treatment frequency index (field level)	-0.242	0.093	6.709	p = 0.0096**
Treatment frequency index in the landscape	-0.293	0.119	6.067	p = 0.014*
Woody SNE area	0.127	0.110	1.325	p = 0.25
Grassland area	0.135	0.083	2.620	p = 0.11
Fallow area	0.018	0.093	0.037	p = 0.85
Oilseed rape area in the current year	-0.070	0.105	0.448	p = 0.5
Oilseed rape area in the previous year	0.162	0.107	2.281	p = 0.13
Area of other flowering crop area in the previous year	-0.090	0.096	0.880	p = 0.35
Year (ref=2023)	0.130	0.213	0.373	p = 0.54
Julian date (observation)	0.230	0.111	4.307	p = 0.038*
<i>Flower area on the quadrat</i>	<i>0.171</i>	<i>0.091</i>	<i>3.539</i>	<i>p = 0.06.</i>
Wind speed during observation	-0.138	0.093	2.185	p = 0.14
Temperature during observation	-0.090	0.085	1.124	p = 0.29
Decimal hour	-0.071	0.081	0.758	p = 0.38
2000m				
Treatment frequency index (field level)	-0.259	0.094	7.686	p = 0.0056**
Treatment frequency index in the landscape	-0.113	0.129	0.770	p = 0.38
Woody SNE area	0.146	0.097	2.283	p = 0.13
Grassland area	0.149	0.108	1.901	p = 0.17
Fallow area	0.054	0.083	0.429	p = 0.51
Oilseed rape area in the current year	-0.130	0.147	0.790	p = 0.37
Oilseed rape area in the previous year	-0.002	0.143	0.000	p = 0.99
Area of other flowering crop area in the previous year	0.057	0.115	0.251	p = 0.62
Year (ref=2023)	0.087	0.231	0.141	p = 0.71
<i>Julian date (observation)</i>	<i>0.183</i>	<i>0.109</i>	<i>2.827</i>	<i>p = 0.093.</i>
Flower area on the quadrat	0.231	0.096	5.771	p = 0.016*
Wind speed during observation	-0.096	0.090	1.134	p = 0.29
Temperature during observation	-0.087	0.088	0.982	p = 0.32
Decimal hour	-0.073	0.082	0.808	p = 0.37

Flea beetle parasitism

Table S5.8. Results of generalized linear mixed models testing the effects of local and landscape variables on flea beetle parasitism rates in oilseed rape fields at three spatial scales with all semi-natural elements classified into a single category.

Each model was fitted using a binomial distribution. Separate models were run at 500 m, 1000 m, and 2000 m landscape buffer scales. Estimates, standard errors, Chi-squared statistics (type II Wald χ^2 tests), and associated *p*-values are reported for each explanatory variable. Bold text indicates significant effects ($p < 0.05$), while italic text highlights marginally significant effects ($0.05 < p < 0.10$).

Variable	Estimate	Std. Error	Chi ² (Anova)	Anova p-value
500m				
<i>Treatment frequency index (field level)</i>	-0.479	0.265	3.300	0.071.
Treatment frequency index in the landscape	-0.077	0.297	0.067	0.8
Total SNE area (woody and herbaceous)	-0.403	0.293	1.900	0.17
Oilseed rape area in the current year	-0.274	0.244	1.300	0.26
Oilseed rape area in the previous year	0.293	0.252	1.400	0.25
Area of other flowering crop area in the previous year	0.166	0.260	0.410	0.52
Julian date (sampling)	1.027	0.119	75.000	< 10^{-3***}
Year (ref=2023)	-0.275	0.474	0.340	0.56
Distance to field margin	-0.070	0.101	0.490	0.48
1000m				
Treatment frequency index (field level)	-0.615	0.240	6.600	0.01*
Treatment frequency index in the landscape	-0.271	0.314	0.740	0.39
<i>Total SNE area (woody and herbaceous)</i>	<i>-0.453</i>	<i>0.255</i>	<i>3.200</i>	<i>0.075.</i>
Oilseed rape area in the current year	-0.301	0.261	1.300	0.25
Oilseed rape area in the previous year	0.565	0.246	5.300	0.022*
Area of other flowering crop area in the previous year	0.057	0.234	0.059	0.81
Julian date (sampling)	0.988	0.117	72.000	< 10^{-3***}
Year (ref=2023)	-0.475	0.438	1.200	0.28
Distance to field margin	-0.061	0.101	0.370	0.54
2000m				
Treatment frequency index (field level)	-0.536	0.259	4.300	0.039*
Treatment frequency index in the landscape	-0.325	0.413	0.620	0.43
Total SNE area (woody and herbaceous)	0.201	0.270	0.550	0.46
Oilseed rape area in the current year	-0.172	0.385	0.200	0.66
Oilseed rape area in the previous year	0.601	0.379	2.500	0.11
Area of other flowering crop area in the previous year	0.597	0.296	4.100	0.044*
Julian date (sampling)	1.044	0.118	79.000	< 10^{-3***}
<i>Year (ref=2023)</i>	<i>-0.874</i>	<i>0.516</i>	<i>2.900</i>	<i>0.09.</i>
Distance to field margin	-0.072	0.101	0.510	0.47

Table S5.9. Results of generalized linear mixed models testing the effects of local and landscape variables on flea beetle parasitism rates in oilseed rape fields at three spatial scales with semi-natural elements classified into two categories: woody and herbaceous.

Each model was fitted using a binomial distribution. Separate models were run at 500 m, 1000 m, and 2000 m landscape buffer scales. Estimates, standard errors, Chi-squared statistics (type II Wald χ^2 tests), and associated *p*-values are reported for each explanatory variable. Bold text indicates significant effects ($p < 0.05$), while italic text highlights marginally significant effects ($0.05 < p < 0.10$).

Variable	Estimate	Std. Error	Chi ² (Anova)	Anova p-value
500m				
Treatment frequency index (field level)	-0.376	0.268	2.000	0.16
Treatment frequency index in the landscape	-0.103	0.289	0.130	0.72
<i>Herbaceous SNE area</i>	<i>-0.396</i>	<i>0.229</i>	<i>3.000</i>	<i>0.084.</i>
Woody SNE area	-0.215	0.279	0.590	0.44
Oilseed rape area in the current year	-0.285	0.238	1.400	0.23
Oilseed rape area in the previous year	0.268	0.246	1.200	0.28
Area of other flowering crop area in the previous year	0.208	0.256	0.660	0.42
Julian date (sampling)	1.037	0.118	77.000	< 10^{-3***}
Year (ref=2023)	-0.152	0.472	0.100	0.75
Distance to field margin	-0.072	0.101	0.520	0.47
1000m				
Treatment frequency index (field level)	-0.549	0.224	6.000	0.014*
Treatment frequency index in the landscape	-0.354	0.296	1.400	0.23
Herbaceous SNE area	-0.539	0.195	7.600	0.0058**
Woody SNE area	-0.077	0.251	0.093	0.76
Oilseed rape area in the current year	-0.344	0.243	2.000	0.16
Oilseed rape area in the previous year	0.611	0.231	7.000	0.0082**
Area of other flowering crop area in the previous year	0.121	0.220	0.300	0.58
Julian date (sampling)	0.992	0.115	74.000	< 10^{-3***}
Year (ref=2023)	-0.358	0.414	0.750	0.39
Distance to field margin	-0.061	0.101	0.370	0.55
2000m				
Treatment frequency index (field level)	-0.369	0.251	2.200	0.14
Treatment frequency index in the landscape	-0.441	0.392	1.300	0.26
Herbaceous SNE area	-0.603	0.267	5.100	0.024*
Woody SNE area	0.208	0.242	0.740	0.39
Oilseed rape area in the current year	-0.370	0.373	0.990	0.32
Oilseed rape area in the previous year	0.556	0.359	2.400	0.12
Area of other flowering crop area in the previous year	0.291	0.302	0.920	0.34
Julian date (sampling)	1.035	0.116	80.000	< 10^{-3***}
Year (ref=2023)	-0.544	0.504	1.200	0.28
Distance to field margin	-0.070	0.101	0.490	0.49

Table S5.10. Results of generalized linear mixed models testing the effects of local and landscape variables on flea beetle parasitism rates in oilseed rape fields at three spatial scales with semi-natural elements classified into three categories: woody, fallows and grasslands.

Each model was fitted using a binomial distribution. Separate models were run at 500 m, 1000 m, and 2000 m landscape buffer scales. Estimates, standard errors, Chi-squared statistics (type II Wald χ^2 tests), and associated p-values are reported for each explanatory variable. Bold text indicates significant effects ($p < 0.05$), while italic text highlights marginally significant effects ($0.05 < p < 0.10$).

Variable	Estimate	Std. Error	Chi ² (Anova)	Anova p-value
500m				
Treatment frequency index (field level)	-0.376	0.268	2.000	0.16
Treatment frequency index in the landscape	-0.100	0.298	0.110	0.74
Fallow area	-0.280	0.245	1.300	0.25
Grassland area	-0.331	0.229	2.100	0.15
Woody SNE area	-0.213	0.283	0.570	0.45
Oilseed rape area in the current year	-0.286	0.239	1.400	0.23
Oilseed rape area in the previous year	0.268	0.246	1.200	0.28
Area of other flowering crop area in the previous year	0.207	0.256	0.650	0.42
Julian date (sampling)	1.038	0.119	76.000	< 10⁻³
Year	-0.153	0.473	0.100	0.75
Distance to field margin	-0.072	0.101	0.520	0.47
1000m				
Treatment frequency index (field level)	-0.546	0.224	5.900	0.015*
Treatment frequency index in the landscape	-0.380	0.308	1.500	0.22
Fallow area	-0.299	0.242	1.500	0.22
Grassland area	-0.532	0.200	7.100	0.0079**
Woody SNE area	-0.111	0.276	0.160	0.69
Oilseed rape area in the current year	-0.325	0.251	1.700	0.19
Oilseed rape area in the previous year	0.596	0.236	6.400	0.012*
Area of other flowering crop area in the previous year	0.130	0.221	0.350	0.56
Julian date (sampling)	0.989	0.115	74.000	< 10^{-3***}
Year	-0.377	0.418	0.810	0.37
Distance to field margin	-0.060	0.101	0.360	0.55
2000m				
Treatment frequency index (field level)	-0.367	0.249	2.200	0.14
Treatment frequency index in the landscape	-0.436	0.388	1.300	0.26
Fallow area	-0.344	0.231	2.200	0.14
Grassland area	-0.689	0.311	4.900	0.027*
Woody SNE area	0.094	0.278	0.110	0.74
Oilseed rape area in the current year	-0.428	0.377	1.300	0.26
Oilseed rape area in the previous year	0.428	0.388	1.200	0.27
Area of other flowering crop area in the previous year	0.187	0.326	0.330	0.57
Julian date (sampling)	1.039	0.116	80.000	< 10^{-3***}
Year	-0.502	0.503	1.000	0.32
Distance to field margin	-0.070	0.101	0.490	0.48

Pollen beetles

Table S5.11. Results of generalized linear mixed models testing the effects of local and landscape variables on pollen beetle parasitism rates in oilseed rape fields at three spatial scales with all semi-natural elements classified into a single category.

Each model was fitted using a binomial distribution. Separate models were run at 500 m, 1000 m, and 2000 m landscape buffer scales. Estimates, standard errors, Chi-squared statistics (type II Wald χ^2 tests), and associated p-values are reported for each explanatory variable. Bold text indicates significant effects ($p < 0.05$), while italic text highlights marginally significant effects ($0.05 < p < 0.10$).

Variable	Estimate	Std. Error	Chi ² (Anova)	Anova p-value
500m				
Treatment frequency index (field level)	-0.039	0.112	0.120	0.72
Treatment frequency index in the landscape	-0.092	0.123	0.560	0.45
Total SNE area (woody and herbaceous)	-0.413	0.115	13.000	< 10^{-3***}
Oilseed rape area in the current year	0.051	0.105	0.240	0.63
Oilseed rape area in the previous year	-0.111	0.110	1.000	0.31
Area of other flowering crop area in the previous year	-0.083	0.115	0.520	0.47
Julian date (sampling)	0.095	0.095	1.000	0.32
Year (ref=2023)	-1.177	0.244	23.000	< 10^{-3***}
Larval stage	1.072	0.053	410.000	< 10^{-3***}
Distance to field margin (ref = 5m)	0.052	0.036	2.100	0.15
1000m				
Treatment frequency index (field level)	-0.029	0.109	0.073	0.79
Treatment frequency index in the landscape	-0.197	0.151	1.700	0.19
Total SNE area (woody and herbaceous)	-0.386	0.125	9.600	0.002**
Oilseed rape area in the current year	0.093	0.127	0.540	0.46
Oilseed rape area in the previous year	-0.038	0.124	0.095	0.76
Area of other flowering crop area in the previous year	-0.127	0.109	1.400	0.24
Julian date (sampling)	0.107	0.095	1.300	0.26
Year (ref=2023)	-1.003	0.250	16.000	< 10^{-3***}
Larval stage	1.072	0.053	410.000	< 10^{-3***}
Distance to field margin (ref = 5m)	0.050	0.036	2.000	0.16
2000m				
Treatment frequency index (field level)	-0.045	0.107	0.170	0.68
Treatment frequency index in the landscape	-0.377	0.178	4.500	0.034*
<i>Total SNE area (woody and herbaceous)</i>	<i>-0.212</i>	<i>0.120</i>	<i>3.100</i>	<i>0.077.</i>
Oilseed rape area in the current year	-0.060	0.173	0.120	0.73
Oilseed rape area in the previous year	0.357	0.170	4.400	0.036*
Area of other flowering crop area in the previous year	0.110	0.114	0.930	0.34
Julian date (sampling)	0.112	0.096	1.400	0.24
Year (ref=2023)	-1.317	0.254	27.000	< 10^{-3***}
Larval stage	1.069	0.053	410.000	< 10^{-3***}
Distance to field margin (ref = 5m)	0.049	0.036	1.900	0.17

Table S5.12. Results of generalized linear mixed models testing the effects of local and landscape variables on pollen beetle parasitism rates in oilseed rape fields at three spatial scales with semi-natural elements classified into two categories: woody and herbaceous.

Each model was fitted using a binomial distribution. Separate models were run at 500 m, 1000 m, and 2000 m landscape buffer scales. Estimates, standard errors, Chi-squared statistics (type II Wald χ^2 tests), and associated p-values are reported for each explanatory variable. Bold text indicates significant effects ($p < 0.05$), while italic text highlights marginally significant effects ($0.05 < p < 0.10$).

Variable	Estimate	Std. Error	Chi ² (Anova)	Anova p-value
500m				
Treatment frequency index (field level)	-0.032	0.114	0.081	0.78
Treatment frequency index in the landscape	-0.075	0.121	0.380	0.54
Woody SNE area	-0.346	0.107	10.000	0.0013
Herbaceous SNE area	-0.082	0.096	0.720	0.39
Oilseed rape area in the current year	0.059	0.107	0.310	0.58
Oilseed rape area in the previous year	-0.081	0.105	0.590	0.44
Julian date (sampling)	0.097	0.096	1.000	0.31
Year (ref=2023)	-1.178	0.248	23.000	< 10⁻³
Larval stage	1.072	0.053	410.000	< 10⁻³
Distance to field margin (ref = 5m)	0.051	0.036	2.100	0.15
1000m				
Treatment frequency index (field level)	-0.032	0.111	0.083	0.77
Treatment frequency index in the landscape	-0.187	0.154	1.500	0.22
Woody SNE area	-0.317	0.116	7.500	0.0062
Herbaceous SNE area	-0.010	0.105	0.009	0.93
Oilseed rape area in the current year	0.118	0.129	0.840	0.36
Oilseed rape area in the previous year	0.003	0.118	0.000	0.98
Julian date (sampling)	0.113	0.096	1.400	0.24
Year (ref=2023)	-1.074	0.248	19.000	< 10⁻³
Larval stage	1.072	0.053	410.000	< 10⁻³
Distance to field margin (ref = 5m)	0.049	0.036	1.900	0.16
2000m				
Treatment frequency index (field level)	-0.036	0.111	0.110	0.75
Treatment frequency index in the landscape	-0.397	0.178	5.000	0.026
Woody SNE area	-0.211	0.107	3.900	0.049
Herbaceous SNE area	-0.158	0.106	2.200	0.14
Oilseed rape area in the current year	-0.092	0.173	0.280	0.59
Oilseed rape area in the previous year	0.338	0.171	3.900	0.048
Julian date (sampling)	0.109	0.096	1.300	0.25
Year (ref=2023)	-1.217	0.252	23.000	< 10⁻³
Larval stage	1.069	0.053	410.000	< 10⁻³
Distance to field margin (ref = 5m)	0.049	0.036	1.900	0.17

Table S5.13. Results of generalized linear mixed models testing the effects of local and landscape variables on pollen beetle parasitism rates in oilseed rape fields at three spatial scales with semi-natural elements classified into three categories: woody, fallows and grasslands.

Each model was fitted using a binomial distribution. Separate models were run at 500 m, 1000 m, and 2000 m landscape buffer scales. Estimates, standard errors, Chi-squared statistics (type II Wald χ^2 tests), and associated p-values are reported for each explanatory variable. Bold text indicates significant effects ($p < 0.05$), while italic text highlights marginally significant effects ($0.05 < p < 0.10$).

Variable	Estimate	Std. Error	Chi ² (Anova)	Anova p-value
500m				
Treatment frequency index (field level)	-0.040	0.112	0.120	0.72
Treatment frequency index in the landscape	-0.045	0.124	0.130	0.72
Woody SNE area	-0.352	0.106	11.000	< 10⁻³
Grassland area	-0.030	0.092	0.110	0.74
Fallow area	-0.124	0.093	1.800	0.18
Oilseed rape area in the current year	0.060	0.105	0.320	0.57
Oilseed rape area in the previous year	-0.079	0.104	0.580	0.45
Julian date (sampling)	0.098	0.096	1.000	0.31
Year (ref=2023)	-1.207	0.247	24.000	< 10⁻³
Larval stage	1.073	0.053	410.000	< 10⁻³
Distance to field margin (ref = 5m)	0.051	0.036	2.100	0.15
1000m				
Treatment frequency index (field level)	-0.014	0.111	0.017	0.9
Treatment frequency index in the landscape	-0.220	0.156	2.000	0.16
Woody SNE area	-0.356	0.122	8.500	0.0035
Grassland area	-0.042	0.104	0.160	0.69
Fallow area	0.076	0.111	0.470	0.49
Oilseed rape area in the current year	0.139	0.129	1.200	0.28
Oilseed rape area in the previous year	-0.036	0.124	0.083	0.77
Julian date (sampling)	0.109	0.096	1.300	0.26
Year (ref=2023)	-1.087	0.247	19.000	< 10⁻³
Larval stage	1.072	0.053	410.000	< 10⁻³
Distance to field margin (ref = 5m)	0.050	0.036	2.000	0.16
2000m				
Treatment frequency index (field level)	-0.022	0.110	0.040	0.84
Treatment frequency index in the landscape	-0.385	0.176	4.800	0.029
Woody SNE area	-0.266	0.116	5.300	0.022
<i>Grassland area</i>	<i>-0.205</i>	<i>0.108</i>	<i>3.600</i>	<i>0.058</i>
Fallow area	-0.025	0.103	0.057	0.81
Oilseed rape area in the current year	-0.113	0.171	0.440	0.51
Oilseed rape area in the previous year	0.264	0.181	2.100	0.14
Julian date (sampling)	0.097	0.096	1.000	0.31
Year (ref=2023)	-1.246	0.250	25.000	< 10⁻³
Larval stage	1.069	0.053	410.000	< 10⁻³
Distance to field margin (ref = 5m)	0.050	0.036	2.000	0.16

Aphid regulation

Table S5.14. Results of generalized linear mixed models testing the effects of local and landscape variables on aphid regulation in oilseed rape fields at three spatial scales with all semi-natural elements classified into a single category.

Each model was fitted using a negative binomial distribution (*nbinom1*). Separate models were run at 500 m, 1000 m, and 2000 m landscape buffer scales. Estimates, standard errors, Chi-squared statistics (type II Wald χ^2 tests), and associated p-values are reported for each explanatory variable. Bold text indicates significant effects ($p < 0.05$), while italic text highlights marginally significant effects ($0.05 < p < 0.10$).

Variable	Estimate	Std. Error	Chi ² (Anova)	Anova p-value
500m				
Flowers per plant (plant size)	0.578	0.051	127.228	< 10⁻³
Julian date (sampling)	0.867	0.585	2.196	0.14
Zone cage (ref = open)	2.577	0.234	118.006	< 10⁻³
Treatment frequency index (field level)	-1.901	0.649	10.017	0.0016
Treatment frequency index in the landscape	1.031	0.963	0.259	0.61
<i>Total SNE area (woody and herbaceous)</i>	<i>-1.034</i>	<i>0.585</i>	<i>0.306</i>	<i>0.58</i>
Oilseed rape area in the current year	-1.015	0.790	0.029	0.86
Oilseed rape area in the previous year	0.126	0.803	0.667	0.41
Area of other flowering crop area in the previous year	0.859	0.702	0.003	0.96
Cage : Treatment frequency index (field level)	-0.129	0.226	0.328	0.57
Cage : Treatment frequency index in the landscape	-0.669	0.298	5.041	0.025
Cage : Total SNE area (woody and herbaceous)	0.804	0.252	10.205	0.0014
Cage : Oilseed rape area in the current year	1.105	0.256	18.618	< 10⁻³
Cage : Oilseed rape area in the previous year	-1.677	0.327	26.350	< 10⁻³
Cage : Area of other flowering crop area in the previous year	-1.148	0.260	19.451	< 10⁻³
1000m				
Flowers per plant (plant size)	0.506	0.054	86.623	< 10⁻³
Julian date (sampling)	0.863	0.668	1.669	0.2
Zone cage (ref = open)	2.365	0.231	118.584	< 10⁻³
Treatment frequency index (field level)	-2.156	0.661	6.320	0.012
Treatment frequency index in the landscape	1.401	0.998	0.505	0.48
Total SNE area (woody and herbaceous)	-0.104	0.565	0.008	0.93
Oilseed rape area in the current year	-1.758	0.855	0.280	0.6
Oilseed rape area in the previous year	0.165	0.801	0.064	0.8
Area of other flowering crop area in the previous year	0.217	0.693	0.673	0.41
Cage : Treatment frequency index (field level)	0.709	0.287	6.083	0.014
Cage : Treatment frequency index in the landscape	-1.022	0.406	6.317	0.012
Cage : Total SNE area (woody and herbaceous)	0.181	0.238	0.579	0.45
Cage : Oilseed rape area in the current year	1.908	0.407	21.986	< 10⁻³
Cage : Oilseed rape area in the previous year	-0.373	0.233	2.555	0.11
Cage : Area of other flowering crop area in the previous year	0.351	0.311	1.270	0.26
2000m				
Flowers per plant (plant size)	0.474	0.048	95.647	< 10⁻³
<i>Julian date (sampling)</i>	<i>1.089</i>	<i>0.590</i>	<i>3.411</i>	<i>0.065</i>
Zone cage (ref = open)	1.741	0.260	90.566	< 10⁻³
Treatment frequency index (field level)	-1.552	0.580	9.559	0.002
Treatment frequency index in the landscape	-0.041	0.926	0.026	0.87
Total SNE area (woody and herbaceous)	-0.882	0.625	0.596	0.44
Oilseed rape area in the current year	-0.358	0.959	0.809	0.37
Oilseed rape area in the previous year	-0.465	0.821	2.058	0.15
Area of other flowering crop area in the previous year	-0.326	0.612	1.501	0.22
Cage : Treatment frequency index (field level)	-0.177	0.358	0.243	0.62
Cage : Treatment frequency index in the landscape	-0.158	0.468	0.114	0.74
Cage : Total SNE area (woody and herbaceous)	2.055	0.361	32.434	< 10⁻³
Cage : Oilseed rape area in the current year	2.888	0.631	20.927	< 10⁻³
Cage : Oilseed rape area in the previous year	-0.776	0.286	7.359	0.0067
Cage : Area of other flowering crop area in the previous year	1.246	0.321	15.088	< 10⁻³

Table S5.15. Results of generalized linear mixed models testing the effects of local and landscape variables on aphid regulation in oilseed rape fields at three spatial scales with semi-natural elements classified into two categories: woody and herbaceous.

Each model was fitted using a negative binomial distribution (*nbinom1*). Separate models were run at 500 m, 1000 m, and 2000 m landscape buffer scales. Estimates, standard errors, Chi-squared statistics (type II Wald χ^2 tests), and associated p-values are reported for each explanatory variable. Bold text indicates significant effects ($p < 0.05$), while italic text highlights marginally significant effects ($0.05 < p < 0.10$).

Variable	Estimate	Std. Error	Chi² (Anova)	Anova p-value
500m				
Flowers per plant (plant size)	0.569	0.050	129.877	< 10⁻³
Julian date (sampling)	0.904	0.592	2.330	0.13
Zone cage (ref = open)	2.514	0.233	112.705	< 10⁻³
Treatment frequency index (field level)	-1.903	0.710	10.494	0.0012
Treatment frequency index in the landscape	1.031	0.980	0.453	0.5
Woody SNE area	-0.982	0.631	1.139	0.29
Herbaceous SNE area	-0.063	0.543	0.650	0.42
Oilseed rape area in the current year	-1.040	0.829	0.272	0.6
Oilseed rape area in the previous year	0.083	0.854	1.010	0.31
Area of other flowering crop area in the previous year	0.893	0.797	0.180	0.67
<i>Cage : Treatment frequency index (field level)</i>	<i>-0.443</i>	<i>0.260</i>	<i>2.914</i>	<i>0.088</i>
Cage : Treatment frequency index in the landscape	-0.472	0.322	2.139	0.14
Cage : Woody SNE area	0.396	0.261	2.305	0.13
Cage : Herbaceous SNE area × ZONEC	0.612	0.192	10.132	0.0015
Cage : Oilseed rape area in the current year	0.813	0.281	8.383	0.0038
Cage : Oilseed rape area in the previous year	-1.951	0.343	32.366	< 10⁻³
Cage : Area of other flowering crop area in the previous year	-1.626	0.336	23.473	< 10⁻³
1000m				
Flowers per plant (plant size)	0.519	0.054	93.154	< 10⁻³
Julian date (sampling)	1.008	0.704	2.050	0.15
Zone cage (ref = open)	2.274	0.225	127.089	< 10⁻³
Treatment frequency index (field level)	-2.044	0.666	5.752	0.016
Treatment frequency index in the landscape	1.312	1.073	0.194	0.66
Woody SNE area	-0.002	0.653	0.174	0.68
Herbaceous SNE area	0.053	0.594	0.576	0.45
Oilseed rape area in the current year	-1.793	0.904	0.201	0.65
Oilseed rape area in the previous year	0.085	0.825	0.127	0.72
Area of other flowering crop area in the previous year	0.343	0.779	0.134	0.71
Cage : Treatment frequency index (field level)	0.645	0.266	5.884	0.015
Cage : Treatment frequency index in the landscape	-1.350	0.434	9.652	0.0019
Cage : Woody SNE area	-0.329	0.295	1.249	0.26
Cage : Herbaceous SNE area	0.495	0.204	5.910	0.015
Cage : Oilseed rape area in the current year	2.284	0.441	26.842	< 10⁻³
Cage : Oilseed rape area in the previous year	-0.373	0.228	2.687	0.1
Cage : Area of other flowering crop area in the previous year	-0.090	0.329	0.075	0.78
2000m				
Flowers per plant (plant size)	0.474	0.048	96.464	< 10⁻³
<i>Julian date (sampling)</i>	<i>1.175</i>	<i>0.657</i>	<i>3.205</i>	<i>0.073</i>
Zone cage (ref = open)	1.739	0.257	91.029	< 10⁻³
Treatment frequency index (field level)	-1.559	0.595	9.232	0.0024
Treatment frequency index in the landscape	-0.113	0.928	0.038	0.85
Woody SNE area	-0.864	0.608	0.624	0.43
Herbaceous SNE area	-0.139	0.590	0.285	0.59
Oilseed rape area in the current year	-0.263	1.025	0.883	0.35
Oilseed rape area in the previous year	-0.543	0.844	2.219	0.14
Area of other flowering crop area in the previous year	-0.312	0.633	1.401	0.24
Cage : Treatment frequency index (field level)	-0.209	0.355	0.346	0.56
Cage : Treatment frequency index in the landscape	-0.091	0.472	0.037	0.85
Cage : Woody SNE area	2.009	0.350	32.861	< 10⁻³
Cage : Herbaceous SNE area	0.591	0.214	7.650	0.0057
Cage : Oilseed rape area in the current year	2.891	0.631	21.011	< 10⁻³
Cage : Oilseed rape area in the previous year	-0.750	0.287	6.848	0.0089
Cage : Area of other flowering crop area in the previous year	1.296	0.327	15.725	< 10⁻³

Table S5.16. Results of generalized linear mixed models testing the effects of local and landscape variables on aphid regulation in oilseed rape fields at three spatial scales with semi-natural elements classified into three categories: woody, fallows and grasslands. Each model was fitted using a negative binomial distribution (*nbinom1*). Separate models were run at 500 m, 1000 m, and 2000 m landscape buffer scales. Estimates, standard errors, Chi-squared statistics (type II Wald χ^2 tests), and associated p-values are reported for each explanatory variable. Bold text indicates significant effects ($p < 0.05$), while italic text highlights marginally significant effects ($0.05 < p < 0.10$).

Variable	Estimate	Std. Error	Chi² (Anova)	Anova p-value
500m				
Flowers per plant (plant size)	0.569	0.050	127.568	< 10⁻³
Julian date (sampling)	2.016	0.735	7.530	0.0061
Zone cage (ref = open)	2.559	0.242	111.118	< 10⁻³
Treatment frequency index (field level)	-1.913	0.659	12.637	< 10⁻³
Treatment frequency index in the landscape	1.391	0.896	1.903	0.17
Woody SNE area	-1.249	0.590	2.333	0.13
Grassland area	1.312	0.754	6.688	0.0097
Fallow area	-0.629	0.444	0.563	0.45
Oilseed rape area in the current year	-1.645	0.804	2.426	0.12
Oilseed rape area in the previous year	-0.451	0.898	2.530	0.11
Area of other flowering crop area in the previous year	0.640	0.724	0.590	0.44
Cage : Treatment frequency index (field level)	-0.373	0.280	1.777	0.18
Cage : Treatment frequency index in the landscape	-0.276	0.359	0.590	0.44
Cage : Woody SNE area	0.468	0.274	2.927	0.087
Cage : Grassland SNE area	0.691	0.271	6.517	0.011
Cage : fallow SNE area	0.364	0.170	4.568	0.033
Cage : Oilseed rape area in the current year	0.619	0.329	3.534	0.06
Cage : Oilseed rape area in the previous year	-2.040	0.345	35.015	< 10⁻³
Cage : Area of other flowering crop area in the previous year	-1.633	0.327	24.995	< 10⁻³
1000m				
Flowers per plant (plant size)	0.526	0.056	87.660	< 10⁻³
Julian date (sampling)	1.685	0.877	3.686	0.055
Zone cage (ref = open)	2.499	0.283	114.216	< 10⁻³
Treatment frequency index (field level)	-2.136	0.623	6.685	0.0097
Treatment frequency index in the landscape	1.343	0.997	0.501	0.48
Woody SNE area	-0.141	0.658	0.025	0.87
Grassland area	0.429	0.710	2.491	0.11
Fallow area	-0.333	0.583	0.532	0.47
Oilseed rape area in the current year	-1.831	0.884	0.522	0.47
Oilseed rape area in the previous year	-0.051	0.759	0.208	0.65
Area of other flowering crop area in the previous year	0.371	0.745	0.010	0.92
Cage : Treatment frequency index (field level)	0.763	0.293	6.764	0.0093
Cage : Treatment frequency index in the landscape	-1.005	0.480	4.381	0.036
Cage : Woody SNE area	0.059	0.385	0.023	0.88
Cage : Grassland SNE area	0.680	0.239	8.121	0.0044
Cage : fallow SNE area	-0.071	0.256	0.076	0.78
Cage : Oilseed rape area in the current year	1.811	0.520	12.125	< 10⁻³
Cage : Oilseed rape area in the previous year	-0.300	0.234	1.644	0.2
Cage : Area of other flowering crop area in the previous year	-0.343	0.364	0.890	0.35
2000m				
Flowers per plant (plant size)	0.524	0.048	118.412	< 10⁻³
Julian date (sampling)	2.047	0.837	5.984	0.014
Zone cage (ref = open)	1.787	0.258	97.844	< 10⁻³
Treatment frequency index (field level)	-1.355	0.580	8.469	0.0036
Treatment frequency index in the landscape	-0.294	0.895	0.006	0.94
Woody SNE area	-0.854	0.634	1.258	0.26
Grassland area	0.299	0.875	1.868	0.17
Fallow area	0.014	0.463	0.248	0.62
Oilseed rape area in the current year	0.247	1.057	1.844	0.17
Oilseed rape area in the previous year	-1.307	0.837	2.734	0.098
Area of other flowering crop area in the previous year	0.068	0.630	2.088	0.15
Cage : Treatment frequency index (field level)	-0.342	0.375	0.829	0.36
Cage : Treatment frequency index in the landscape	0.436	0.508	0.737	0.39
Cage : Woody SNE area	2.623	0.411	40.838	< 10⁻³
Cage : Grassland SNE area	1.549	0.284	29.673	< 10⁻³
Cage : fallow SNE area	-0.602	0.228	6.994	0.0082
Cage : Oilseed rape area in the current year	2.872	0.614	21.845	< 10⁻³
Cage : Oilseed rape area in the previous year	0.007	0.320	0.000	0.98
Cage : Area of other flowering crop area in the previous year	0.944	0.324	8.505	0.0035

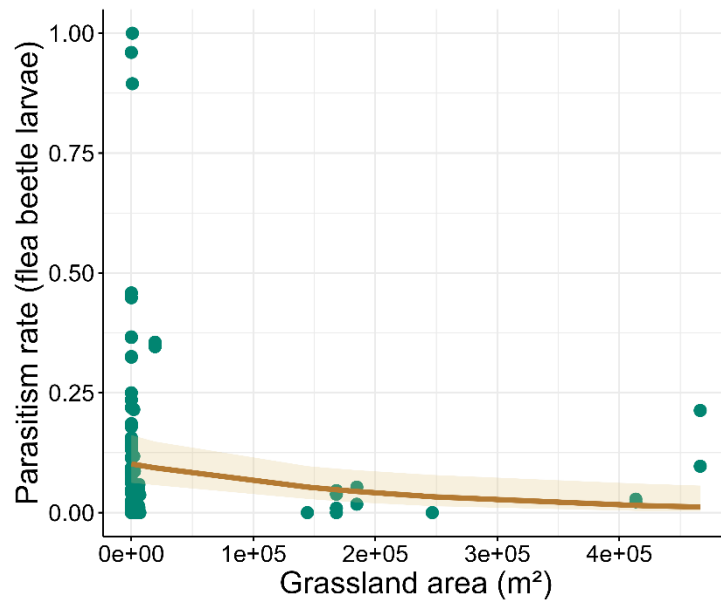


Figure S5.1. Effect of grassland area on the parasitism rate of flea beetle larvae. Predicted marginal effects (solid line) and 95% confidence intervals (shaded area) derived from a GLMM, illustrating the influence of surrounding grassland area on parasitism rates of flea beetle larvae. Raw observed values (proportions) are overlaid as points and show an uneven distribution along the grassland gradient.

6

General Discussion



Anthrax anthrax, in the Cévennes, 2021, © Thibault Gandara

We live in a world where human activities strongly impact biodiversity, and agricultural landscapes stand at the crossroads of multiple social challenges, including food production, economic sustainability, and biodiversity conservation. The recent IPBES Nexus Assessment (McElwee et al., 2025) further emphasizes how these issues are deeply interconnected, linking biodiversity with climate change, food and water security, and human health. Pollinators are keystone to both agricultural productivity and ecosystem functioning, such that assessing their response to landscape and agricultural practices is a powerful tool to evaluate sustainability of agricultural environments. Such assessments help identify where ecological imbalances occur and guide the transition toward more resilient and biodiversity-friendly agricultural models. In this context, understanding where pollinators and their associated pollination services are most altered, and by which factors, is essential to anticipate and design the agriculture of tomorrow.

This thesis aimed to spatially map pollination services, to investigate how landscape structure and farming practices influence their distribution, and to examine their correlations with another ecosystem service, i.e. conservation biological control. We studied the services in simplified, intensive agricultural landscapes using complementary approaches. The objectives were defined as follow:

Objective 1 – Assessing pollination using non-lethal methods and exploring its determinants: We aimed to evaluate the effectiveness of non-lethal approaches, ranging from direct observations of plant–pollinator interactions to measurements of pollination outcomes through yield components of oilseed rape and strawberries, and to explore their complementarity. This also included examining how pollination metrics relate to environmental variables, encompassing both landscape composition and farming practices.

Objective 2 – Spatializing pollination services: We developed and applied indices of pollination to capture the spatial variability of pollination across the landscape.

Objective 3 – Correlating pollination and conservation biological control: We investigated the relationships between pollination and conservation biological control to assess how crop and landscape management can promote synergies between ecosystem services.

In the following sections, I will revisit our main results in relation to the objectives of this thesis and put them into perspective with the existing literature. The discussion of results is structured around major thematic areas rather than strictly following the original objectives. First, I will present an overview of the methods developed and implemented in this thesis, focusing on the relevance and effectiveness of non-lethal monitoring approaches for pollinators and pollination, as well as strategies to spatialize pollination services using both field observations and yield-based indices, including the limitations we encountered. Second, I will examine the drivers and spatial dynamics of pollination services in intensive agricultural landscapes,

focusing on how landscape composition, local floral resources, and agricultural practices shape pollinator communities and pollination outcomes, and exploring the potential synergies with biological pest control. Third, I will present existing initiatives for pollinator and pollination conservation and discuss how our work could potentially inform and be integrated into these programs and then be translated into concrete actions. Fourth, I will briefly outline some broader reflections raised by the experiences and findings of this thesis.

1. Overview of the methods developed and implemented

1.1. Using non-lethal methods to study pollinators and pollination

Growing ethical and methodological concerns are questioning the continued reliance on lethal sampling as the main approach to studying pollinators and pollination. While such lethal approaches, allowing a determination to species level, are often mandatory to establish conservation baselines such as Red Lists (Rasmont et al., 2017), they raise more and more ethical concerns (Barrett and Fischer, 2024). It is quite paradoxical to kill insects in order to protect them, particularly knowing that the past years ecological surveys on wild bees sacrificed hundreds of thousands of individuals (Montgomery et al., 2021). This issue is particularly concerning given that many specimens collected through pan trapping surveys remain unidentified (Gonzalez et al., 2020), due to the shortage of taxonomic expertise and the limited knowledge of certain abundant insect groups like Diptera. Additionally, the small number of taxonomists makes these studies particularly time consuming and costly. In this context, the development and use of non-lethal monitoring methods deserve particular attention (Lövei et al., 2023).

In this thesis, we were very careful to apply non-lethal methods to assess pollination across large-scale intensive agricultural landscapes, while accounting for the whole panel of flower-visitors such as non-syrphid flies (Orford et al., 2015). It should be noted that our analyses included all flower–visitor interactions except those involving pollen beetles, although pollination efficiency can vary greatly among insect groups. Future work could build on this by weighting the contribution of different morphogroups according to their pollination effectiveness, to provide a more accurate assessment of the pollination services. As shown earlier, these approaches are consistent within the existing literature on pollination services, and they provide protocols that are simpler, ethically non-invasive, easily replicable, and less time-consuming than lethal ones. Such methods are particularly suited for large-scale applications when taxonomic identification is not the central objective. They can also be readily transposed into participatory science initiatives, which play a crucial role in broadening knowledge production and enhancing the dissemination of scientific understanding (Bedessem et al., 2021). However, no single method can address all research or outreach objectives. In our

study systems, such as the large agricultural plains where pollinator communities are already declining abruptly but are relatively well documented, non-lethal approaches are particularly suitable. In contrast, in other regions, such as the Mediterranean zone, where many pollinator species remain poorly known (Nieto et al., 2014), both non-lethal and specimen-based methods are complementary and should be chosen according to the research question. In these areas, many studies are still needed to improve our understanding of pollinator diversity, ecology, and conservation.

Nonetheless, despite these advantages, several methodological challenges remain when linking observations on pollinator activity to actual pollination outcomes with small-scale field surveys, highlighting the need for continuous and innovative monitoring methods. Our observations of plant–pollinator interactions did not reveal any correlation with the yield differences observed between open and closed treatments on the phytometer plants studied, except for the number of seeds per silique in oilseed rape. This may be explained by the limited number of replicates available and by the fact that our observations of interactions between morphogroups and plants only capture a snapshot at a given time of day. Continuous monitoring methods, such as ecoacoustics (Crochard, 2023) or camera traps (Naqvi et al., 2022), appear to be promising alternatives for future studies, as they would allow for non-destructive, long-term recording of interactions across the full phenological range of pollinators. At the landscape scale, environmental DNA (eDNA) approaches are increasingly applied, particularly for wild bees, and could provide a non-lethal means to characterize wild bee communities visiting specific plants (Ollivier et al., 2025). However, these methods also present their limitations. Ecoacoustics, for instance, currently does not allow precise taxonomic identification and is restricted to a narrow range of pollinators. Camera traps are generally limited to a single flower or small patch of flowers to ensure sufficient resolution for recognition, which restricts their representativeness at larger scales. Similarly, eDNA provides only a static picture of species presence in a given landscape, without capturing the dynamics of pollinator activity, visitation rates, or actual interaction strengths. More broadly, these approaches remain costly, need high-tech equipment, require cross-validation with traditional field methods, and are not yet directly comparable across studies.

Beyond improving temporal coverage, continuous monitoring approaches and other methods would also enable the inclusion of pollinator groups that are often overlooked in field studies, such as nocturnal pollinators. We did not have the ability to take these specific pollinators into account in our field work even if evidence shows that moths and other night-active insects can make substantial contributions to crop pollination especially for small fruit productions (Buxton et al., 2022; Blareau and Requier, 2025). These pollinators remain largely underconsidered in most studies, and this gap is particularly concerning since regulations on

pesticide use frequently allow applications during evening or night hours, precisely when these pollinators are most active, potentially exposing them to elevated risks.

1.2. Using phytometers pollination

Our study allowed us to implement two pollinator exclusion experiments on plants we used as phytometers, by measuring differences in yield components between open- and closed-pollination treatments. The two focal species were oilseed rape (*Brassica napus*) and strawberry (*Fragaria × ananassa*). We detail for both pollination phytometers the limitations encountered and how we think phytometer studies could be improved.

For strawberries, results from Chapters 2 and 3 showed lower than expected yield differences attributable to pollination. This species and the ‘Charlotte’ cultivar had been chosen due to the ease of handling and transportation, due to the opportunity to measure fruit deformation and based on several successful previous studies (e.g. Castle et al., 2019; Nicholls et al., 2023). According to the general approach adopted in Chapter 3 along an urban–agricultural gradient, few patterns were detected, possibly attributable to high self-pollination in the strawberry plants, which may obscure the signal of interest. Similarly, in Chapter 3, no significant relationship was found between pollinator visits and yield components, indicating limited evidence of pollination effects on strawberries, despite observable yield differences between open and closed pollination treatments. Finally, the experiment aimed at estimating maximum pollination through hand-pollination proved largely unsuccessful, which is surprising given that previous studies applying similar methods reported clear hand-pollination effects in strawberries (Connelly et al., 2015; Wietzke et al., 2018; Miranda et al., 2025). These mixed results lead us to recommend alternative phytometer species in future studies, as mentioned in the Discussion of Chapter 3. Following the feedback from our strawberry experiments, I discussed with Axelle Boizet and Alice Michelot-Antalik the development of pollinometers using species with greater pollinator dependence, such as *Centaurea jacea* — a highly pollinator-dependent plant species (Albrecht et al., 2009). This experiment is currently underway and is expected to yield more sensitive results. Moreover, the strawberry flowering period was not synchronous with that of oilseed rape, meaning that the pollinator communities observed on strawberries may have differed from those active during oilseed rape flowering. Nevertheless, this provided us the opportunity to examine the responses of pollinator communities that were not observed on wild flora or oilseed rape to environmental drivers.

For oilseed rape, our experiments were conducted directly in the field over a single year, as the experimental process was extremely time-consuming. In total, more than seven weeks were required for cage installation, removal, and yield component assessment, not including data entry. This effort was carried out across 20 fields with the support of a team of technicians.

Given these constraints, we could not deploy experiments over as broad a panel of fields as in Perrot et al. (2018) or Leroy et al. (2025). Overall, these experiments allowed us to detect clear differences in yield components—such as total seed mass per plant and the number of seeds per silique—linked to pollination, similar to findings from more detailed studies focusing on seed quality and composition (Perrot et al., 2024). These variations suggest that pollination contributes meaningfully to yield formation in oilseed rape. Moreover, they appear to be influenced by both agricultural practices and landscape composition.

1.3. Spatializing pollination services

In this thesis, we addressed pollination assessment from multiple perspectives. We investigated pollination in the field through direct observations and the implementation of exclusion experiments using phytometers in the SCARABEE farmer network in the Paris Basin. These data provide the opportunity to spatialize pollination services at local scale by combining numerous observations of plant–pollinator interactions and on phytometers across different habitats throughout the landscape. This spatialization approach allowed us to establish relationships between pollinator and pollination measurements and the surrounding agricultural practices and landscape composition.

In parallel with this field work, we developed a pollination index based on yield data collected between 2007 and 2019 in the Fénay landscape monitoring platform near Dijon. This index builds on the approach proposed by (Martin et al., 2019) at the French national scale, which we adapted to the territorial scale. We compared our results with another established method based on land cover and land use (LCLU) to predict pollinator presence (especially wild bees) and their probability of visit. This predictive approach was initially developed by (Lonsdorf et al., 2009) and has since been adapted and modified in many studies (e.g. (Polce et al., 2013; Zulian et al., 2013b; Rahimi and Jung, 2024)). Our yield-based method correlated well with the LCLU-based predictions at the resolution of large agricultural landscapes. Our yield-based method brings forward promising results for spatializing pollination in agricultural landscapes, as it does not require expert knowledge of how LCLU elements contribute to pollinator food and nesting resources.

Initially, the robustness of our yield-based index was supposed to be compared to the field experiments we conducted like other studies did for the LCLU based method (Desaegher et al., 2021). We originally intended to deploy the yield-based index within the SCARABEE farmer network, but this objective could not be met. This was mainly due to missing historical yield data at the plot scale from surveyed farmers. Moreover, data protection regulations restrict access to and sharing of electronically recorded yield information from farmers, and we lacked time to interview all farmers individually. As a result, this work contributes in two different

and complementary directions to pollination service estimation. On the one hand, by comparing different approaches to measure pollination services under field conditions, and on the other hand, by developing more automated and spatialized tools to assess pollination at larger territorial scales. I think that future research should build upon this work to build links between these two directions bridging field-based indicators to spatialized estimation of pollination based on yields. Moreover, I think that the development of this index could be strengthened through its appropriation by agricultural organizations. Indeed, access to high-quality yield data at the plot scale falls within the remit of some entities such as agricultural chambers, which could test the index within other small agricultural regions. Furthermore, to refine the index, it would be valuable to complement the large-scale syntheses currently available (Klein et al., 2007; Siopa et al., 2024) with more detailed information on the pollinator dependence of different cultivated varieties, developed in collaboration with seed companies. Finally, the integration of covariates such as input use, pesticide applications, meteorological conditions or soil quality into the calculations could provide further improvements to the robustness and applicability of the index. To encourage diffusion towards the agricultural sector as well as to organizations such as the OFB, we submitted an article in the *Innovations agronomiques* journal.

2. Drivers and spatial dynamics of pollination services in intensive agricultural landscapes

Across our study regions in the southwestern Paris Basin and south of Dijon, several key landscape elements consistently emerged as drivers of pollination services. These results were captured through different metrics (observations of plant–pollinator interactions, differences in yield components measured via exclusion experiments, and realized pollination index derived from yield data) and converged to the conclusion that the composition of agricultural landscapes strongly shapes pollinator communities and the pollination services they provide.

2.1. Landscape elements and composition impact pollinator communities and pollination services

1.3.1. Landscape composition affects the spatial distribution of pollination services

Semi-natural elements exerted the strongest and most consistent positive influence on pollinators and pollination. The area they covered in the surroundings of our experiments were identified as major predictors in number and diversity of plant-pollinator interactions and in pollination outcomes as shown in Chapters 2, 4, and 5. Our findings are consistent with the existing literature showing that semi-natural elements play a central role in supporting

pollinators and pollination (Carvalho et al., 2011; Rivers-Moore et al., 2020; Eeraerts, 2023). They are key elements in agricultural landscapes through the provision of both floral and nesting resources (Rollin et al., 2015; Cole et al., 2017), that are scarce in intensively cultivated landscapes. Timberlake et al. (2019) highlighted a lack of nectar production for bumblebees during March and August-September on Southwestern UK farms. And more recently, Bishop et al. (2024) found floral resource limitations for bumblebees and solitary bees in late June and July at both local and landscape scales. This scarcity of resources is particularly pronounced in our study area, as Eure-et-Loir is the French department with by far the highest proportion of land area occupied by large-scale monocultures (68% of its total surface, source: www.insee.fr). Concerning semi-natural elements, hedgerows and forest edges host plant species that are not present in fields and ensure continuous floral availability throughout the season (Donkersley, 2019), while also offering nesting sites in stable elements such as trees (Ouin et al., 2015), bare soil, and offer nesting construction resources for pollinators such as wild bees (Requier and Leonhardt, 2020). Grassland can also enhance pollinator abundance and spillover into surrounding croplands, by providing key habitats for bees pollinator, especially for larger grassland areas (Klaus et al., 2021). By combining these functions, semi-natural elements enhance pollinator diversity and resilience, thereby sustaining and possibly improving pollination services in intensive agricultural landscapes (Eeraerts et al., 2019; Raderschall et al., 2021).

Oilseed rape also had a strong effect on pollinator communities and pollination. This mass-flowering crops provides abundant floral resources in March-April for early active pollinators, and our analysis revealed that continuity of oilseed rape in the landscape from one year to another enhanced both the number of plant–pollinator interactions and the yield differences between open and pollinator-excluded treatments. This pattern supports the hypothesis that oilseed rape in the previous year can influence pollinator abundance and activity in the following year. Pollinators that benefited from the abundant floral resources provided by oilseed rape are more likely to be more abundant near these past mass-flowering areas in the subsequent year. These observed responses can be linked to the annual dynamics and spillover of pollinators associated with oilseed rape (Riedinger et al., 2015). Similarly to Van Reeth et al. (2019) who tested the influence of oilseed rape area on the abundance of wild bees in grasslands, we observed in Chapter 2 a slight negative trend in the number of pollinator visits to wild plants when the area of oilseed rape increased. We also found that oilseed rape area tended to increase the yield difference between open and pollinator-excluded treatments. This pattern may indicate a stronger attraction of pollinators towards the crop.

By contrast, the effect of past crop diversity was limited in our analyses, probably due to the generally low crop heterogeneity and very low area of flowering crops other than oilseed rape.

Crop heterogeneity, calculated through a Shannon index, is generally low in the large monocultures of the Paris Basin, which are dominated by a wheat–barley–oilseed rape rotation. Moreover, the combined benefits of crop heterogeneity and semi-natural elements for pollinators (Aguilera et al., 2020) are also limited by the scarcity of such habitats in these landscapes. Nevertheless, crop diversification remains a powerful lever to enhance biodiversity in agricultural landscapes (Sirami et al., 2019; Beillouin et al., 2021). Implementing both crop and landscape heterogeneity in particularly homogeneous territories could therefore represent a promising strategy to restore more biodiversity friendly-farmland and reinforce ecological functions (Priyadarshana et al., 2024). Moreover, reducing field size while increasing heterogeneity in the landscape has been shown to enhance natural pest control (Tibi et al., 2023). Such structural diversification could also benefit pollination services by promoting habitat connectivity and resource availability for pollinators, thereby contributing to the multifunctionality of agroecosystems (Lundin et al., 2021).

1.3.2. Herbaceous field margins can provide complementary floral resources for pollinators.

The results presented in Chapter 2 indicate that wildflowers along herbaceous field margins host distinct pollinator assemblages compared to oilseed rape, highlighting their potential role in complementing crop resources. This effect is all the more remarkable given that the studied herbaceous field margins were relatively poor in species composition, since we chose the most similar plant species compositions possible. Wild plants are essential for pollinator conservation (Williams et al., 2015; Grass et al., 2016). Previous studies have already highlighted the importance of weeds in maintaining diverse plant–pollinator communities and interaction networks (Gibson et al., 2006; Carvalheiro et al., 2011). Such floral resources are thus crucial in agricultural landscapes, particularly in intensively managed systems where they remain scarce, whether along field margins (Lowe et al., 2021), within fields (Balfour and Ratnieks, 2022), or in dedicated agroecological structures (Scheper et al., 2015) and can even be useful for neighbor flowering crops (Sutter et al., 2018a).

1.3.3. Broader spatialization approaches and their relationship with the landscape

Finally, our spatialized index of pollination, which was based not on *in situ observations* but on yield data obtained from farmers, provided an innovative perspective. In Chapter 2, we assessed differences in yields between open and caged pollination treatments on oilseed rape, and in Chapter 4 we compared a yield-based pollination index with the potential pollination index derived from the InVEST landscape model (Sharp et al., 2018). These complementary approaches allowed us to establish important links between crop yields, landscape predictors, and modelled pollinator supply. To further explore the potential applications of the realized

pollination index, it could be used to quantify pollination in areas where pollinator-friendly practices are implemented, such as reduced pesticide use or the establishment of biodiversity-enhancing structures such as flower strips. With further refinement, the index could directly quantify the contribution of these structures, including small landscape features, to pollination and their cumulative benefits for pollinator-dependent crops. In this way, the realized pollination index offers a way to evaluate how landscape and crop diversity jointly influence pollination services and the possible resulting yield gains. In doing so, it opens perspective to design agricultural landscapes that better support pollinators and pollination services with an index based on crop yields, echoing recent advances in landscape modeling based on land use, land cover, and expert knowledge (Desaegher et al., 2021).

2.2. Effects of pesticide use on pollinator communities and resulting pollination services

While numerous studies have addressed the effects of pesticides on pollinator abundance and diversity (e.g. Main et al., 2020; Dicks et al., 2021), far fewer have directly examined their consequences on realized pollination (e.g. Gillespie et al., 2014; Das et al., 2025). This work therefore provides an original contribution by linking pesticide use to both pollinator communities and the pollination service itself. Beyond the effects of landscape composition, pesticide use had consistent negative impacts on pollinators and pollination services across both field and landscape scales. The field data we collected, together with the national Solagro database, allowed us to estimate the impacts of pesticide use on pollinator communities and pollination at both the field and landscape scales. The results presented in Chapters 2, 4, and 5 consistently demonstrate a negative effect of pesticides on pollinators and the pollination services. Few studies have simultaneously considered pesticide use at both the field and landscape levels (Bloom et al., 2021). Our findings suggest that exposure of some landscapes, or more locally some fields, to intensive pesticide use negatively affects pollinator presence and the resulting pollination service, as highlighted by the impact of local practices on pollination index in Chapter 4. These results are consistent with the existing literature and corroborate studies showing negative impacts of pesticide use on wild bees at different scales. For instance, (C. A. Brittain et al., 2010b) demonstrated that on the long run, applications of insecticides within the same fields over a season can lead to cumulative effects, progressively reducing wild bee species richness and abundance. This effect is particularly strong when pollinators are exposed to a constant pressure year after year, highlighting their potential for long-term declines under sustained pesticide pressure (Woodcock et al., 2016; Janousek et al., 2023). Contamination of the pollinators can be caused through multiple ways from direct spraying to contaminated pollen and nectar (Stanley and Preetha, 2016), and laboratory experiments confirm these results proving that pesticides cause direct mortality and less

effective visitation (Siviter et al., 2024). In addition to insecticides, herbicide use can also indirectly affect pollinators by reducing the availability and diversity of floral resources within and around fields (Bretagnolle and Gaba, 2015), thereby limiting foraging opportunities and weakening the overall resilience of pollinator communities.

In our work, we considered agricultural practices through the (narrow) lens of pesticide use, acknowledging that, together with habitat loss, they are the main drivers of biodiversity loss in agricultural landscapes (Brunet and Fragoso, 2024). Beyond the use of pesticides calculated through the Treatment Frequency Index, future work could benefit from refined metrics, such as indicators of pesticides toxicity, as not all products exert equal effects. Linking the toxicity of specific active ingredients, mixtures and possible cocktail effects to the use made on the field would allow for a more detailed assessment of how particular products impact biodiversity (Cairo et al., 2024; Carozzi et al., 2024). A greater availability of data regarding pesticide application rates would further enhance the capacity to investigate these effects in depth. Moreover, these effects can also be confounded with those of other associated practices. For instance, tillage is well known to strongly impact beneficial insect populations, including pollinators (Ullmann et al., 2016; Christmann, 2022), while nitrogen fertilization can influence pollinators indirectly through its effects on plant communities in fields and field margins (Fried et al., 2018).

2.3. Synergies between pollination and biological pest control

An important question for the multifunctionality of agroecosystems is whether the ecological contexts that promote pollination also favor biological pest control, thereby generating synergies between these two services. Our results provide partial support for such complementarities: pollination and biological control were positively correlated, although these relationships were not always significant and their strength varied across landscapes and farming practices. These potential synergies likely arise because both services are mediated by insect communities that respond similarly to ecological drivers—being enhanced by floral resource availability within and around fields and constrained by pesticide use and habitat simplification. This pattern echoes findings from previous studies showing that pollination and biological pest control can respond in similar ways to landscape heterogeneity and farming practices, but not systematically (Gonthier et al., 2014; Kovács-Hostyánszki et al., 2017; Lundin et al., 2021). Their response to biodiversity-friendly measures may also vary, as shown by Hussain et al. (2021), who reported a positive response of pollinators to the establishment of grasslands, whereas biological pest control showed no such effect. These relationships can be very context dependent, which limits their generalization, as most studies are conducted like ours in specific crop and landscape settings—here in intensive monoculture systems—where local effects may be strongly modulated by surrounding landscape composition and

configuration. Together, these results highlight that while opportunities exist to foster both services simultaneously, their joint management requires a nuanced understanding of ecological trade-offs and synergies across agricultural landscapes (Bartual et al., 2019) and agricultural practices.

An important limitation of our study lies in the way we assessed biological pest control. Our measurements were restricted to parasitism rates, without quantifying the pest populations themselves on the fields. A broader framework, integrating both pollinators, crop pests, and their natural enemies, would allow a more comprehensive understanding of the environmental parameters and mechanisms driving the dynamics of multiple ecosystem services simultaneously, but it will require even more field work. Such an approach seems particularly relevant in the current context of increasing pest resistance to pesticides (Hervé, 2018), especially considering that our results highlight strong negative impacts of chemical applications on non-target organisms. Furthermore, our observations in Chapter 2 revealed a high affinity of parasitoid wasps for wildflowers along herbaceous field margins, underscoring the importance of these floral resources for the conservation of natural enemies. This pattern aligns with results from a study in apple orchards, where trees associated with *Veronica persica* exhibited a higher parasitism rate (Laffon et al., 2025). Our findings suggest that enhancing semi-natural habitats and floral resources can be a good way to improve conservation biological control (Serée et al., 2023). Altogether, these considerations point toward a broader reflection on agricultural practices, emphasizing the need to design management strategies that simultaneously support multiple services, including pollination and biological pest control (Lundin et al., 2021). As we have shown, even small habitats, such as field and road margins, can play a crucial role in this regard and should be managed to maximize their potential for biodiversity.

2.4. Conclusion

Taken together, our work and the existing literature highlight that the mechanisms driving pollinator presence and pollination services are inherently complex. While pesticide use exerts consistent negative effects, these impacts do not occur in isolation but interact with other agricultural practices and with the structure of the surrounding landscape (Nicholson et al., 2017). Semi-natural elements can buffer pesticide impacts to some extent, mitigating pollinator declines and supporting the persistence of pollination services (Park et al., 2015; Gebhardt et al., 2025). However, we showed that presence of semi-natural elements doesn't neutralize totally the effect of pesticides. As recently emphasized by Gebhardt et al. (2025), rethinking agricultural landscapes cannot be achieved by considering pesticide use and landscape composition as separate drivers; instead, it requires an integrated perspective that accounts for their synergistic and often interacting effects on pollinators and the services they provide.

3. Perspectives opened by this work and possible integration in public policies.

3.1. An ambitious national plan for the conservation of pollinating insects.

This thesis was embedded within the broader framework of European and national strategies for the protection of pollinators and pollination. These policy strategies play a crucial role in the translation of scientific research into concrete measures. At the national level, the French Pollinator Plan sets out a series of actions for the preservation of pollinators and pollination, structured around six thematic axes that combine knowledge acquisition with operational measures. I did not conduct species level inventories and identification that directly contribute to Red List assessments and/or targeted conservation of endangered species. Instead, I developed a framework for measuring pollination services in agricultural landscapes. By linking pollination to crop yields and to landscape management, our results highlight the agronomic importance of pollinators, thus providing indirect but useful arguments for their conservation within policy frameworks through the services they provide. This thesis is directly in line with the actions outlined in section 1.1, which aims to develop and strengthen knowledge on the ecology of wild pollinators, as well as to Action 1.3, dedicated to studying the impacts of global change, human activities, and sanitary risks on pollinators and on the ecological function of pollination in both wild plants and agricultural systems. This first axis, centered on the production of scientific knowledge, provides a fundamental basis for more applied actions within the National Plan, such as the revision of pesticide use during flowering periods or the technical and economic support for agricultural practices and landscape management favorable to pollinators and pollination services.

In the same vein, other national programs can operate in synergy with the French National Pollinator Plan. For instance, my thesis contributes to the Ecophyto 2030 strategy, a national framework aimed at reducing pesticide use by 50% by 2030. Within this strategic plan, our research provides scientific evidence of the negative impacts of pesticides on pollination and biological pest control services, thereby supporting the development of alternative solutions to pesticide use and reinforcing the objectives of the National Pollinator Plan. National strategies need to be supported by elected representatives, who play a decisive role in decision-making. For example, (Meunier and Hott, 2024) conducted a fact-finding mission on the integration of biodiversity into agricultural landscapes, aimed at synthesizing scientific knowledge for their peers to inform further decisions.

At the European level, the EU Pollinator Monitoring Scheme (EU-PoMS) was recently launched. It is a standardized, EU-wide initiative designed to track the status and trends of key

pollinator groups (bees, butterflies, hoverflies, moths, and threatened species) through cost-effective monitoring of more than 2,000 sites across Europe. Its aim is to provide robust indicators for biodiversity policy and the Common Agricultural Policy, while mobilizing both scientists and citizen science to generate high-quality data for conservation and decision-making. Beyond improving our knowledge of pollinator populations, one of the most urgent priorities is to ensure the preservation of all pollinators, regardless of their conservation status, given that the main drivers of their decline are already well identified and documented.

3.2. ...with applications and policy decisions that fail to follow

Despite these numerous ambitious national and European strategies, the situation remains concerning. Even with our simplified assessment of plant–pollinator interactions, the deleterious effects of pesticide use were clearly detectable. However, the translation of scientific data and ecological knowledge into strong political decisions is still limited (Gemmell-Herren et al., 2021). The evaluation of the first French National Pollinator Plan (2016–2021) illustrates this, noting that the measures implemented were insufficient to halt the decline of pollinating insects (Plan national d'action, 2021). Similarly, the Ecophyto plan (2008–2018), which aimed to significantly reduce pesticide use, did not achieve its objectives, as no substantial decrease in sales or applications was observed (Hossard et al., 2017). The subsequent plan, initially targeting 2025, also failed, and the current goal now aims for a 50% reduction in pesticide use by 2030. Our results, however, clearly demonstrate that pesticide use strongly affects the spatial distribution of pollinators and pollination services, indicating that reducing pesticide pressure represents an urgent lever for action. While it costs little to state that pesticides harm pollinators, the economic incentive for action remains limited: the yield benefits provided by pollinators are often difficult to quantify, the price of insecticides is particularly low and most of the high-revenue crops (such as cereals, sugar beet, or potatoes) are only marginally or not dependent on animal pollination (Klein et al., 2007). To move forward, it may be more effective to focus on territories where agriculture strongly relies on pollinators, such as fruit orchards and vegetable production, and to capitalize on the growing public awareness regarding biodiversity, food quality and local production. In this perspective, the re-location of food production appears central and is supported by recent foresight on the future of agriculture (Billen et al., 2021; Mora et al., 2023). Supporting pollinator-dependent crops at the territorial scale could not only strengthen local food systems but also engage consumers in promoting production models that rely on functional biodiversity.

These failures highlight a structural difficulty: most of these strategies rely on voluntary participation by stakeholders, without real regulatory enforcement. Yet, despite the accumulation of scientific evidence documenting the deleterious effects of pesticides and intensive agricultural practices on biodiversity (Geiger et al., 2010; Akinsorotan et al., 2023;

Rigal et al., 2023), production systems continue to rely on a model that is destructive to living organisms. In the absence of binding measures and genuine support for the transition, biodiversity is rarely given the opportunity to recover, and decline dynamics continue unabated. Implementing a precautionary principle to protect pollinators is therefore essential, yet such measures face significant challenges due to competing economic interests (Drivdal and van der Sluijs, 2021).

More recently, there has even been a certain backsliding in some France's compared to its past record of environmental and health decisions. A striking example is the proposed law to reauthorize acetamiprid, a neonicotinoid known for its particularly harmful impact on pollinators and primarily used on non-food crops such as sugar beet (Ligtelijn et al., 2024; Mamy et al., 2025). These decisions illustrate how the scope of conservation efforts is often constrained by political trade-offs that favour economic interests over ecosystem preservation. Our results, together with the existing scientific literature, highlight the negative impacts of these pesticides on pollinators and pollination, raising a more fundamental question: should the agricultural model not be reconsidered, prioritizing local food crops rather than industrialized productions such as rapeseed for biofuels or processed sugar beet, which require pesticide use, in order to allow biodiversity to recover while ensuring food security?

Overall, political decisions tend to favour agro-industrial interests and increasing simplification of agricultural landscapes, whereas the conclusions of most ecological studies such as ours point in the exact opposite direction.

3.3. Disseminate local knowledge and experiences to generalize effective models.

My thesis is embedded in a broader context of national and European research initiatives aiming to deepen scientific knowledge on pollinators and pollination. Increasingly, these projects adopt participatory approaches, co-designing solutions with local stakeholders. For instance, the BE-CREATIVE project (Built pEstiCide-free agRoecosystEms At TerrItory leVEL) seeks to develop pesticide-free agricultural territories by combining agronomic, ecological, and organizational innovations with the active involvement of local actors. Similarly, European initiatives such as RestPoll (<https://restpoll.eu/>) integrate scientific knowledge production with horizontal, participatory approaches, exploring the relationships between pollinators, landscapes, and farming practices, and addressing pesticide reduction in direct connection with pollinator conservation.

In this context, our work contributes directly to these efforts. We worked with farmers on experimental schemes and tried to extend our plant pollinator observations through a collaborative protocol with INRAE Gotheron. This collaboration also gave us the opportunity

to participate in a *Café Agro*, a horizontal exchange platform between researchers and farmers, and the one I participated in focused on biodiversity assessment within agricultural fields. These local initiatives, combined with our tools, could be further developed to design agricultural landscapes that explicitly account for pollination from the outset, ensuring that ecosystem services are considered in land-use planning.

Beyond these initiatives, local research efforts and participatory experiments could further benefit from the tools developed in my thesis to design agricultural arrangements that integrate pollination considerations from the outset. It is crucial to document and scientifically support all approaches that promote biodiversity, particularly pollinators, while ensuring that knowledge is disseminated, simplified, and horizontally transferred. Several initiatives already contribute to this effort, such as the national mapping of pollinator-friendly actions developed within the framework of the *Plan national pollinisateurs* (<https://www.contratsolutions-agriculture-pollinisateurs.fr/>), or digital resource-sharing platforms like OSAÉ (<https://osez-agroecologie.org>), which draws on concrete and diverse examples of agroecological practices implemented on farms. Promoting ecologically sustainable, locally adapted food crops rather than industrial monocultures for export or processing is also crucial. Participatory approaches with farmers, such as flower strip plantings, have shown promising results (Hölting et al., 2022), but scaling up these actions, creating collectives, and linking them to policy frameworks will be essential to strengthen local dynamics and achieve meaningful conservation outcomes. Beyond academic and institutional initiatives, associations also play a key role in bridging the gap between science and practice. Through awareness-raising, knowledge dissemination, and on-farm support, organizations such as Arthropologia (<https://www.arthropologia.org/#>) or Réensauvager la ferme (<https://reensauvagerlaferme.fr/>) actively help farmers to better understand, welcome, and value biodiversity within their production systems. These initiatives illustrate how collective action can complement scientific research by fostering practical changes and long-term commitment to more ecological farming practices.

4. More general thoughts opened during this thesis

In line with our values of biodiversity conservation and reducing impacts of climate change, we also experimented with a combination of cycling and train travel to replace the numerous car journeys required for fieldwork (over 20,000 km in total). These trials showed that while travel between sites was slower, it was still possible to complete all scheduled surveys within a single day under favourable weather conditions. However, as pollinator observations depended on the presence of sunshine, the timing became too tight to finish all the surveys on time when we needed to wait for an observation session. Beyond logistics, these experiences allowed us to approach fieldwork with less stress and to value travel time differently (Munch,

2020). They highlight the potential of moving towards a form of “slow science,” in which protocols and sampling designs should be rethought so that research can be carried out using low-carbon modes of transportation (Nathans and Sterling, 2016; Ro, 2023). Such a shift would represent an important step towards making ecological research more consistent with its own objectives of environmental responsibility.

Moreover, our fieldwork often generated curiosity among local residents and neighbouring farmers we encountered. Most people expressed genuine interest and frequently asked questions about our activities, which reinforced the idea that scientific protocols should be designed in a way that allows anyone to engage with pollinators and assess potential impacts. This experience underlined the importance of making research approaches more open and accessible, not only to the scientific community but also to the broader public.

References

- Abdala-Roberts, L., Puentes, A., Finke, D.L., Marquis, R.J., Montserrat, M., Poelman, E.H., Rasmann, S., Sentis, A., Van Dam, N.M., Wimp, G., Mooney, K., Björkman, C., 2019. Tri-trophic interactions: bridging species, communities and ecosystems. *Ecol. Lett.* 22, 2151–2167. <https://doi.org/10.1111/ele.13392>
- Abrahamczyk, S., Kessler, M., Roth, T., Heer, N., 2022. Temporal changes in the Swiss flora: implications for flower-visiting insects. *BMC Ecol. Evol.* 22, 109. <https://doi.org/10.1186/s12862-022-02061-2>
- Aguilera, G., Roslin, T., Miller, K., Tamburini, G., Birkhofer, K., Caballero-Lopez, B., Lindström, S.A.-M., Öckinger, E., Rundlöf, M., Rusch, A., Smith, H.G., Bommarco, R., 2020. Crop diversity benefits carabid and pollinator communities in landscapes with semi-natural habitats. *J. Appl. Ecol.* 57, 2170–2179. <https://doi.org/10.1111/1365-2664.13712>
- Aizen, M.A., Aguiar, S., Biesmeijer, J.C., Garibaldi, L.A., Inouye, D.W., Jung, C., Martins, D.J., Medel, R., Morales, C.L., Ngo, H., Pauw, A., Paxton, R.J., Sáez, A., Seymour, C.L., 2019. Global agricultural productivity is threatened by increasing pollinator dependence without a parallel increase in crop diversification. *Glob. Change Biol.* 25, 3516–3527. <https://doi.org/10.1111/gcb.14736>
- Akinsorotan, O.A., Akinsorotan, A.M., Adewale, R.O., Akande, A.B., 2023. Detrimental Effects of Agrochemical-Based Agricultural Intensification on Biodiversity: Evidence from Some Past Studies, in: Ogwu, M.C., Chibueze Izah, S. (Eds.), *One Health Implications of Agrochemicals and Their Sustainable Alternatives*. Springer Nature, Singapore, pp. 275–298. https://doi.org/10.1007/978-981-99-3439-3_10
- Albrecht, M., Duelli, P., Obrist, M.K., Kleijn, D., Schmid, B., 2009. Effective Long-Distance Pollen Dispersal in *Centaurea jacea*. *PLOS ONE* 4, e6751. <https://doi.org/10.1371/journal.pone.0006751>
- Albrecht, M., Kleijn, D., Williams, N.M., Tschumi, M., Blaauw, B.R., Bommarco, R., Campbell, A.J., Dainese, M., Drummond, F.A., Entling, M.H., Ganser, D., Arjen de Groot, G., Goulson, D., Grab, H., Hamilton, H., Herzog, F., Isaacs, R., Jacot, K., Jeanneret, P., Jonsson, M., Knop, E., Kremen, C., Landis, D.A., Loeb, G.M., Marini, L., McKerchar, M., Morandin, L., Pfister, S.C., Potts, S.G., Rundlöf, M., Sardiñas, H., Sciligo, A., Thies, C., Tschamntke, T., Venturini, E., Veromann, E., Vollhardt, I.M.G., Wäckers, F., Ward, K., Westbury, D.B., Wilby, A., Woltz, M., Wratten, S., Sutter, L., 2020. The effectiveness of flower strips and hedgerows on pest control, pollination services and crop yield: a quantitative synthesis. *Ecol. Lett.* 23, 1488–1498. <https://doi.org/10.1111/ele.13576>
- Albrecht, M., Schmid, B., Hautier, Y., Müller, C.B., 2012. Diverse pollinator communities enhance plant reproductive success. *Proc. R. Soc. B Biol. Sci.* 279, 4845–4852. <https://doi.org/10.1098/rspb.2012.1621>
- Alignier, A., Solé-Senan, X.O., Robleño, I., Baraibar, B., Fahrig, L., Giralt, D., Gross, N., Martin, J.-L., Recasens, J., Sirami, C., Siriwardena, G., Bøsem Baillod, A., Bertrand, C., Carrié, R., Hass, A., Henckel, L., Miquet, P., Badenhauer, I., Baudry, J., Bota, G., Bretagnolle, V., Brotons, L., Burel, F., Calatayud, F., Clough, Y., Georges, R., Gibon, A., Girard, J., Lindsay, K., Minano, J., Mitchell, S., Patry, N., Poulin, B., Tschamntke, T., Vialatte, A., Violle, C., Yaverscovski, N., Batáry, P., 2020. Configurational crop

- heterogeneity increases within-field plant diversity. *J. Appl. Ecol.* 57, 654–663. <https://doi.org/10.1111/1365-2664.13585>
- Allart, R., Ricci, B., Poggi, S., 2021. Procédure alm de cartographie automatique du paysage. *Cah. Tech. INRA* 103, 12.
- Ammann, L., Boser-Baillod, A., Herzog, F., Frey, D., Entling, M.H., Albrecht, M., 2024. Spatio-temporal complementarity of floral resources sustains wild bee pollinators in agricultural landscapes. *Agric. Ecosyst. Environ.* 359, 108754. <https://doi.org/10.1016/j.agee.2023.108754>
- Ansquer, P., Al Haj Khaled, R., Cruz, P., Theau, J.-P., Therond, O., Duru, M., 2009. Characterizing and predicting plant phenology in species-rich grasslands. *Grass Forage Sci.* 64, 57–70. <https://doi.org/10.1111/j.1365-2494.2008.00670.x>
- Anstett, M.-C., Duchet-Annez, M., Denis, C., 2022. Projet Cassis : Approche pluridisciplinaire pour des mesures agro écologiques. *Bourgogne-Franche-Comté Nat.*
- Aviron, S., Nitsch, H., Jeanneret, P., Buholzer, S., Luka, H., Pfiffner, L., Pozzi, S., Schüpbach, B., Walter, T., Herzog, F., 2009. Ecological cross compliance promotes farmland biodiversity in Switzerland. *Front. Ecol. Environ.* 7, 247–252. <https://doi.org/10.1890/070197>
- Balbuena, M.S., Tison, L., Hahn, M.-L., Greggers, U., Menzel, R., Farina, W.M., 2015. Effects of sublethal doses of glyphosate on honeybee navigation. *J. Exp. Biol.* 218, 2799–2805. <https://doi.org/10.1242/jeb.117291>
- Baldock, K.C., 2020. Opportunities and threats for pollinator conservation in global towns and cities. *Curr. Opin. Insect Sci., Ecology • Parasites/Parasitoids/Biological control* 38, 63–71. <https://doi.org/10.1016/j.cois.2020.01.006>
- Baldock, K.C.R., Goddard, M.A., Hicks, D.M., Kunin, W.E., Mitschunas, N., Osgathorpe, L.M., Potts, S.G., Robertson, K.M., Scott, A.V., Stone, G.N., Vaughan, I.P., Memmott, J., 2015. Where is the UK's pollinator biodiversity? The importance of urban areas for flower-visiting insects. *Proc. R. Soc. B Biol. Sci.* 282, 20142849. <https://doi.org/10.1098/rspb.2014.2849>
- Balfour, N.J., Ratnieks, F.L.W., 2022. The disproportionate value of ‘weeds’ to pollinators and biodiversity. *J. Appl. Ecol.* 59, 1209–1218. <https://doi.org/10.1111/1365-2664.14132>
- Ball, L., Still, R., Riggs, A., Skilbeck, A., Shardlow, M., Whitehouse, A., Tinsley-Marshall, P., 2022. Bugs Matter: Citizen Science Survey of Insect Decline Using Vehicle Number Plates.
- Banaszak-Cibicka, W., Żmihorski, M., 2020. Are cities hotspots for bees? Local and regional diversity patterns lead to different conclusions. *Urban Ecosyst.* 23, 713–722. <https://doi.org/10.1007/s11252-020-00972-w>
- Banks, J.E., Banks, H.T., Myers, N., Laubmeier, A.N., Bommarco, R., 2020. Lethal and sublethal effects of toxicants on bumble bee populations: a modelling approach. *Ecotoxicology* 29, 237–245. <https://doi.org/10.1007/s10646-020-02162-y>
- Bänsch, S., Tschardtke, T., Gabriel, D., Westphal, C., 2021. Crop pollination services: Complementary resource use by social vs solitary bees facing crops with contrasting flower supply. *J. Appl. Ecol.* 58, 476–485. <https://doi.org/10.1111/1365-2664.13777>
- Barrett, M., Fischer, B., 2024. Ethical issues in lethal insect monitoring. *Curr. Opin. Insect Sci.* 66, 101279. <https://doi.org/10.1016/j.cois.2024.101279>

- Bartholomée, O., Aullo, A., Becquet, J., Vannier, C., Lavorel, S., 2020. Pollinator presence in orchards depends on landscape-scale habitats more than in-field flower resources. *Agric. Ecosyst. Environ.* 293, 106806. <https://doi.org/10.1016/j.agee.2019.106806>
- Bartholomée, O., Lavorel, S., 2019. Disentangling the diversity of definitions for the pollination ecosystem service and associated estimation methods. *Ecol. Indic.* 107, 105576. <https://doi.org/10.1016/j.ecolind.2019.105576>
- Bartomeus, I., Gagic, V., Bommarco, R., 2015. Pollinators, pests and soil properties interactively shape oilseed rape yield. *Basic Appl. Ecol.* 16, 737–745. <https://doi.org/10.1016/j.baae.2015.07.004>
- Bartual, A.M., Sutter, L., Bocci, G., Moonen, A.-C., Cresswell, J., Entling, M., Giffard, B., Jacot, K., Jeanneret, P., Holland, J., Pfister, S., Pintér, O., Veromann, E., Winkler, K., Albrecht, M., 2019. The potential of different semi-natural habitats to sustain pollinators and natural enemies in European agricultural landscapes. *Agric. Ecosyst. Environ.* 279, 43–52. <https://doi.org/10.1016/j.agee.2019.04.009>
- Basu, P., Ngo, H.T., Aizen, M.A., Garibaldi, L.A., Gemmill-Herren, B., Imperatriz-Fonseca, V., Klein, A.M., Potts, S.G., Seymour, C.L., Vanbergen, A.J., 2024. Pesticide impacts on insect pollinators: Current knowledge and future research challenges. *Sci. Total Environ.* 954, 176656. <https://doi.org/10.1016/j.scitotenv.2024.176656>
- Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting Linear Mixed-Effects Models Using lme4. *J. Stat. Softw.* 67, 1–48. <https://doi.org/10.18637/jss.v067.i01>
- Bedessem, B., Julliard, R., Montuschi, E., 2021. Measuring epistemic success of a biodiversity citizen science program: A citation study. *PLOS ONE* 16, e0258350. <https://doi.org/10.1371/journal.pone.0258350>
- Begg, G.S., Cook, S.M., Dye, R., Ferrante, M., Franck, P., Lavigne, C., Lövei, G.L., Mansion-Vaquie, A., Pell, J.K., Petit, S., Quesada, N., Ricci, B., Wratten, S.D., Birch, A.N.E., 2017. A functional overview of conservation biological control. *Crop Prot., Pesticide use and risk reduction with IPM* 97, 145–158. <https://doi.org/10.1016/j.cropro.2016.11.008>
- Beillouin, D., Ben-Ari, T., Malézieux, E., Seufert, V., Makowski, D., 2021. Positive but variable effects of crop diversification on biodiversity and ecosystem services. *Glob. Change Biol.* 27, 4697–4710. <https://doi.org/10.1111/gcb.15747>
- Bennett, A.B., Lovell, S., 2019. Landscape and local site variables differentially influence pollinators and pollination services in urban agricultural sites. *PLOS ONE* 14, e0212034. <https://doi.org/10.1371/journal.pone.0212034>
- Bennett, J.M., Steets, J.A., Burns, J.H., Burkle, L.A., Vamosi, J.C., Wolowski, M., Arceo-Gómez, G., Burd, M., Durka, W., Ellis, A.G., Freitas, L., Li, J., Rodger, J.G., Ștefan, V., Xia, J., Knight, T.M., Ashman, T.-L., 2020. Land use and pollinator dependency drives global patterns of pollen limitation in the Anthropocene. *Nat. Commun.* 11, 3999. <https://doi.org/10.1038/s41467-020-17751-y>
- Benvenuti, S., 2024. Weed Role for Pollinator in the Agroecosystem: Plant–Insect Interactions and Agronomic Strategies for Biodiversity Conservation. *Plants* 13, 2249. <https://doi.org/10.3390/plants13162249>
- Berger, J.S., Birkhofer, K., Hanson, H.I., Hedlund, K., 2018. Landscape configuration affects herbivore–parasitoid communities in oilseed rape. *J. Pest Sci.* 91, 1093–1105. <https://doi.org/10.1007/s10340-018-0965-1>

- Beyer, N., Gabriel, D., Westphal, C., 2021. Contrasting effects of past and present mass-flowering crop cultivation on bee pollinators shaping yield components in oilseed rape. *Agric. Ecosyst. Environ.* 319, 107537. <https://doi.org/10.1016/j.agee.2021.107537>
- Biesmeijer, J.C., Roberts, S.P.M., Reemer, M., Ohlemüller, R., Edwards, M., Peeters, T., Schaffers, A.P., Potts, S.G., Kleukers, R., Thomas, C.D., Settele, J., Kunin, W.E., 2006. Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. *Science* 313, 351–354. <https://doi.org/10.1126/science.1127863>
- Billen, G., Aguilera, E., Einarsson, R., Garnier, J., Gingrich, S., Grizzetti, B., Lassaletta, L., Le Noë, J., Sanz-Cobena, A., 2021. Reshaping the European agro-food system and closing its nitrogen cycle: The potential of combining dietary change, agroecology, and circularity. *One Earth* 4, 839–850. <https://doi.org/10.1016/j.oneear.2021.05.008>
- Biodiversity for food and agriculture and ecosystem services, 2020. . FAO. <https://doi.org/10.4060/cb0649en>
- Birdshire, K.R., Carper, A.L., Briles, C.E., 2020. Bee community response to local and landscape factors along an urban-rural gradient. *Urban Ecosyst.* 23, 689–702. <https://doi.org/10.1007/s11252-020-00956-w>
- Bishop, G.A., Fijen, T.P.M., Raemakers, I., van Kats, R.J.M., Kleijn, D., 2024. Bees go up, flowers go down: Increased resource limitation from late spring to summer in agricultural landscapes. *J. Appl. Ecol.* 61, 431–441. <https://doi.org/10.1111/1365-2664.14576>
- Blaauw, B.R., Isaacs, R., 2014. Flower plantings increase wild bee abundance and the pollination services provided to a pollination-dependent crop. *J. Appl. Ecol.* 51, 890–898. <https://doi.org/10.1111/1365-2664.12257>
- Blareau, E., Requier, F., 2025. Is Nocturnal Pollination Important for Crop Production? Experimental Evidence From Small Fruit Crops. *J. Appl. Entomol.* <https://doi.org/10.1111/jen.70019>
- Blareau, E., Sy, P., Daoud, K., Requier, F., 2023. Insect-Mediated Pollination of Strawberries in an Urban Environment. *Insects* 14, 877. <https://doi.org/10.3390/insects14110877>
- Bloom, E.H., Wood, T.J., Hung, K.-L.J., Ternest, J.J., Ingwell, L.L., Goodell, K., Kaplan, I., Szendrei, Z., 2021. Synergism between local- and landscape-level pesticides reduces wild bee floral visitation in pollinator-dependent crops. *J. Appl. Ecol.* 58, 1187–1198. <https://doi.org/10.1111/1365-2664.13871>
- Bommarco, R., 2024. Ecological redesign of crop ecosystems for reliable crop protection. A review. *Agron. Sustain. Dev.* 44, 51. <https://doi.org/10.1007/s13593-024-00987-z>
- Bommarco, R., Kleijn, D., Potts, S.G., 2013. Ecological intensification: harnessing ecosystem services for food security. *Trends Ecol. Evol.* 28, 230–238. <https://doi.org/10.1016/j.tree.2012.10.012>
- Bosch, J., Martín González, A.M., Rodrigo, A., Navarro, D., 2009. Plant–pollinator networks: adding the pollinator’s perspective. *Ecol. Lett.* 12, 409–419. <https://doi.org/10.1111/j.1461-0248.2009.01296.x>
- Bowler, D.E., Bjorkman, A.D., Dornelas, M., Myers-Smith, I.H., Navarro, L.M., Niamir, A., Supp, S.R., Waldock, C., Winter, M., Vellend, M., Blowes, S.A., Böhning-Gaese, K., Bruelheide, H., Elahi, R., Antão, L.H., Hines, J., Isbell, F., Jones, H.P., Magurran, A.E., Cabral, J.S., Bates, A.E., 2020. Mapping human pressures on biodiversity across the planet uncovers anthropogenic threat complexes. *People Nat.* 2, 380–394. <https://doi.org/10.1002/pan3.10071>

- Brandes, M., Heimbach, U., Ulber, B., 2018. Effects of insecticide application on parasitism rates of pollen beetle larvae (*Brassicogethes aeneus* (Fabricius)) by tersilochine parasitoids. *Arthropod-Plant Interact.* 12, 799–809. <https://doi.org/10.1007/s11829-017-9580-y>
- Breeze, T.D., Bailey, A.P., Balcombe, K.G., Potts, S.G., 2011. Pollination services in the UK: How important are honeybees? *Agric. Ecosyst. Environ.* 142, 137–143. <https://doi.org/10.1016/j.agee.2011.03.020>
- Bretagnolle, V., Gaba, S., 2015. Weeds for bees? A review. *Agron. Sustain. Dev.* 35, 891–909. <https://doi.org/10.1007/s13593-015-0302-5>
- Brévault, T., Clouvel, P., 2019. Pest management: Reconciling farming practices and natural regulations. *Crop Prot.* 115, 1–6. <https://doi.org/10.1016/j.cropro.2018.09.003>
- Brittain, C., Bommarco, R., Vighi, M., Barmaz, S., Settele, J., Potts, S.G., 2010. The impact of an insecticide on insect flower visitation and pollination in an agricultural landscape. *Agric. For. Entomol.* 12, 259–266. <https://doi.org/10.1111/j.1461-9563.2010.00485.x>
- Brittain, C.A., Vighi, M., Bommarco, R., Settele, J., Potts, S.G., 2010a. Impacts of a pesticide on pollinator species richness at different spatial scales. *Basic Appl. Ecol.* 11, 106–115. <https://doi.org/10.1016/j.baae.2009.11.007>
- Brittain, C.A., Vighi, M., Bommarco, R., Settele, J., Potts, S.G., 2010b. Impacts of a pesticide on pollinator species richness at different spatial scales. *Basic Appl. Ecol.* 11, 106–115. <https://doi.org/10.1016/j.baae.2009.11.007>
- Brooks, M., Bolker, B., Kristensen, K., Maechler, M., Magnusson, A., McGillicuddy, M., Skaug, H., Nielsen, A., Berg, C., Benthams, K. van, Sadat, N., Lüdecke, D., Lenth, R., O'Brien, J., Geyer, C.J., Jagan, M., Wiernik, B., Stouffer, D.B., Agronah, M., Akdur, H.T.K., 2025. glmmTMB: Generalized Linear Mixed Models using Template Model Builder.
- Brooks, M.E., Kristensen, K., van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A., Skaug, H.J., Maechler, M., Bolker, B., 2017. glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modelling. *The R Journal.* 9, 378–400. <https://doi.org/10.32614/RJ-2017-066>
- Bruce, T.J.A., 2010. Tackling the threat to food security caused by crop pests in the new millennium. *Food Secur.* 2, 133–141. <https://doi.org/10.1007/s12571-010-0061-8>
- Bruckner, S., Wilson, M., Aurell, D., Rennich, K., vanEngelsdorp, D., Steinhauer, N., Williams, G.R., 2023. A national survey of managed honey bee colony losses in the USA: results from the Bee Informed Partnership for 2017–18, 2018–19, and 2019–20. *J. Apic. Res.* 62, 429–443. <https://doi.org/10.1080/00218839.2022.2158586>
- Brunet, J., Fragoso, F.P., 2024. What are the main reasons for the worldwide decline in pollinator populations? *CABI Rev.* 19. <https://doi.org/10.1079/cabireviews.2024.0016>
- Burkle, L.A., Alarcón, R., 2011. The future of plant–pollinator diversity: Understanding interaction networks across time, space, and global change. *Am. J. Bot.* 98, 528–538. <https://doi.org/10.3732/ajb.1000391>
- Buxton, M.N., Gaskett, A.C., Lord, J.M., Pattemore, D.E., 2022. A global review demonstrating the importance of nocturnal pollinators for crop plants. *J. Appl. Ecol.* 59, 2890–2901. <https://doi.org/10.1111/1365-2664.14284>
- Cabernard, L., Pfister, S., Hellweg, S., 2024. Biodiversity impacts of recent land-use change driven by increases in agri-food imports. *Nat. Sustain.* 7, 1512–1524. <https://doi.org/10.1038/s41893-024-01433-4>

- Cáceres, M.D., Jansen, F., Endicott, S., Dell, N., 2025. *indicspecies: Relationship Between Species and Groups of Sites*.
- Cairo, M., Monnet, A.-C., Robin, S., Porcher, E., Fontaine, C., 2024. Identifying pesticide mixtures at country-wide scale. *Peer Community J.* 4. <https://doi.org/10.24072/pcjournal.472>
- Calderini, D.F., Slafer, G.A., 1998. Changes in yield and yield stability in wheat during the 20th century. *Field Crops Res.* 57, 335–347. [https://doi.org/10.1016/S0378-4290\(98\)00080-X](https://doi.org/10.1016/S0378-4290(98)00080-X)
- Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., Narwani, A., Mace, G.M., Tilman, D., Wardle, D.A., Kinzig, A.P., Daily, G.C., Loreau, M., Grace, J.B., Larigauderie, A., Srivastava, D.S., Naeem, S., 2012. Biodiversity loss and its impact on humanity. *Nature* 486, 59–67. <https://doi.org/10.1038/nature11148>
- Carozzi, M., Descout, M., Lungarska, A., Girault, B., Poméon, T., Martin, P., 2024. Combining methods and knowledges for monitoring environmental policies on a territorial scale: spatial disaggregation of pesticides sales through land use data, reglementary information and expert knowledges, in: *Proceedings of the XVIII International Congress of the European Society of Agronomy*. INRAE, Rennes, France.
- Carvalho, L.G., Veldtman, R., Shenkute, A.G., Tesfay, G.B., Pirk, C.W.W., Donaldson, J.S., Nicolson, S.W., 2011. Natural and within-farmland biodiversity enhances crop productivity. *Ecol. Lett.* 14, 251–259. <https://doi.org/10.1111/j.1461-0248.2010.01579.x>
- Casanelles-Abella, J., Fontana, S., Fournier, B., Frey, D., Moretti, M., 2023. Low resource availability drives feeding niche partitioning between wild bees and honeybees in a European city. *Ecol. Appl.* 33, e2727. <https://doi.org/10.1002/eap.2727>
- Castle, D., Grass, I., Westphal, C., 2019. Fruit quantity and quality of strawberries benefit from enhanced pollinator abundance at hedgerows in agricultural landscapes. *Agric. Ecosyst. Environ.* 275, 14–22. <https://doi.org/10.1016/j.agee.2019.01.003>
- Catarino, R., Bretagnolle, V., Perrot, T., Vialloux, F., Gaba, S., 2019. Bee pollination outperforms pesticides for oilseed crop production and profitability. *Proc. R. Soc. B.* <https://doi.org/10.1098/rspb.2019.1550>
- Ceballos, G., Ehrlich, P.R., Barnosky, A.D., García, A., Pringle, R.M., Palmer, T.M., 2015. Accelerated modern human-induced species losses: Entering the sixth mass extinction. *Sci. Adv.* 1, e1400253. <https://doi.org/10.1126/sciadv.1400253>
- Celis-Diez, J.L., García, C.B., Armesto, J.J., Abades, S., Garratt, M.P.D., Fontúrbel, F.E., 2023. Wild Floral Visitors Are More Important Than Honeybees as Pollinators of Avocado Crops. *Agronomy* 13, 1722. <https://doi.org/10.3390/agronomy13071722>
- Chayre, A., Gibert, C., Mezilet, Y., Pointereau, P., 2024. Carte adonis présentant par commune l'usage des pesticides au travers de l'indice de fréquence de traitement (ift).
- Chen, Y., Zhang, C., van der Werf, W., 2024. Pollination services in the North China Plain measured using buckwheat sentinel plants; is there a deficit? *Agric. Ecosyst. Environ.* 373, 109129. <https://doi.org/10.1016/j.agee.2024.109129>
- Cheng G., Yunhui L.I.U., Jiyong M. a. N., Yuhui Q., Ji L.I., 2020. Preliminary study on landscape design of ecological farms based on biodiversity and ecosystem service. *Chin. J. Eco-Agric.* 28, 1499–1508. <https://doi.org/10.13930/j.cnki.cjea.200068>
- Christmann, S., 2022. Regard and protect ground-nesting pollinators as part of soil biodiversity. *Ecol. Appl.* 32, e2564. <https://doi.org/10.1002/eap.2564>

- Cohen, H., Philpott, S.M., Liere, H., Lin, B.B., Jha, S., 2021. The relationship between pollinator community and pollination services is mediated by floral abundance in urban landscapes. *Urban Ecosyst.* 24, 275–290. <https://doi.org/10.1007/s11252-020-01024-z>
- Cole, L.J., Baddeley, J.A., Robertson, D., Topp, C.F.E., Walker, R.L., Watson, C.A., 2022. Supporting wild pollinators in agricultural landscapes through targeted legume mixtures. *Agric. Ecosyst. Environ.* 323, 107648. <https://doi.org/10.1016/j.agee.2021.107648>
- Cole, L.J., Brocklehurst, S., Robertson, D., Harrison, W., McCracken, D.I., 2017. Exploring the interactions between resource availability and the utilisation of semi-natural habitats by insect pollinators in an intensive agricultural landscape. *Agric. Ecosyst. Environ.* 246, 157–167. <https://doi.org/10.1016/j.agee.2017.05.007>
- Combes, C., 1996. Parasites, biodiversity and ecosystem stability. *Biodivers. Conserv.* 5, 953–962. <https://doi.org/10.1007/BF00054413>
- Connelly, H., Poveda, K., Loeb, G., 2015. Landscape simplification decreases wild bee pollination services to strawberry. *Agric. Ecosyst. Environ.* 211, 51–56. <https://doi.org/10.1016/j.agee.2015.05.004>
- Cowie, R.H., Bouchet, P., Fontaine, B., 2022. The Sixth Mass Extinction: fact, fiction or speculation? *Biol. Rev.* 97, 640–663. <https://doi.org/10.1111/brv.12816>
- Crochard, L., 2023. Du suivi des pollinisateurs et de leurs interactions au service de pollinisation en milieu agricole : influence des champs cultivés (phdthesis). Museum national d'Histoire naturelle.
- Crochard, L., Julliard, R., Gaba, S., Bretagnolle, V., Baude, M., Fontaine, C., 2022. Weeds from non-flowering crops as potential contributors to oilseed rape pollination. *Agric. Ecosyst. Environ.* 336, 108026. <https://doi.org/10.1016/j.agee.2022.108026>
- Cusser, S., Jha, S., Lonsdorf, E., Ricketts, T., 2023. Public and private economic benefits of adopting conservation tillage for cotton pollination. *Agric. Ecosyst. Environ.* 342, 108251. <https://doi.org/10.1016/j.agee.2022.108251>
- Das, M., Paul, A., Bhattacharya, S., Basu, P., 2025. Pollinator visitation decline due to pesticide application beyond threshold frequency brings down crop yield. *Ecol. Entomol.* 50, 33–42. <https://doi.org/10.1111/een.13375>
- de Chazal, J., Rounsevell, M.D.A., 2009. Land-use and climate change within assessments of biodiversity change: A review. *Glob. Environ. Change, Traditional Peoples and Climate Change* 19, 306–315. <https://doi.org/10.1016/j.gloenvcha.2008.09.007>
- Deguines, N., Jono, C., Baude, M., Henry, M., Julliard, R., Fontaine, C., 2014. Large-scale trade-off between agricultural intensification and crop pollination services. *Front. Ecol. Environ.* 12, 212–217. <https://doi.org/10.1890/130054>
- Deguines, N., Julliard, R., de Flores, M., Fontaine, C., 2016. Functional homogenization of flower visitor communities with urbanization. *Ecol. Evol.* 6, 1967–1976. <https://doi.org/10.1002/ece3.2009>
- Desaegher, J., Chiron, F., Bessa-Gomes, C., 2023. Nationwide study of the triple landscape gradient across natural, agricultural and urban areas for the richness of flower-visiting insects. *Biol. Conserv.* 288, 110355. <https://doi.org/10.1016/j.biocon.2023.110355>
- Desaegher, J., Ouin, A., Sheeren, D., 2022a. How far is enough? Prediction of the scale of effect for wild bees. *Ecography* 2022, e05758. <https://doi.org/10.1111/ecog.05758>
- Desaegher, J., Ouin, A., Sheeren, D., 2022b. How far is enough? Prediction of the scale of effect for wild bees. *Ecography* 2022, e05758. <https://doi.org/10.1111/ecog.05758>

- Desaegher, J., Sheeren, D., Ouin, A., 2021. Optimising spatial distribution of mass-flowering patches at the landscape scale to increase crop pollination. *J. Appl. Ecol.* 58, 1876–1887. <https://doi.org/10.1111/1365-2664.13949>
- Devienne, S., 2018. Les révolutions agricoles contemporaines en France, in: Chouquer, G., Maurel, M.-C. (Eds.), *Les mutations récentes du foncier et des agricultures en Europe*, Les Cahiers de la MSHE Ledoux. Presses universitaires de Franche-Comté, Besançon, pp. 25–52. <https://doi.org/10.4000/books.pufc.5643>
- Dicks, L.V., Breeze, T.D., Ngo, H.T., Senapathi, D., An, J., Aizen, M.A., Basu, P., Buchori, D., Galetto, L., Garibaldi, L.A., Gemmill-Herren, B., Howlett, B.G., Imperatriz-Fonseca, V.L., Johnson, S.D., Kovács-Hostyánszki, A., Kwon, Y.J., Lattorff, H.M.G., Lungharwo, T., Seymour, C.L., Vanbergen, A.J., Potts, S.G., 2021. A global-scale expert assessment of drivers and risks associated with pollinator decline. *Nat. Ecol. Evol.* 5, 1453–1461. <https://doi.org/10.1038/s41559-021-01534-9>
- Dietzel, S., Rojas-Botero, S., Kollmann, J., Fischer, C., 2023. Enhanced urban roadside vegetation increases pollinator abundance whereas landscape characteristics drive pollination. *Ecol. Indic.* 147, 109980. <https://doi.org/10.1016/j.ecolind.2023.109980>
- Diyaolu, C.O., Folarin, I.O., 2024. The Role of Biodiversity in Agricultural Resilience: Protecting Ecosystem Services for Sustainable Food Production. *Int. J. Res. Publ. Rev.* 5, 1560–1573. <https://doi.org/10.55248/gengpi.5.1024.2741>
- Donkersley, P., 2019. Trees for bees. *Agric. Ecosyst. Environ.* 270–271, 79–83. <https://doi.org/10.1016/j.agee.2018.10.024>
- Dormann, C.F., Fruend, J., Gruber, B., Bauer, T., Beckett, S., Devoto, M., Felix, G.M.F., Iriondo, J.M., Opsahl, T., Pinheiro, R.B.P., Strauss, R., Vazquez, D.P., 2025. bipartite: Visualising Bipartite Networks and Calculating Some (Ecological) Indices.
- Douglas, M.R., Baisley, P., Soba, S., Kammerer, M., Lonsdorf, E.V., Grozinger, C.M., 2022. Putting pesticides on the map for pollinator research and conservation. *Sci. Data* 9, 571. <https://doi.org/10.1038/s41597-022-01584-z>
- Dover, J.W., 2019. Introduction to hedgerows and field margins, in: *The Ecology of Hedgerows and Field Margins*. Routledge.
- Dray, S., Dufour, A., 2007. The ade4 Package: Implementing the Duality Diagram for Ecologists. *J. Stat. Softw.* 22, 1–20. <https://doi.org/10.18637/jss.v086.i01>
- Drivdal, L., van der Sluijs, J.P., 2021. Pollinator conservation requires a stronger and broader application of the precautionary principle. *Curr. Opin. Insect Sci., Special Section on Pollinator decline: human and policy dimensions* * *Social insects* 46, 95–105. <https://doi.org/10.1016/j.cois.2021.04.005>
- Dwyer, G., Dushoff, J., Yee, S.H., 2004. The combined effects of pathogens and predators on insect outbreaks. *Nature* 430, 341–345. <https://doi.org/10.1038/nature02569>
- Eeraerts, M., 2023. A minimum of 15% semi-natural habitat facilitates adequate wild pollinator visitation to a pollinator-dependent crop. *Biol. Conserv.* 278, 109887. <https://doi.org/10.1016/j.biocon.2022.109887>
- Eeraerts, M., Smagghe, G., Meeus, I., 2019. Pollinator diversity, floral resources and semi-natural habitat, instead of honey bees and intensive agriculture, enhance pollination service to sweet cherry. *Agric. Ecosyst. Environ.* 284, 106586. <https://doi.org/10.1016/j.agee.2019.106586>

- Egan, P.A., Dicks, L.V., Hokkanen, H.M.T., Stenberg, J.A., 2020. Delivering Integrated Pest and Pollinator Management (IPPM). *Trends Plant Sci.* 25, 577–589. <https://doi.org/10.1016/j.tplants.2020.01.006>
- Eggleton, P., Belshaw, R., 1997. Insect parasitoids: an evolutionary overview. *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* 337, 1–20. <https://doi.org/10.1098/rstb.1992.0079>
- Eggleton, P., Gaston, K.J., 1990. “Parasitoid” Species and Assemblages: Convenient Definitions or Misleading Compromises? *Oikos* 59, 417–421. <https://doi.org/10.2307/3545155>
- Ehlers, B.K., Bataillon, T., Damgaard, C.F., 2021. Ongoing decline in insect-pollinated plants across Danish grasslands. *Biol. Lett.* 17, 20210493. <https://doi.org/10.1098/rsbl.2021.0493>
- Ekbohm, B., 2010. Pests and Their Enemies in Spring Oilseed Rape in Europe and Challenges to Integrated Pest Management, in: Williams, I.H. (Ed.), *Biocontrol-Based Integrated Management of Oilseed Rape Pests*. Springer Netherlands, Dordrecht, pp. 151–165. https://doi.org/10.1007/978-90-481-3983-5_5
- Emmerson, M., Morales, M.B., Oñate, J.J., Batáry, P., Berendse, F., Liira, J., Aavik, T., Guerrero, I., Bommarco, R., Eggers, S., Pärt, T., Tscharntke, T., Weisser, W., Clement, L., Bengtsson, J., 2016. Chapter Two - How Agricultural Intensification Affects Biodiversity and Ecosystem Services, in: Dumbrell, A.J., Kordas, R.L., Woodward, G. (Eds.), *Advances in Ecological Research, Large-Scale Ecology: Model Systems to Global Perspectives*. Academic Press, pp. 43–97. <https://doi.org/10.1016/bs.aecr.2016.08.005>
- Farina, W.M., Balbuena, M.S., Herbert, L.T., Mengoni Goñalons, C., Vázquez, D.E., 2019. Effects of the Herbicide Glyphosate on Honey Bee Sensory and Cognitive Abilities: Individual Impairments with Implications for the Hive. *Insects* 10, 354. <https://doi.org/10.3390/insects10100354>
- Fauviau, A., Baude, M., Bazin, N., Fiordaliso, W., Fisogni, A., Fortel, L., Garrigue, J., Geslin, B., Goulnik, J., Guilbaud, L., Hautekète, N., Heiniger, C., Kuhlmann, M., Lambert, O., Langlois, D., Le Féon, V., Lopez Vaamonde, C., Maillet, G., Massol, F., Michel, N., Michelot-Antalik, A., Michez, D., Mouret, H., Piquot, Y., Potts, S.G., Roberts, S., Ropars, L., Schurr, L., Van Reeth, C., Villalta, I., Zaninotto, V., Dajoz, I., Henry, M., 2022. A large-scale dataset reveals taxonomic and functional specificities of wild bee communities in urban habitats of Western Europe. *Sci. Rep.* 12, 18866. <https://doi.org/10.1038/s41598-022-21512-w>
- Fikadu, Z., 2019. The Contribution of Managed Honey Bees to Crop Pollination, Food Security, and Economic Stability: Case of Ethiopia. *Open Agric. J.* 13, 175–181. <https://doi.org/10.2174/1874331501913010175>
- Fitriana, N.A., Lutpi, N.A., Abdeljawad, N.S., 2024. Impact of air pollution on agricultural productivity in urban area. *Environ. Toxicol. Manag.* 4, 17–22. <https://doi.org/10.33086/etm.v4i3.7091>
- Fried, G., Villers, A., Porcher, E., 2018. Assessing non-intended effects of farming practices on field margin vegetation with a functional approach. *Agric. Ecosyst. Environ.* 261, 33–44. <https://doi.org/10.1016/j.agee.2018.03.021>
- Frøslev, T.G., Nielsen, I.B., Santos, S.S., Barnes, C.J., Bruun, H.H., Ejrnæs, R., 2022. The biodiversity effect of reduced tillage on soil microbiota. *Ambio* 51, 1022–1033. <https://doi.org/10.1007/s13280-021-01611-0>

- Gagic, V., Kleijn, D., Báldi, A., Boros, G., Jørgensen, H.B., Elek, Z., Garratt, M.P.D., de Groot, G.A., Hedlund, K., Kovács-Hostyánszki, A., Marini, L., Martin, E., Pevere, I., Potts, S.G., Redlich, S., Senapathi, D., Steffan-Dewenter, I., Świtek, S., Smith, H.G., Takács, V., Tryjanowski, P., van der Putten, W.H., van Gils, S., Bommarco, R., 2017. Combined effects of agrochemicals and ecosystem services on crop yield across Europe. *Ecol. Lett.* 20, 1427–1436. <https://doi.org/10.1111/ele.12850>
- Gagic, V., Marcora, A., Howie, L., 2019. Additive and interactive effects of pollination and biological pest control on crop yield. *J. Appl. Ecol.* 56, 2528–2535. <https://doi.org/10.1111/1365-2664.13482>
- Gagnon, A.-È., Audette, C., Duval, B., Boisclair, J., 2017. Can the Use of *Trichogramma ostrinae* (Hymenoptera: Trichogrammatidae) to Control *Ostrinia nubilalis* (Lepidoptera: Crambidae) Be Economically Sustainable for Processing Sweet Corn? *J. Econ. Entomol.* 110, 59–66. <https://doi.org/10.1093/jee/tow293>
- Gámez-Virués, S., Perović, D.J., Gossner, M.M., Börschig, C., Blüthgen, N., de Jong, H., Simons, N.K., Klein, A.-M., Krauss, J., Maier, G., Scherber, C., Steckel, J., Rothenwöhrer, C., Steffan-Dewenter, I., Weiner, C.N., Weisser, W., Werner, M., Tschardt, T., Westphal, C., 2015. Landscape simplification filters species traits and drives biotic homogenization. *Nat. Commun.* 6, 8568. <https://doi.org/10.1038/ncomms9568>
- Gandara, T., Gardarin, A., Desaegher, J., Petit, S., Porcher, E., Michelot-Antalik, A., 2025. A crop yield-based pollination index reveals the impacts of land cover and pesticide use on realized pollination at a landscape scale. *Agric. Ecosyst. Environ.* 392, 109747. <https://doi.org/10.1016/j.agee.2025.109747>
- Gardarin, A., Pigot, J., Valantin-Morison, M., 2021. The hump-shaped effect of plant functional diversity on the biological control of a multi-species pest community. *Sci. Rep.* 11, 21635. <https://doi.org/10.1038/s41598-021-01160-2>
- Garibaldi, L.A., Andersson, G.K.S., Requier, F., Fijen, T.P.M., Hipólito, J., Kleijn, D., Pérez-Méndez, N., Rollin, O., 2018. Complementarity and synergisms among ecosystem services supporting crop yield. *Glob. Food Secur.* 17, 38–47. <https://doi.org/10.1016/j.gfs.2018.03.006>
- Garibaldi, L.A., Steffan-Dewenter, I., Kremen, C., Morales, J.M., Bommarco, R., Cunningham, S.A., Carvalheiro, L.G., Chacoff, N.P., Dudenhöffer, J.H., Greenleaf, S.S., Holzschuh, A., Isaacs, R., Krewenka, K., Mandelik, Y., Mayfield, M.M., Morandin, L.A., Potts, S.G., Ricketts, T.H., Szentgyörgyi, H., Viana, B.F., Westphal, C., Winfree, R., Klein, A.M., 2011. Stability of pollination services decreases with isolation from natural areas despite honey bee visits. *Ecol. Lett.* 14, 1062–1072. <https://doi.org/10.1111/j.1461-0248.2011.01669.x>
- Garibaldi, Lucas A., Steffan-Dewenter, I., Winfree, R., Aizen, M.A., Bommarco, R., Cunningham, S.A., Kremen, C., Carvalheiro, L.G., Harder, L.D., Afik, O., Bartomeus, I., Benjamin, F., Boreux, V., Cariveau, D., Chacoff, N.P., Dudenhöffer, J.H., Freitas, B.M., Ghazoul, J., Greenleaf, S., Hipólito, J., Holzschuh, A., Howlett, B., Isaacs, R., Javorek, S.K., Kennedy, C.M., Krewenka, K.M., Krishnan, S., Mandelik, Y., Mayfield, M.M., Motzke, I., Munyuli, T., Nault, B.A., Otieno, M., Petersen, J., Pisanty, G., Potts, S.G., Rader, R., Ricketts, T.H., Rundlöf, M., Seymour, C.L., Schüepp, C., Szentgyörgyi, H., Taki, H., Tschardt, T., Vergara, C.H., Viana, B.F., Wanger, T.C., Westphal, C., Williams, N., Klein, A.M., 2013. Wild Pollinators Enhance Fruit Set of Crops Regardless of Honey Bee Abundance. *Science* 339, 1608–1611. <https://doi.org/10.1126/science.1230200>

- Garibaldi, L. A., Steffan-Dewenter, I., Winfree, R., Aizen, M.A., Bommarco, R., Cunningham, S.A., Kremen, C., Carvalheiro, L.G., Harder, L.D., Afik, O., Bartomeus, I., Benjamin, F., Boreux, V., Cariveau, D., Chacoff, N.P., Dudenhoffer, J.H., Freitas, B.M., Ghazoul, J., Greenleaf, S., Hipolito, J., Holzschuh, A., Howlett, B., Isaacs, R., Javorek, S.K., Kennedy, C.M., Krewenka, K.M., Krishnan, S., Mandelik, Y., Mayfield, M.M., Motzke, I., Munyuli, T., Nault, B.A., Otieno, M., Petersen, J., Pisanty, G., Potts, S.G., Rader, R., Ricketts, T.H., Rundlof, M., Seymour, C.L., Schuepp, C., Szentgyorgyi, H., Taki, H., Tscharntke, T., Vergara, C.H., Viana, B.F., Wanger, T.C., Westphal, C., Williams, N., Klein, A.M., 2013. Wild Pollinators Enhance Fruit Set of Crops Regardless of Honey Bee Abundance. *Science* 339, 1608–1611. <https://doi.org/10.1126/science.1230200>
- Garnault, M., Barbu, C., Aulagnier, A., Bockstaller, C., Gouy Boussada, V., Per, K., Baptiste, L., Le Bellec, F., Dachbrodt-Saaydeh, S., Freddie-Jeanne, R., Marc, G., Benoît, G., Alfred, K., Tanguy, L., Maugin, E., Harry, O.-L., Strassemeyer, J., Walker, A.-S., Laura, H., François, O., Aubertot, J.-N., Cst Ecophyto, ., 2024. Evaluation of two indicators according to the objectives of the Sustainable Use of pesticides Directive (SUD). A French case study.
- Garratt, M.P.D., Groot, G.A., Albrecht, M., Bosch, J., Breeze, T.D., Fountain, M.T., Klein, A.M., McKerchar, M., Park, M., Paxton, R.J., Potts, S.G., Pufal, G., Rader, R., Senapathi, D., Andersson, G.K.S., Bernauer, O.M., Blitzer, E.J., Boreux, V., Campbell, A.J., Carvell, C., Földesi, R., García, D., Garibaldi, L.A., Hambäck, P.A., Kirkitadze, G., Kovács-Hostyánszki, A., Martins, K.T., Miñarro, M., O'Connor, R., Radzeviciute, R., Roquer-Bení, L., Samnegård, U., Scott, L., Vereecken, N.J., Wäckers, F., Webber, S.M., Japoshvili, G., Zhusupbaeva, A., 2021. Opportunities to reduce pollination deficits and address production shortfalls in an important insect-pollinated crop. *Ecol. Appl.* 31. <https://doi.org/10.1002/eap.2445>
- Gay, C., Gaba, S., Bretagnolle, V., 2024. The structure of plant–pollinator networks is affected by crop type in a highly intensive agricultural landscape. *Agric. Ecosyst. Environ.* 359, 108759. <https://doi.org/10.1016/j.agee.2023.108759>
- Gebhardt, S., van Dijk, J., Lof, M.E., Wassen, M.J., Bakker, M., 2025. Understanding interactive effects between habitat configuration and pesticide use for pollination: towards better informed landscape management. *Ecol. Process.* 14, 25. <https://doi.org/10.1186/s13717-025-00587-z>
- Geiger, F., Bengtsson, J., Berendse, F., Weisser, W.W., Emmerson, M., Morales, M.B., Ceryngier, P., Liira, J., Tscharntke, T., Winqvist, C., Eggers, S., Bommarco, R., Pärt, T., Bretagnolle, V., Plantegenest, M., Clement, L.W., Dennis, C., Palmer, C., Oñate, J.J., Guerrero, I., Hawro, V., Aavik, T., Thies, C., Flohre, A., Hänke, S., Fischer, C., Goedhart, P.W., Inchausti, P., 2010. Persistent negative effects of pesticides on biodiversity and biological control potential on European farmland. *Basic Appl. Ecol.* 11, 97–105. <https://doi.org/10.1016/j.baae.2009.12.001>
- Gemmill-Herren, B., Garibaldi, L.A., Kremen, C., Ngo, H.T., 2021. Building effective policies to conserve pollinators: translating knowledge into policy. *Curr. Opin. Insect Sci., Special Section on Pollinator decline: human and policy dimensions * Social insects* 46, 64–71. <https://doi.org/10.1016/j.cois.2021.02.012>
- Geslin, B., Le Féon, V., Folschweiller, M., Flacher, F., Carmignac, D., Motard, E., Perret, S., Dajoz, I., 2016. The proportion of impervious surfaces at the landscape scale structures wild bee assemblages in a densely populated region. *Ecol. Evol.* 6, 6599–6615. <https://doi.org/10.1002/ece3.2374>

- Geslin, B., Mouillard-Lample, L., Zakardjian, M., Dajoz, I., Flacher, F., Henry, M., Perrard, A., Requier, F., Ropars, L., Schatz, B., Vereecken, N.J., Gauzens, B., 2023. Chapter Four - New insights on massively introduced managed species and their consequences for plant–pollinator interactions, in: Bohan, D.A., Dumbrell, A.J. (Eds.), *Advances in Ecological Research*, *Advances in Ecological Research: Roadmaps: Part A*. Academic Press, pp. 63–89. <https://doi.org/10.1016/bs.aecr.2023.09.003>
- Ghisbain, G., Thiery, W., Massonnet, F., Erazo, D., Rasmont, P., Michez, D., Dellicour, S., 2024. Projected decline in European bumblebee populations in the twenty-first century. *Nature* 628, 337–341. <https://doi.org/10.1038/s41586-023-06471-0>
- Gibson, R.H., Nelson, I.L., Hopkins, G.W., Hamlett, B.J., Memmott, J., 2006. Pollinator webs, plant communities and the conservation of rare plants: arable weeds as a case study. *J. Appl. Ecol.* 43, 246–257. <https://doi.org/10.1111/j.1365-2664.2006.01130.x>
- Gillespie, S., Long, R., Seitz, N., Williams, N., 2014. Insecticide Use in Hybrid Onion Seed Production Affects Pre- and Postpollination Processes. *J. Econ. Entomol.* 107, 29–37. <https://doi.org/10.1603/EC13044>
- Godara, N., Williamson, R.C., Koo, D., Askew, S.D., 2023. Effect of herbicides on pollinator foraging behavior and flower morphology in white clover (*Trifolium repens* L.)–infested turfgrass. *Weed Technol.* 37, 221–225. <https://doi.org/10.1017/wet.2023.33>
- Gonthier, D.J., Ennis, K.K., Farinas, S., Hsieh, H.-Y., Iverson, A.L., Batáry, P., Rudolphi, J., Tschardtke, T., Cardinale, B.J., Perfecto, I., 2014. Biodiversity conservation in agriculture requires a multi-scale approach. *Proc. R. Soc. B Biol. Sci.* 281, 20141358. <https://doi.org/10.1098/rspb.2014.1358>
- Gontijo, L.M., Beers, E.H., Snyder, W.E., 2013. Flowers promote aphid suppression in apple orchards. *Biol. Control* 66, 8–15. <https://doi.org/10.1016/j.biocontrol.2013.03.007>
- Gonzalez, V.H., Osborn, A.L., Brown, E.R., Pavlick, C.R., Enríquez, E., Tscheulin, T., Petanidou, T., Hranitz, J.M., Barthell, J.F., 2020. Effect of pan trap size on the diversity of sampled bees and abundance of bycatch. *J. Insect Conserv.* 24, 409–420. <https://doi.org/10.1007/s10841-020-00224-4>
- Goulnik, J., Plantureux, S., Théry, M., Baude, M., Delattre, M., van Reeth, C., Villerd, J., Michelot-Antalik, A., 2020. Floral trait functional diversity is related to soil characteristics and positively influences pollination function in semi-natural grasslands. *Agric. Ecosyst. Environ.* 301, 107033. <https://doi.org/10.1016/j.agee.2020.107033>
- Goulson, D., Nicholls, E., Botías, C., Rotheray, E.L., 2015. Bee declines driven by combined stress from parasites, pesticides, and lack of flowers. *Science* 347. <https://doi.org/10.1126/science.1255957>
- Grass, I., Albrecht, J., Jauker, F., Diekötter, T., Warzecha, D., Wolters, V., Farwig, N., 2016. Much more than bees—Wildflower plantings support highly diverse flower-visitor communities from complex to structurally simple agricultural landscapes. *Agric. Ecosyst. Environ.* 225, 45–53. <https://doi.org/10.1016/j.agee.2016.04.001>
- Grass, I., Batáry, P., Tschardtke, T., 2021. Chapter Six - Combining land-sparing and land-sharing in European landscapes, in: Bohan, D.A., Vanbergen, A.J. (Eds.), *Advances in Ecological Research*, *The Future of Agricultural Landscapes*, Part II. Academic Press, pp. 251–303. <https://doi.org/10.1016/bs.aecr.2020.09.002>
- Grass, I., Loos, J., Baensch, S., Batáry, P., Librán-Embid, F., Ficiciyan, A., Klaus, F., Riechers, M., Rosa, J., Tiede, J., Udy, K., Westphal, C., Wurz, A., Tschardtke, T., 2019. Land-sharing/-sparing connectivity landscapes for ecosystem services and biodiversity conservation. *People Nat.* 1, 262–272. <https://doi.org/10.1002/pan3.21>

- Gray, A., Brodschneider, R., Adjlane, N., Ballis, A., Brusbardis, V., Charrière, J.-D., Chlebo, R., F. Coffey, M., Cornelissen, B., Amaro da Costa, C., Csáki, T., Dahle, B., Danihlík, J., Dražić, M.M., Evans, G., Fedoriak, M., Forsythe, I., de Graaf, D., Gregorc, A., Johannesen, J., Kauko, L., Kristiansen, P., Martikkala, M., Martín-Hernández, R., Medina-Flores, C.A., Mutinelli, F., Patalano, S., Petrov, P., Raudmets, A., Ryzhikov, V.A., Simon-Delso, N., Stevanovic, J., Topolska, G., Uzunov, A., Vejsnaes, F., Williams, A., Zammit-Mangion, M., Soroker, V., 2019. Loss rates of honey bee colonies during winter 2017/18 in 36 countries participating in the COLOSS survey, including effects of forage sources. *J. Apic. Res.* 58, 479–485. <https://doi.org/10.1080/00218839.2019.1615661>
- Gudowska, A., Cwajna, A., Marjańska, E., Moroń, D., 2024. Pollinators enhance the production of a superior strawberry – A global review and meta-analysis. *Agric. Ecosyst. Environ.* 362, 108815. <https://doi.org/10.1016/j.agee.2023.108815>
- Guzman, L.M., Elle, E., Morandin, L.A., Cobb, N.S., Chesshire, P.R., McCabe, L.M., Hughes, A., Orr, M., M’Gonigle, L.K., 2024. Impact of pesticide use on wild bee distributions across the United States. *Nat. Sustain.* 7, 1324–1334. <https://doi.org/10.1038/s41893-024-01413-8>
- Haines-Young, R., Potschin, M., 2010. The links between biodiversity, ecosystem services and human well-being, in: Raffaelli, D.G., Frid, C.L.J. (Eds.), *Ecosystem Ecology*. Cambridge University Press, pp. 110–139. <https://doi.org/10.1017/CBO9780511750458.007>
- Hallmann, C.A., Sorg, M., Jongejans, E., Siepel, H., Hofland, N., Schwan, H., Stenmans, W., Müller, A., Sumser, H., Hörrén, T., Goulson, D., Kroon, H. de, 2017. More than 75 percent decline over 27 years in total flying insect biomass in protected areas. *PLOS ONE* 12, e0185809. <https://doi.org/10.1371/journal.pone.0185809>
- Hanson, H.I., Smith, H.G., Hedlund, K., 2015. Agricultural management reduces emergence of pollen beetle parasitoids. *Agric. Ecosyst. Environ.* 205, 9–14. <https://doi.org/10.1016/j.agee.2015.03.001>
- Hartig, F., Lohse, L., leite, M. de S., 2024. DHARMA: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models.
- Herrmann, J.D., Beye, H., De La Broise, C., Hartlep, H., Diekötter, T., 2019. Positive effects of the pollinators *Osmia cornuta* (Megachilidae) and *Lucilia sericata* (Calliphoridae) on strawberry quality. *Arthropod-Plant Interact.* 13, 71–77. <https://doi.org/10.1007/s11829-018-9636-7>
- Hervé, M.R., 2018. Breeding for insect resistance in oilseed rape: Challenges, current knowledge and perspectives. *Plant Breed.* 137, 27–34. <https://doi.org/10.1111/pbr.12552>
- Hevia, V., Carmona, C.P., Azcárate, F.M., Heredia, R., González, J.A., 2021. Role of floral strips and semi-natural habitats as enhancers of wild bee functional diversity in intensive agricultural landscapes. *Agric. Ecosyst. Environ.* 319, 107544. <https://doi.org/10.1016/j.agee.2021.107544>
- Holland, J.M., Douma, J.C., Crowley, L., James, L., Kor, L., Stevenson, D.R.W., Smith, B.M., 2017. Semi-natural habitats support biological control, pollination and soil conservation in Europe. A review. *Agron. Sustain. Dev.* 37, 31. <https://doi.org/10.1007/s13593-017-0434-x>

- Hölting, L., Beckmann, M., Volk, M., Cord, A.F., 2019. Multifunctionality assessments – More than assessing multiple ecosystem functions and services? A quantitative literature review. *Ecol. Indic.* 103, 226–235. <https://doi.org/10.1016/j.ecolind.2019.04.009>
- Hölting, L., Busse, M., Bülow, S., Engler, J.O., Hagemann, N., Joormann, I., Kernecker, M.L., Larondelle, N., Sturm, A., Turkelboom, F., Wätzold, F., Cord, A.F., 2022. Co-design: Working with farmers in Europe to halt the loss of biological diversity. *Ecol. Solut. Evid.* 3, e12169. <https://doi.org/10.1002/2688-8319.12169>
- Holzschuh, A., Dainese, M., González-Varo, J.P., Mudri-Stojnić, S., Riedinger, V., Rundlöf, M., Scheper, J., Wickens, J.B., Wickens, V.J., Bommarco, R., Kleijn, D., Potts, S.G., Roberts, S.P.M., Smith, H.G., Vilà, M., Vujić, A., Steffan-Dewenter, I., 2016. Mass-flowering crops dilute pollinator abundance in agricultural landscapes across Europe. *Ecol. Lett.* 19, 1228–1236. <https://doi.org/10.1111/ele.12657>
- Hossard, L., Guichard, L., Pelosi, C., Makowski, D., 2017. Lack of evidence for a decrease in synthetic pesticide use on the main arable crops in France. *Sci. Total Environ.* 575, 152–161. <https://doi.org/10.1016/j.scitotenv.2016.10.008>
- Hudewenz, A., Pufal, G., Bögeholz, A.-L., Klein, A.-M., 2014. Cross-pollination benefits differ among oilseed rape varieties. *J. Agric. Sci.* 152, 770–778. <https://doi.org/10.1017/S0021859613000440>
- Hussain, R.I., Brandl, M., Maas, B., Rabl, D., Walcher, R., Krautzer, B., Entling, M.H., Moser, D., Frank, T., 2021. Re-established grasslands on farmland promote pollinators more than predators. *Agric. Ecosyst. Environ.* 319, 107543. <https://doi.org/10.1016/j.agee.2021.107543>
- Inglada, J., Vincent, A., Thierion, V., 2018. Theia OSO Land Cover Map 2018. <https://doi.org/10.5281/zenodo.3613415>
- IPBES, 2016. The assessment report of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services on pollinators, pollination and food production. Zenodo. <https://doi.org/10.5281/ZENODO.3402856>
- IUCN, 2025. The IUCN Red List of Threatened Species [WWW Document]. IUCN Red List Threat. Species. URL <https://www.iucnredlist.org/en> (accessed 6.4.25).
- Jacquet, F., Jeuffroy, M.-H., Jouan, J., Le Cadre, E., Litrico, I., Malausa, T., Reboud, X., Huyghe, C., 2022. Pesticide-free agriculture as a new paradigm for research. *Agron. Sustain. Dev.* 42, 8. <https://doi.org/10.1007/s13593-021-00742-8>
- Janousek, W.M., Douglas, M.R., Cannings, S., Clément, M.A., Delphia, C.M., Everett, J.G., Hatfield, R.G., Keinath, D.A., Koch, J.B.U., McCabe, L.M., Mola, J.M., Ogilvie, J.E., Rangwala, I., Richardson, L.L., Rohde, A.T., Strange, J.P., Tronstad, L.M., Graves, T.A., 2023. Recent and future declines of a historically widespread pollinator linked to climate, land cover, and pesticides. *Proc. Natl. Acad. Sci.* 120, e2211223120. <https://doi.org/10.1073/pnas.2211223120>
- Jenkins, D.G., Quintana-Ascencio, P.F., 2020. A solution to minimum sample size for regressions. *PLOS ONE* 15, e0229345. <https://doi.org/10.1371/journal.pone.0229345>
- Johnson, S.D., Steiner, K.E., 2000. Generalization versus specialization in plant pollination systems. *Trends Ecol. Evol.* 15, 140–143. [https://doi.org/10.1016/S0169-5347\(99\)01811-X](https://doi.org/10.1016/S0169-5347(99)01811-X)
- Kassambara, A., Mundt, F., 2020. factoextra: Extract and Visualize the Results of Multivariate Data Analyses.

- Katumo, D.M., Liang, H., Ochola, A.C., Lv, M., Wang, Q.-F., Yang, C.-F., 2022. Pollinator diversity benefits natural and agricultural ecosystems, environmental health, and human welfare. *Plant Divers.* 44, 429–435. <https://doi.org/10.1016/j.pld.2022.01.005>
- Kehoe, L., Romero-Muñoz, A., Polaina, E., Estes, L., Kreft, H., Kuemmerle, T., 2017. Biodiversity at risk under future cropland expansion and intensification. *Nat. Ecol. Evol.* 1, 1129–1135. <https://doi.org/10.1038/s41559-017-0234-3>
- Kendall, L.K., Mola, J.M., Portman, Z.M., Cariveau, D.P., Smith, H.G., Bartomeus, I., 2022. The potential and realized foraging movements of bees are differentially determined by body size and sociality. *Ecology* 103, e3809. <https://doi.org/10.1002/ecy.3809>
- Kennedy, C.M., Lonsdorf, E., Neel, M.C., Williams, N.M., Ricketts, T.H., Winfree, R., Bommarco, R., Brittain, C., Burley, A.L., Cariveau, D., Carvalheiro, L.G., Chacoff, N.P., Cunningham, S.A., Danforth, B.N., Dudenhöffer, J., Elle, E., Gaines, H.R., Garibaldi, L.A., Gratton, C., Holzschuh, A., Isaacs, R., Javorek, S.K., Jha, S., Klein, A.M., Krewenka, K., Mandelik, Y., Mayfield, M.M., Morandin, L., Neame, L.A., Otieno, M., Park, M., Potts, S.G., Rundlöf, M., Saez, A., Steffan-Dewenter, I., Taki, H., Viana, B.F., Westphal, C., Wilson, J.K., Greenleaf, S.S., Kremen, C., 2013. A global quantitative synthesis of local and landscape effects on wild bee pollinators in agroecosystems. *Ecol. Lett.* 16, 584–599. <https://doi.org/10.1111/ele.12082>
- Klatt, B.K., Holzschuh, A., Westphal, C., Clough, Y., Smit, I., Pawelzik, E., Tschamtker, T., 2014. Bee pollination improves crop quality, shelf life and commercial value. *Proc. R. Soc. B Biol. Sci.* 281, 20132440. <https://doi.org/10.1098/rspb.2013.2440>
- Klaus, F., Tschamtker, T., Uhler, J., Grass, I., 2021. Calcareous grassland fragments as sources of bee pollinators for the surrounding agricultural landscape. *Glob. Ecol. Conserv.* 26, e01474. <https://doi.org/10.1016/j.gecco.2021.e01474>
- Klein, A.-M., Vaissière, B.E., Cane, J.H., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C., Tschamtker, T., 2007. Importance of pollinators in changing landscapes for world crops. *Proc. Biol. Sci.* 274, 303–313. <https://doi.org/10.1098/rspb.2006.3721>
- Kovács-Hostyánszki, A., Espíndola, A., Vanbergen, A.J., Settele, J., Kremen, C., Dicks, L.V., 2017. Ecological intensification to mitigate impacts of conventional intensive land use on pollinators and pollination. *Ecol. Lett.* 20, 673–689. <https://doi.org/10.1111/ele.12762>
- Kratschmer, S., Milchram, M., Landler, L., Burgstaller, S., Spießberger, M., Schuller, N., Grötcke, D., Wacker, H., Dönn, V., Planitzer, A., Ihle, F., Suarez-Rubio, M., Lanner, J., 2025. Tracking large bees in open landscapes with active radio tags—Advantages and challenges using stationary receivers. *J. Anim. Ecol.* 94, 1638–1649. <https://doi.org/10.1111/1365-2656.70061>
- Lacombe, C., Couix, N., Hazard, L., 2018. Designing agroecological farming systems with farmers: A review. *Agric. Syst.* 165, 208–220. <https://doi.org/10.1016/j.agry.2018.06.014>
- Laffon, L., Bischoff, A., Lescourret, F., Mujica-Fuentes, D., Olivares, J., Rasmussen, B., Rasplus, J.-Y., Franck, P., 2025. Temporal snapshot of parasitoid wasp communities on three flowering plant species and implications for the rosy apple aphid regulation (*Dysaphis plantaginea*) in apple orchards. *Agric. For. Entomol.* 27, 403–414. <https://doi.org/10.1111/afe.12674>
- Le Féon, V., Schermann-Legionnet, A., Delettre, Y., Aviron, S., Billeter, R., Bugter, R., Hendrickx, F., Burel, F., 2010. Intensification of agriculture, landscape composition and wild bee communities: A large scale study in four European countries. *Agric.*

- Ecosyst. Environ., Special section Harvested perennial grasslands: Ecological models for farming's perennial future 137, 143–150. <https://doi.org/10.1016/j.agee.2010.01.015>
- Lefebvre, V., Fontaine, C., Villemant, C., Daugeron, C., 2014. Are empidine dance flies major flower visitors in alpine environments? A case study in the Alps, France. *Biol. Lett.* 10, 20140742. <https://doi.org/10.1098/rsbl.2014.0742>
- Lenth, R., 2024. emmeans: Estimated Marginal Means, aka Least-Squares Means.
- Leroy, A., Martin, O., Gautier, J.-L., Bretagnolle, V., Gaba, S., 2025. The surrounding landscape affects ecosystem multifunctionality in oilseed rape fields. *J. Appl. Ecol.* 62, 2283–2295. <https://doi.org/10.1111/1365-2664.70105>
- Li, Z., Costamagna, A.C., Beran, F., You, M., 2024. Biology, Ecology, and Management of Flea Beetles in *Brassica* Crops. *Annu. Rev. Entomol.* 69, 199–217. <https://doi.org/10.1146/annurev-ento-033023-015753>
- Ligtelijn, M., Henrik Barmantlo, S., van Gestel, C.A.M., 2024. Field-realistic doses of the neonicotinoid acetamiprid impact natural soil arthropod community diversity and structure. *Environ. Pollut.* 359, 124568. <https://doi.org/10.1016/j.envpol.2024.124568>
- Liss, K.N., Mitchell, M.G., MacDonald, G.K., Mahajan, S.L., Méthot, J., Jacob, A.L., Maguire, D.Y., Metson, G.S., Ziter, C., Dancose, K., Martins, K., Terrado, M., Bennett, E.M., 2013. Variability in ecosystem service measurement: a pollination service case study. *Front. Ecol. Environ.* 11, 414–422. <https://doi.org/10.1890/120189>
- Lonsdorf, E., Kremen, C., Ricketts, T., Winfree, R., Williams, N., Greenleaf, S., 2009. Modelling pollination services across agricultural landscapes. *Ann. Bot.* 103, 1589–1600. <https://doi.org/10.1093/aob/mcp069>
- Lövei, G.L., Ferrante, M., Möller, D., Möller, G., Vincze, É., 2023. The need for a (non-destructive) method revolution in entomology. *Biol. Conserv.* 282, 110075. <https://doi.org/10.1016/j.biocon.2023.110075>
- Lowe, E.B., Groves, R., Gratton, C., 2021. Impacts of field-edge flower plantings on pollinator conservation and ecosystem service delivery – A meta-analysis. *Agric. Ecosyst. Environ.* 310, 107290. <https://doi.org/10.1016/j.agee.2020.107290>
- Lowenstein, D.M., Matteson, K.C., Minor, E.S., 2015. Diversity of wild bees supports pollination services in an urbanized landscape. *Oecologia* 179, 811–821. <https://doi.org/10.1007/s00442-015-3389-0>
- Loy, X., Brosi, B.J., 2022. The effects of pollinator diversity on pollination function. *Ecology* 103, e3631. <https://doi.org/10.1002/ecy.3631>
- Lüdtke, D., 2018. ggeffects: tidy data frames of marginal effects from regression models. *J. Open Source Softw.* 3, 772. <https://doi.org/10.21105/joss.00772>
- Lüdtke, D., Makowski, D., Ben-Shachar, M.S., Patil, I., Waggoner, P., Wiernik, B.M., Thériault, R., Arel-Bundock, V., Jullum, M., gjo11, Bacher, E., Luchman, J., 2025. performance: Assessment of Regression Models Performance.
- Lundin, O., Rundlöf, M., Jonsson, M., Bommarco, R., Williams, N.M., 2021. Integrated pest and pollinator management – expanding the concept. *Front. Ecol. Environ.* 19, 283–291. <https://doi.org/10.1002/fee.2325>
- MacInnis, G., Forrest, J.R.K., 2020. Field design can affect cross-pollination and crop yield in strawberry (*Fragaria x ananassa* D.). *Agric. Ecosyst. Environ.* 289, 106738. <https://doi.org/10.1016/j.agee.2019.106738>

- MacLaren, C., Storkey, J., Menegat, A., Metcalfe, H., Dehnen-Schmutz, K., 2020. An ecological future for weed science to sustain crop production and the environment. A review. *Agron. Sustain. Dev.* 40, 24. <https://doi.org/10.1007/s13593-020-00631-6>
- Mahon, N., Hodge, S., 2022. Evaluating the effects of observation period, floral density, and weather conditions on the consistency and accuracy of timed pollinator counts. *J. Pollinat. Ecol.* 32, 124–138. [https://doi.org/10.26786/1920-7603\(2022\)699](https://doi.org/10.26786/1920-7603(2022)699)
- Main, A.R., Hladik, M.L., Webb, E.B., Goyne, K.W., Mengel, D., 2020. Beyond neonicotinoids – Wild pollinators are exposed to a range of pesticides while foraging in agroecosystems. *Sci. Total Environ.* 742, 140436. <https://doi.org/10.1016/j.scitotenv.2020.140436>
- Mamy, L., Pesce, S., Sanchez, W., Aviron, S., Bedos, C., Berny, P., Bertrand, C., Betoulle, S., Charles, S., Chaumot, A., Coeurdassier, M., Coutellec, M.-A., Crouzet, O., Faburé, J., Fritsch, C., Gonzalez, P., Hedde, M., Leboulanger, C., Margoum, C., Mougin, C., Munaron, D., Nélieu, S., Pelosi, C., Rault, M., Sucré, E., Thomas, M., Tournébiz, J., Leenhardt, S., 2025. Impacts of neonicotinoids on biodiversity: a critical review. *Environ. Sci. Pollut. Res.* 32, 2794–2829. <https://doi.org/10.1007/s11356-023-31032-3>
- Mänd, M., Williams, I.H., Viik, E., Karise, R., 2010. Oilseed Rape, Bees and Integrated Pest Management, in: Williams, I.H. (Ed.), *Biocontrol-Based Integrated Management of Oilseed Rape Pests*. Springer Netherlands, Dordrecht, pp. 357–379. https://doi.org/10.1007/978-90-481-3983-5_14
- Manning, P., van der Plas, F., Soliveres, S., Allan, E., Maestre, F.T., Mace, G., Whittingham, M.J., Fischer, M., 2018. Redefining ecosystem multifunctionality. *Nat. Ecol. Evol.* 2, 427–436. <https://doi.org/10.1038/s41559-017-0461-7>
- Marja, R., Tschardtke, T., Batáry, P., 2022. Increasing landscape complexity enhances species richness of farmland arthropods, agri-environment schemes also abundance – A meta-analysis. *Agric. Ecosyst. Environ.* 326, 107822. <https://doi.org/10.1016/j.agee.2021.107822>
- Martin, G., Fontaine, C., Accatino, F., Porcher, E., 2019. New indices for rapid assessment of pollination services based on crop yield data: France as a case study. *Ecol. Indic.* 101, 355–363. <https://doi.org/10.1016/j.ecolind.2019.01.022>
- Maurer, C., Sutter, L., Martínez-Núñez, C., Pellissier, L., Albrecht, M., 2022. Different types of semi-natural habitat are required to sustain diverse wild bee communities across agricultural landscapes. *J. Appl. Ecol.* 59, 2604–2615. <https://doi.org/10.1111/1365-2664.14260>
- McElwee, P.D., Harrison, P.A., van Huysen, T.L., Alonso Roldán, V., Barrios, E., Dasgupta, P., DeClerck, F., Harmáčková, Z., Hayman, D.T.S., Herrero, M., Kumar, R., Ley, D., Mangalagiu, D., McFarlane, R.A., Paukert, C., Pengue, W.A., Prist, P.R., Ricketts, T.H., Rounsevell, M.D.A., Saito, O., Selomane, O., Seppelt, R., Singh, P.K., Sitas, N., Smith, P., Vause, J., Molua, E.L., Zambrana-Torrel, C., Obura, D., 2025. IPBES Nexus Assessment: Summary for Policymakers. Zenodo. <https://doi.org/10.5281/zenodo.15673657>
- Meehan, T.D., Werling, B.P., Landis, D.A., Gratton, C., 2011. Agricultural landscape simplification and insecticide use in the Midwestern United States. *Proc. Natl. Acad. Sci.* 108, 11500–11505. <https://doi.org/10.1073/pnas.1100751108>
- Meijaard, E., Virah-Sawmy, M., Newing, H.S., Ingram, V., Holle, M.J.M., Pasmans, T., Omar, S., Van Den Hombergh, H., Unus, N., Fosch, A., Ferraz De Arruda, H., Allen, J., Tsagarakis, K., Ogwu, M.C., Diaz-Ismael, A., Hance, J., Moreno, Y., O’Keefe, S.,

- Slavin, J., Slingerland, M., Meijaard, E.M., Macfarlane, N., Jimenez, R., Wich, S., Sheil, D., 2024. Exploring the future of vegetable oils : oil crop implications : fats, forests, forecasts, and futures, 1st ed. IUCN, International Union for Conservation of Nature. <https://doi.org/10.2305/KFJA1910>
- Merle, I., Hipólito, J., Requier, F., 2022. Towards integrated pest and pollinator management in tropical crops. *Curr. Opin. Insect Sci.* 50, 100866. <https://doi.org/10.1016/j.cois.2021.12.006>
- Meunier, E., Smith, P., Griessinger, T., Robert, C., 2024. Understanding changes in reducing pesticide use by farmers: Contribution of the behavioural sciences. *Agric. Syst.* 214, 103818. <https://doi.org/10.1016/j.agry.2023.103818>
- Meunier, M., Hott, H., 2024. Rapport d'information déposé en application de l'article 145 du règlement, par la commission du développement durable et de l'aménagement du territoire, en conclusion des travaux d'une mission d'information sur les dynamiques de la biodiversité dans les paysages agricoles et l'évaluation des politiques publiques associées (Mme Manon Meunier et M. Hubert Ott), n° 2113 [WWW Document]. URL https://www.assemblee-nationale.fr/dyn/16/rapports/cion-dvp/116b2113_rapport-information (accessed 9.27.25).
- Meynard, J.-M., Charrier, F., Fares, M., Le Bail, M., Magrini, M.-B., Charlier, A., Messéan, A., 2018. Socio-technical lock-in hinders crop diversification in France. *Agron. Sustain. Dev.* 38, 54. <https://doi.org/10.1007/s13593-018-0535-1>
- Michelot-Antalik, A., Langlois, A., de Bello, F., Desaegher, J., Genty, L., Goulnik, J., Grosjean, J., Jacquemart, A.-L., Kergunteuil, A., Junker, R.R., Jeannerod, L., Odoux, J.-F., Proffit, M., Schatz, B., Vanderplanck, M., E-Vojtkó, A., Baude, M., 2025. Handbook of protocols for standardized measurements of floral traits for pollinators in temperate communities. *Methods Ecol. Evol.* 16, 988–1001. <https://doi.org/10.1111/2041-210X.70031>
- Millennium Ecosystem Assessment (Ed.), 2005. Ecosystems and human well-being: synthesis, The Millennium Ecosystem Assessment series. Island Press, Washington, DC.
- Miranda, P.S., Lima, Z.C.M., Pérez-Maluf, R., Oliveira, E.P.D., Monroe, P.H.M., Moreira, A.A., 2025. Influence of pollination mechanisms on the physical-chemical quality of strawberry (*Fragaria x ananassa*) cv. San Andreas. *An. Acad. Bras. Ciênc.* 97, e20240799. <https://doi.org/10.1590/0001-3765202520240799>
- Møller, A.P., 2019. Parallel declines in abundance of insects and insectivorous birds in Denmark over 22 years. *Ecol. Evol.* 9, 6581–6587. <https://doi.org/10.1002/ece3.5236>
- Montgomery, G.A., Belitz, M.W., Guralnick, R.P., Tingley, M.W., 2021. Standards and Best Practices for Monitoring and Benchmarking Insects. *Front. Ecol. Evol.* 8. <https://doi.org/10.3389/fevo.2020.579193>
- Montgomery, I., Caruso, T., Reid, N., 2020. Hedgerows as Ecosystems: Service Delivery, Management, and Restoration. *Annu. Rev. Ecol. Evol. Syst.* 51, 81–102. <https://doi.org/10.1146/annurev-ecolsys-012120-100346>
- Mora, O., Berne, J.-A., Drouet, J.-L., Le Mouël, C., Meunier, C., 2023. Foresight: European Chemical Pesticide-Free Agriculture in 2050. <https://doi.org/10.17180/CA9N-2P17>
- Morandin, L.A., Long, R.F., Kremen, C., 2016. Pest Control and Pollination Cost–Benefit Analysis of Hedgerow Restoration in a Simplified Agricultural Landscape. *J. Econ. Entomol.* 109, 1020–1027. <https://doi.org/10.1093/jee/tow086>

- Mouratiadou, I., Wezel, A., Kamilia, K., Marchetti, A., Paracchini, M.L., Bàrberi, P., 2024. The socio-economic performance of agroecology. A review. *Agron. Sustain. Dev.* 44, 19. <https://doi.org/10.1007/s13593-024-00945-9>
- Muff, S., Nilsen, E.B., O'Hara, R.B., Nater, C.R., 2022. Rewriting results sections in the language of evidence. *Trends Ecol. Evol.* 37, 203–210. <https://doi.org/10.1016/j.tree.2021.10.009>
- Munch, E., 2020. Réduire la vitesse et l'empreinte écologique des déplacements de terrain. *Carnets Géographes*. <https://doi.org/10.4000/cdg.6392>
- Naqvi, Q., Wolff, P.J., Molano-Flores, B., Sperry, J.H., 2022. Camera traps are an effective tool for monitoring insect–plant interactions. *Ecol. Evol.* 12, e8962. <https://doi.org/10.1002/ece3.8962>
- Nathans, J., Sterling, P., 2016. How scientists can reduce their carbon footprint. *eLife* 5, e15928. <https://doi.org/10.7554/eLife.15928>
- Neumann, A.E., Conitz, F., Karlebowski, S., Sturm, U., Schmack, J.M., Egerer, M., 2024. Flower richness is key to pollinator abundance: The role of garden features in cities. *Basic Appl. Ecol.* 79, 102–113. <https://doi.org/10.1016/j.baae.2024.06.004>
- Neumüller, U., Burger, H., Krausch, S., Blüthgen, N., Ayasse, M., 2020. Interactions of local habitat type, landscape composition and flower availability moderate wild bee communities. *Landsc. Ecol.* 35, 2209–2224. <https://doi.org/10.1007/s10980-020-01096-4>
- Neuwirth, E., 2022. RColorBrewer: ColorBrewer Palettes.
- Newbold, T., Hudson, L.N., Hill, S.L.L., Contu, S., Lysenko, I., Senior, R.A., Börger, L., Bennett, D.J., Choimes, A., Collen, B., Day, J., De Palma, A., Díaz, S., Echeverria-Londoño, S., Edgar, M.J., Feldman, A., Garon, M., Harrison, M.L.K., Alhusseini, T., Ingram, D.J., Itescu, Y., Kattge, J., Kemp, V., Kirkpatrick, L., Kleyer, M., Correia, D.L.P., Martin, C.D., Meiri, S., Novosolov, M., Pan, Y., Phillips, H.R.P., Purves, D.W., Robinson, A., Simpson, J., Tuck, S.L., Weiher, E., White, H.J., Ewers, R.M., Mace, G.M., Scharlemann, J.P.W., Purvis, A., 2015. Global effects of land use on local terrestrial biodiversity. *Nature* 520, 45–50. <https://doi.org/10.1038/nature14324>
- Nicholls, C.I., Altieri, M.A., 2013. Plant biodiversity enhances bees and other insect pollinators in agroecosystems. A review. *Agron. Sustain. Dev.* 33, 257–274. <https://doi.org/10.1007/s13593-012-0092-y>
- Nicholls, E., Griffiths-Lee, J., Basu, P., Chatterjee, S., Goulson, D., 2023. Crop–pollinator interactions in urban and peri-urban farms in the United Kingdom. *Plants People Planet* 5, 759–775. <https://doi.org/10.1002/ppp3.10376>
- Nicholson, C.C., Knapp, J., Kiljanek, T., Albrecht, M., Chauzat, M.-P., Costa, C., De la Rúa, P., Klein, A.-M., Mänd, M., Potts, S.G., Schweiger, O., Bottero, I., Cini, E., de Miranda, J.R., Di Prisco, G., Dominik, C., Hodge, S., Kaunath, V., Knauer, A., Laurent, M., Martínez-López, V., Medrzycki, P., Pereira-Peixoto, M.H., Raimets, R., Schwarz, J.M., Senapathi, D., Tamburini, G., Brown, M.J.F., Stout, J.C., Rundlöf, M., 2024a. Pesticide use negatively affects bumble bees across European landscapes. *Nature* 628, 355–358. <https://doi.org/10.1038/s41586-023-06773-3>
- Nicholson, C.C., Knapp, J., Kiljanek, T., Albrecht, M., Chauzat, M.-P., Costa, C., De la Rúa, P., Klein, A.-M., Mänd, M., Potts, S.G., Schweiger, O., Bottero, I., Cini, E., de Miranda, J.R., Di Prisco, G., Dominik, C., Hodge, S., Kaunath, V., Knauer, A., Laurent, M., Martínez-López, V., Medrzycki, P., Pereira-Peixoto, M.H., Raimets, R., Schwarz, J.M., Senapathi, D., Tamburini, G., Brown, M.J.F., Stout, J.C., Rundlöf, M., 2024b. Pesticide

- use negatively affects bumble bees across European landscapes. *Nature* 628, 355–358. <https://doi.org/10.1038/s41586-023-06773-3>
- Nicholson, C.C., Knapp, J., Kiljanek, T., Albrecht, M., Chauzat, M.-P., Costa, C., De la Rúa, P., Klein, A.-M., Mänd, M., Potts, S.G., Schweiger, O., Bottero, I., Cini, E., de Miranda, J.R., Di Prisco, G., Dominik, C., Hodge, S., Kaunath, V., Knauer, A., Laurent, M., Martínez-López, V., Medrzycki, P., Pereira-Peixoto, M.H., Raimets, R., Schwarz, J.M., Senapathi, D., Tamburini, G., Brown, M.J.F., Stout, J.C., Rundlöf, M., 2023. Pesticide use negatively affects bumble bees across European landscapes. *Nature* 1–4. <https://doi.org/10.1038/s41586-023-06773-3>
- Nicholson, C.C., Koh, I., Richardson, L.L., Beauchemin, A., Ricketts, T.H., 2017. Farm and landscape factors interact to affect the supply of pollination services. *Agric. Ecosyst. Environ.* 250, 113–122. <https://doi.org/10.1016/j.agee.2017.08.030>
- Nielsen, A., Reitan, T., Rinvoll, A.W., Brysting, A.K., 2017. Effects of competition and climate on a crop pollinator community. *Agric. Ecosyst. Environ.* 246, 253–260. <https://doi.org/10.1016/j.agee.2017.06.006>
- Nunes, L.A., Tai, T., Zuckerberg, B., Clare, J.D., Jepsen, S., Strange, J., Gratton, C., 2024. Local floral abundance influences bumble bee occupancy more than urban-agricultural landscape context. *Insect Conserv. Divers.* 17, 215–228. <https://doi.org/10.1111/icad.12719>
- Ockermüller, E., Kratschmer, S., Hainz-Renetzeder, C., Sauberer, N., Meimberg, H., Frank, T., Pascher, K., Pachinger, B., 2023. Agricultural land-use and landscape composition: Response of wild bee species in relation to their characteristic traits. *Agric. Ecosyst. Environ.* 353, 108540. <https://doi.org/10.1016/j.agee.2023.108540>
- O'Connor, R.S., Kunin, W.E., Garratt, M.P.D., Potts, S.G., Roy, H.E., Andrews, C., Jones, C.M., Peyton, J.M., Savage, J., Harvey, M.C., Morris, R.K.A., Roberts, S.P.M., Wright, I., Vanbergen, A.J., Carvell, C., 2019. Monitoring insect pollinators and flower visitation: The effectiveness and feasibility of different survey methods. *Methods Ecol. Evol.* 10, 2129–2140. <https://doi.org/10.1111/2041-210X.13292>
- OECD, 2021. Agricultural Policy Monitoring and Evaluation 2021: Addressing the Challenges Facing Food Systems, Agricultural Policy Monitoring and Evaluation. OECD. <https://doi.org/10.1787/2d810e01-en>
- Oksanen, J., Simpson, G.L., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Solymos, P., Stevens, M.H.H., Szoecs, E., Wagner, H., Barbour, M., Bedward, M., Bolker, B., Borcard, D., Borman, T., Carvalho, G., Chirico, M., Caceres, M.D., Durand, S., Evangelista, H.B.A., FitzJohn, R., Friendly, M., Furneaux, B., Hannigan, G., Hill, M.O., Lahti, L., Martino, C., McGlinn, D., Ouellette, M.-H., Cunha, E.R., Smith, T., Stier, A., Braak, C.J.F.T., Weedon, J., 2025. *vegan: Community Ecology Package*.
- Ollerton, J., Winfree, R., Tarrant, S., 2011. How many flowering plants are pollinated by animals? *Oikos* 120, 321–326. <https://doi.org/10.1111/j.1600-0706.2010.18644.x>
- Ollivier, M., Cilia, G., Cejas, D., 2025. Molecular Identification of Wild Bees, in: Cilia, G., Ranalli, R., Zavatta, L., Flaminio, S. (Eds.), *Hidden and Wild: An Integrated Study of European Wild Bees*. Springer Nature Switzerland, Cham, pp. 151–185. https://doi.org/10.1007/978-3-031-76742-5_6
- Orford, K.A., Vaughan, I.P., Memmott, J., 2015. The forgotten flies: the importance of non-syrphid Diptera as pollinators. *Proc. R. Soc. B Biol. Sci.* 282, 20142934. <https://doi.org/10.1098/rspb.2014.2934>

- Orsini, F., Pennisi, G., Michelon, N., Minelli, A., Bazzocchi, G., Sanyé-Mengual, E., Gianquinto, G., 2020. Features and Functions of Multifunctional Urban Agriculture in the Global North: A Review. *Front. Sustain. Food Syst.* 4, 562513. <https://doi.org/10.3389/fsufs.2020.562513>
- Ortega-Ramos, P.A., Coston, D.J., Seimandi-Corda, G., Mauchline, A.L., Cook, S.M., 2022. Integrated pest management strategies for cabbage stem flea beetle (*Psylliodes chrysocephala*) in oilseed rape. *Glob. Change Biol. Bioenergy* 14, 267–286. <https://doi.org/10.1111/gcbb.12918>
- Osterman, J., Theodorou, P., Radzevičiūtė, R., Schnitker, P., Paxton, R.J., 2021. Apple pollination is ensured by wild bees when honey bees are drawn away from orchards by a mass co-flowering crop, oilseed rape. *Agric. Ecosyst. Environ.* 315, 107383. <https://doi.org/10.1016/j.agee.2021.107383>
- Ouin, A., Cabanettes, A., Andrieu, E., Deconchat, M., Roume, A., Vigan, M., Larrieu, L., 2015. Comparison of tree microhabitat abundance and diversity in the edges and interior of small temperate woodlands. *For. Ecol. Manag.* 340, 31–39. <https://doi.org/10.1016/j.foreco.2014.12.009>
- Outhwaite, C.L., McCann, P., Newbold, T., 2022. Agriculture and climate change are reshaping insect biodiversity worldwide. *Nature* 605, 97–102. <https://doi.org/10.1038/s41586-022-04644-x>
- Page, M.L., Nicholson, C.C., Brennan, R.M., Britzman, A.T., Greer, J., Hemberger, J., Kahl, H., Müller, U., Peng, Y., Rosenberger, N.M., Stuligross, C., Wang, L., Yang, L.H., Williams, N.M., 2021. A meta-analysis of single visit pollination effectiveness comparing honeybees and other floral visitors. *Am. J. Bot.* 108, 2196–2207. <https://doi.org/10.1002/ajb2.1764>
- Park, M.G., Blitzer, E.J., Gibbs, J., Losey, J.E., Danforth, B.N., 2015. Negative effects of pesticides on wild bee communities can be buffered by landscape context. *Proc. R. Soc. B Biol. Sci.* 282, 20150299. <https://doi.org/10.1098/rspb.2015.0299>
- Paudel, Y.P., Mackereth, R., Hanley, R., Qin, W., 2015. Honey Bees (*Apis mellifera* L.) and Pollination Issues: Current status, impacts and potential drivers of decline. *J. Agric. Sci.* 7. <https://doi.org/10.5539/jas.v7n6p93>
- Pebesma, E., Bivand, R., 2023. *Spatial Data Science: With Applications in R*. Chapman and Hall/CRC, New York. <https://doi.org/10.1201/9780429459016>
- Penuelas, J., Coello, F., Sardans, J., 2023. A better use of fertilizers is needed for global food security and environmental sustainability. *Agric. Food Secur.* 12, 5. <https://doi.org/10.1186/s40066-023-00409-5>
- Perrot, T., Bretagnolle, V., Acar, N., Febvret, V., Matejcek, A., Grégoire, S., Gaba, S., 2024. Bees improve oil quality of oilseed rape. *Basic Appl. Ecol.* 76, 41–49. <https://doi.org/10.1016/j.baae.2024.02.002>
- Perrot, T., Bretagnolle, V., Gaba, S., 2022. Environmentally friendly landscape management improves oilseed rape yields by increasing pollinators and reducing pests. *J. Appl. Ecol.* 59, 1825–1836. <https://doi.org/10.1111/1365-2664.14190>
- Perrot, T., Gaba, S., Roncoroni, M., Gautier, J.-L., Bretagnolle, V., 2018. Bees increase oilseed rape yield under real field conditions. *Agric. Ecosyst. Environ.* 266, 39–48. <https://doi.org/10.1016/j.agee.2018.07.020>
- Perrot, T., Möhring, N., Rusch, A., Gaba, S., Bretagnolle, V., 2025. Crop yield loss under high insecticide regime driven by reduction in natural pest control. *Proc. R. Soc. B Biol. Sci.* 292, 20250138. <https://doi.org/10.1098/rspb.2025.0138>

- Petit, S., Boursault, A., Le Guilloux, M., Munier-Jolain, N., Reboud, X., 2011. Weeds in agricultural landscapes. A review. *Agron. Sustain. Dev.* 31, 309–317. <https://doi.org/10.1051/agro/2010020>
- Pigot, J., Gardarin, A., Doré, T., Morisseau, A., Valantin-Morison, M., 2024. Unlike woodland edges, flower strips do not act as a refuge for cabbage stem flea beetle aestivation. *Pest Manag. Sci.* 80, 2325–2332. <https://doi.org/10.1002/ps.7558>
- Pimentel, D., 1975. *Insects, Science & Society*. Elsevier.
- Pimm, S.L., Jenkins, C.N., Abell, R., Brooks, T.M., Gittleman, J.L., Joppa, L.N., Raven, P.H., Roberts, C.M., Sexton, J.O., 2014. The biodiversity of species and their rates of extinction, distribution, and protection. *Science* 344, 1246752. <https://doi.org/10.1126/science.1246752>
- Plan national d'action, 2021. Plan national en faveur des insectes pollinisateurs et de la pollinisation 2021-2026.
- Polce, C., Termansen, M., Aguirre-Gutiérrez, J., Boatman, N.D., Budge, G.E., Crowe, A., Garratt, M.P., Pietravalle, S., Potts, S.G., Ramirez, J.A., Somerwill, K.E., Biesmeijer, J.C., 2013. Species Distribution Models for Crop Pollination: A Modelling Framework Applied to Great Britain. *PLOS ONE* 8, e76308. <https://doi.org/10.1371/journal.pone.0076308>
- Popic, T.J., Davila, Y.C., Wardle, G.M., 2013. Evaluation of Common Methods for Sampling Invertebrate Pollinator Assemblages: Net Sampling Out-Perform Pan Traps. *PLoS ONE* 8, e66665. <https://doi.org/10.1371/journal.pone.0066665>
- Porcher, E., Bonnet, P., Damgaard, C., De Frenne, P., Deguines, N., Ehlers, B.K., Frei, J., García, M.B., Gros, C., Jandt, U., Joly, A., Martin, G., Michez, D., Pescott, O.L., Roth, T., Waller, D., 2024. Can we harmonize the monitoring of plants and pollinators?: Meeting report on the symposium ‘New solutions to monitor plants, pollinators and their interactions in a changing world’, held at Collège de France and Muséum national d'Histoire naturelle, Paris, France, 23–24 May 2024. *New Phytol.* 244, 39–42. <https://doi.org/10.1111/nph.20038>
- Potter, A., LeBuhn, G., 2015. Pollination service to urban agriculture in San Francisco, CA. *Urban Ecosyst.* 18, 885–893. <https://doi.org/10.1007/s11252-015-0435-y>
- Potts, S.G., Biesmeijer, J.C., Kremen, C., Neumann, P., Schweiger, O., Kunin, W.E., 2010. Global pollinator declines: trends, impacts and drivers. *Trends Ecol. Evol.* 25, 345–353. <https://doi.org/10.1016/j.tree.2010.01.007>
- Potts, S.G., Imperatriz-Fonseca, V., Ngo, H.T., Aizen, M.A., Biesmeijer, J.C., Breeze, T.D., Dicks, L.V., Garibaldi, L.A., Hill, R., Settele, J., Vanbergen, A.J., 2016. Safeguarding pollinators and their values to human well-being. *Nature* 540, 220–229. <https://doi.org/10.1038/nature20588>
- Powney, G.D., Carvell, C., Edwards, M., Morris, R.K.A., Roy, H.E., Woodcock, B.A., Isaac, N.J.B., 2019. Widespread losses of pollinating insects in Britain. *Nat. Commun.* 10, 1018. <https://doi.org/10.1038/s41467-019-08974-9>
- Priyadarshana, T.S., Martin, E.A., Sirami, C., Woodcock, B.A., Goodale, E., Martínez-Núñez, C., Lee, M.-B., Pagani-Núñez, E., Raderschall, C.A., Brotons, L., Rege, A., Ouin, A., Tschamtkke, T., Slade, E.M., 2024. Crop and landscape heterogeneity increase biodiversity in agricultural landscapes: A global review and meta-analysis. *Ecol. Lett.* 27, e14412. <https://doi.org/10.1111/ele.14412>
- QGIS Development Team, 2024. QGIS Geographic Information System [WWW Document]. URL <https://www.qgis.org/> (accessed 1.28.25).

- R Core Team, 2025. R: A language and environment for statistical computing.
- R Development Core Team, 2017. R Development Core Team. (2017). R: A language and environment for statistical computing, version 3.3.3. Vienna, Austria: R Foundation for Statistical Computing.
- Rader, R., Bartomeus, I., Garibaldi, L.A., Garratt, M.P.D., Howlett, B.G., Winfree, R., Cunningham, S.A., Mayfield, M.M., Arthur, A.D., Andersson, G.K.S., Bommarco, R., Brittain, C., Carneiro, L.G., Chacoff, N.P., Entling, M.H., Foully, B., Freitas, B.M., Gemmill-Herren, B., Ghazoul, J., Griffin, S.R., Gross, C.L., Herbertsson, L., Herzog, F., Hipólito, J., Jagger, S., Jauker, F., Klein, A.-M., Kleijn, D., Krishnan, S., Lemos, C.Q., Lindström, S.A.M., Mandelik, Y., Monteiro, V.M., Nelson, W., Nilsson, L., Pattemore, D.E., de O. Pereira, N., Pisanty, G., Potts, S.G., Reemer, M., Rundlöf, M., Sheffield, C.S., Scheper, J., Schüepp, C., Smith, H.G., Stanley, D.A., Stout, J.C., Szentgyörgyi, H., Taki, H., Vergara, C.H., Viana, B.F., Wojciechowski, M., 2016. Non-bee insects are important contributors to global crop pollination. *Proc. Natl. Acad. Sci.* 113, 146–151. <https://doi.org/10.1073/pnas.1517092112>
- Rader, R., Cunningham, S.A., Howlett, B.G., Inouye, D.W., 2020. Non-Bee Insects as Visitors and Pollinators of Crops: Biology, Ecology, and Management. *Annu. Rev. Entomol.* 65, 391–407. <https://doi.org/10.1146/annurev-ento-011019-025055>
- Raderschall, C.A., Bommarco, R., Lindström, S.A.M., Lundin, O., 2021. Landscape crop diversity and semi-natural habitat affect crop pollinators, pollination benefit and yield. *Agric. Ecosyst. Environ.* 306, 107189. <https://doi.org/10.1016/j.agee.2020.107189>
- Rahimi, E., Jung, C., 2024. Spatial Modeling of Insect Pollination Services in Fragmented Landscapes. *Insects* 15, 662. <https://doi.org/10.3390/insects15090662>
- Rani, L., Thapa, K., Kanojia, N., Sharma, N., Singh, S., Grewal, A.S., Srivastav, A.L., Kaushal, J., 2021. An extensive review on the consequences of chemical pesticides on human health and environment. *J. Clean. Prod.* 283, 124657. <https://doi.org/10.1016/j.jclepro.2020.124657>
- Rasmont, P., Devalez, J., Pauly, A., Michez, D., Radchenko, V.G., 2017. Addition to the checklist of IUCN European wild bees (Hymenoptera: Apoidea). *Ann. Société Entomol. Fr.* NS 53, 17–32. <https://doi.org/10.1080/00379271.2017.1307696>
- Ratsimba, N., Therond, O., Parry, H., Monteil, C., Vialatte, A., 2022. Inconsistent responses of conservation biocontrol to landscape structure: new insights from a network-based review. *Ecol. Appl. Publ. Ecol. Soc. Am.* 32, e2456. <https://doi.org/10.1002/eap.2456>
- Redlich, S., Martin, E.A., Steffan-Dewenter, I., 2018. Landscape-level crop diversity benefits biological pest control. *J. Appl. Ecol.* 55, 2419–2428. <https://doi.org/10.1111/1365-2664.13126>
- Renaud, E., Heraudet, V., Deparis, M., Basquin, H., Bessa-Gomes, C., Baudry, E., 2022. Non-linear effects of landscape on pollination service and plant species richness in a peri-urban territory with urban and agricultural land use. *Urban For. Urban Green.* 68, 127454. <https://doi.org/10.1016/j.ufug.2021.127454>
- Requier, F., Leonhardt, S.D., 2020. Beyond flowers: including non-floral resources in bee conservation schemes. *J. Insect Conserv.* 24, 5–16. <https://doi.org/10.1007/s10841-019-00206-1>
- Requier, F., Sibaja Leyton, M., Morales, C.L., Garibaldi, L.A., Giacobino, A., Porrini, M.P., Rosso-Londoño, J.M., Velarde, R.A., Aignasse, A., Aldea-Sánchez, P., Allasino, M.L., Arredondo, D., Audisio, C., Cagnolo, N.B., Basualdo, M., Branchiccela, B., Calderón, R.A., Castelli, L., Castilhos, D., Escareño, F.C., Correa-Benítez, A., da Silva, F.O.,

- Garnica, D.S., de Groot, G., Delgado-Cañedo, A., Fernández-Marín, H., Freitas, B.M., Galindo-Cardona, A., Garcia, N., Garrido, P.M., Giray, T., Gonçalves, L.S., Landi, L., Malusá Gonçalves, D., Martinez, S.I., Moja, P.J., Molineri, A., Müller, P.F., Nogueira, E., Pacini, A., Palacio, M.A., Parra, G.N., Parra-H, A., Peres Gramacho, K., Castro, E.P., Pires, C.S.S., Reynaldi, F.J., Luis, A.R., Rossini, C., Sánchez Armijos, M., Santos, E., Scannapieco, A., Spina, Y.M., Tapia González, J.M., Vargas Fernández, A.M., Viana, B.F., Vieli, L., Yadró García, C.A., Antúnez, K., 2024. First large-scale study reveals important losses of managed honey bee and stingless bee colonies in Latin America. *Sci. Rep.* 14, 10079. <https://doi.org/10.1038/s41598-024-59513-6>
- Rey Benayas, J.M., Bullock, J.M., 2012. Restoration of Biodiversity and Ecosystem Services on Agricultural Land. *Ecosystems* 15, 883–899. <https://doi.org/10.1007/s10021-012-9552-0>
- Ribeiro, A.P., Silva, N.F.F. da, Mesquita, F.N., Araújo, P. de C.S., Rosa, T.C., Mesquita-Neto, J.N., 2021. Machine learning approach for automatic recognition of tomato-pollinating bees based on their buzzing-sounds. *PLOS Comput. Biol.* 17, e1009426. <https://doi.org/10.1371/journal.pcbi.1009426>
- Ricci, B., Lavigne, C., Alignier, A., Aviron, S., Biju-Duval, L., Bouvier, J.C., Choisis, J.-P., Franck, P., Joannon, A., Ladet, S., Mezerette, F., Plantegenest, M., Savary, G., Thomas, C., Vialatte, A., Petit, S., 2019. Local pesticide use intensity conditions landscape effects on biological pest control. *Proc. R. Soc. B Biol. Sci.* 286, 20182898. <https://doi.org/10.1098/rspb.2018.2898>
- Ricou, C., Schneller, C., Amiaud, B., Plantureux, S., Bockstaller, C., 2014. A vegetation-based indicator to assess the pollination value of field margin flora. *Ecol. Indic.* 45, 320–331. <https://doi.org/10.1016/j.ecolind.2014.03.022>
- Riedinger, V., Mitesser, O., Hovestadt, T., Steffan-Dewenter, I., Holzschuh, A., 2015. Annual dynamics of wild bee densities: attractiveness and productivity effects of oilseed rape. *Ecology* 96, 1351–1360. <https://doi.org/10.1890/14-1124.1>
- Rigal, S., Dakos, V., Alonso, H., Auniņš, A., Benkő, Z., Brotons, L., Chodkiewicz, T., Chylarecki, P., de Carli, E., del Moral, J.C., Domşa, C., Escandell, V., Fontaine, B., Foppen, R., Gregory, R., Harris, S., Herrando, S., Husby, M., Ieronymidou, C., Jiguet, F., Kennedy, J., Klvaňová, A., Kmecl, P., Kuczyński, L., Kurlavičius, P., Kálás, J.A., Lähikainen, A., Lindström, Å., Lorrillièr, R., Moshøj, C., Nellis, R., Noble, D., ESKILDSEN, D.P., Paquet, J.-Y., Péliissié, M., Pladevall, C., Portolou, D., Reif, J., Schmid, H., Seaman, B., Szabo, Z.D., Szép, T., Florenzano, G.T., Teufelbauer, N., Trautmann, S., van Turnhout, C., Vermouzek, Z., Vikstrøm, T., Voříšek, P., Weiserbs, A., Devictor, V., 2023. Farmland practices are driving bird population decline across Europe. *Proc. Natl. Acad. Sci.* 120, e2216573120. <https://doi.org/10.1073/pnas.2216573120>
- Riggi, L.G., Gagic, V., Rusch, A., Malsher, G., Ekbom, B., Bommarco, R., 2017. Pollen beetle mortality is increased by ground-dwelling generalist predators but not landscape complexity. *Agric. Ecosyst. Environ.* 250, 133–142. <https://doi.org/10.1016/j.agee.2017.06.039>
- Ripple, W.J., Beschta, R.L., Wolf, C., Painter, L.E., Wirsing, A.J., 2025. The strength of the Yellowstone trophic cascade after wolf reintroduction. *Glob. Ecol. Conserv.* 58, e03428. <https://doi.org/10.1016/j.gecco.2025.e03428>
- Rivers-Moore, J., Andrieu, E., Vialatte, A., Ouin, A., 2020. Wooded Semi-Natural Habitats Complement Permanent Grasslands in Supporting Wild Bee Diversity in Agricultural Landscapes. *Insects* 11, 812. <https://doi.org/10.3390/insects11110812>

- Rivers-Moore, J., Ouin, A., Vialatte, A., Carrié, R., Ladet, S., Andrieu, E., 2023. Contrasting effects of wooded and herbaceous semi-natural habitats on supporting wild bee diversity. *Agric. Ecosyst. Environ.* 356, 108644. <https://doi.org/10.1016/j.agee.2023.108644>
- Ro, C., 2023. Why a climate researcher pushed the limits of low-carbon travel — and his employer's patience. *Nature* 624, 215–216. <https://doi.org/10.1038/d41586-023-03496-3>
- Rollin, O., Bretagnolle, V., Fortel, L., Guilbaud, L., Henry, M., 2015. Habitat, spatial and temporal drivers of diversity patterns in a wild bee assemblage. *Biodivers. Conserv.* 24, 1195–1214. <https://doi.org/10.1007/s10531-014-0852-x>
- Romero, H., Ihl, M., Rivera, A., Zalazar, P., Azocar, P., 1999. Rapid urban growth, land-use changes and air pollution in Santiago, Chile. *Atmos. Environ.* 33, 4039–4047. [https://doi.org/10.1016/S1352-2310\(99\)00145-4](https://doi.org/10.1016/S1352-2310(99)00145-4)
- Ropars, L., Affre, L., Thébault, É., Geslin, B., 2022. Seasonal dynamics of competition between honey bees and wild bees in a protected Mediterranean scrubland. *Oikos* 2022. <https://doi.org/10.1111/oik.08915>
- Ropars, L., Dajoz, I., Fontaine, C., Muratet, A., Geslin, B., 2019. Wild pollinator activity negatively related to honey bee colony densities in urban context. *PLOS ONE* 14, e0222316. <https://doi.org/10.1371/journal.pone.0222316>
- Roquer-Beni, L., Arnan, X., Rodrigo, A., Bosch, J., 2022. What makes a good pollinator? Relationship between pollinator traits and pollination effectiveness in apple flowers. *Entomol. Gen.* 42, 875–882. <https://doi.org/10.1127/entomologia/2022/1571>
- Rouabah, A., Rabolin-Meinrad, C., Gay, C., Therond, O., 2024. Models of bee responses to land use and land cover changes in agricultural landscapes - a review and research agenda. *Biol. Rev. Camb. Philos. Soc.* <https://doi.org/10.1111/brv.13109>
- Rousset, F., Ferdy, J.-B., Courtiol, A., 2025. spaMM: Mixed-Effect Models, with or without Spatial Random Effects.
- Rusch, A., Valantin-Morison, M., Roger-Estrade, J., Sarthou, J.-P., 2012. Local and landscape determinants of pollen beetle abundance in overwintering habitats. *Agric. For. Entomol.* 14, 37–47. <https://doi.org/10.1111/j.1461-9563.2011.00547.x>
- Rusch, A., Valantin-Morison, M., Sarthou, J.-P., Roger-Estrade, J., 2011. Multi-scale effects of landscape complexity and crop management on pollen beetle parasitism rate. *Landsc. Ecol.* 26, 473–486. <https://doi.org/10.1007/s10980-011-9573-7>
- Rusch, A., Valantin-Morison, M., Sarthou, J.-P., Roger-Estrade, J., 2010. Chapter six - Biological Control of Insect Pests in Agroecosystems: Effects of Crop Management, Farming Systems, and Seminal Habitats at the Landscape Scale: A Review, in: Sparks, D.L. (Ed.), *Advances in Agronomy*. Academic Press, pp. 219–259. <https://doi.org/10.1016/B978-0-12-385040-9.00006-2>
- Ruser, R., Fuß, R., Andres, M., Hegewald, H., Kesenheimer, K., Köbke, S., Rübiger, T., Quinones, T.S., Augustin, J., Christen, O., Dittert, K., Kage, H., Lewandowski, I., Prochnow, A., Stichnothe, H., Flessa, H., 2017. Nitrous oxide emissions from winter oilseed rape cultivation. *Agric. Ecosyst. Environ.* 249, 57–69. <https://doi.org/10.1016/j.agee.2017.07.039>
- Sánchez-Bayo, F., Wyckhuys, K.A.G., 2021. Further evidence for a global decline of the entomofauna. *Austral Entomol.* 60, 9–26. <https://doi.org/10.1111/aen.12509>

- Sanderson, R.A., Goffe, L.A., Leifert, C., 2015. Time-series models to quantify short-term effects of meteorological conditions on bumblebee forager activity in agricultural landscapes. *Agric. For. Entomol.* 17, 270–276. <https://doi.org/10.1111/afe.12102>
- Schauberger, B., Ben-Ari, T., Makowski, D., Kato, T., Kato, H., Ciais, P., 2018. Yield trends, variability and stagnation analysis of major crops in France over more than a century. *Sci. Rep.* 8, 16865. <https://doi.org/10.1038/s41598-018-35351-1>
- Scheper, J., Badenhausser, I., Kantelhardt, J., Kirchweyer, S., Bartomeus, I., Bretagnolle, V., Clough, Y., Gross, N., Raemakers, I., Vilà, M., Zaragoza-Trello, C., Kleijn, D., 2023. Biodiversity and pollination benefits trade off against profit in an intensive farming system. *Proc. Natl. Acad. Sci.* 120, e2212124120. <https://doi.org/10.1073/pnas.2212124120>
- Scheper, J., Bommarco, R., Holzschuh, A., Potts, S.G., Riedinger, V., Roberts, S.P.M., Rundlöf, M., Smith, H.G., Steffan-Dewenter, I., Wickens, J.B., Wickens, V.J., Kleijn, D., 2015. Local and landscape-level floral resources explain effects of wildflower strips on wild bees across four European countries. *J. Appl. Ecol.* 52, 1165–1175. <https://doi.org/10.1111/1365-2664.12479>
- Schipanski, M.E., Barbercheck, M., Douglas, M.R., Finney, D.M., Haider, K., Kaye, J.P., Kemanian, A.R., Mortensen, D.A., Ryan, M.R., Tooker, J., White, C., 2014. A framework for evaluating ecosystem services provided by cover crops in agroecosystems. *Agric. Syst.* 125, 12–22. <https://doi.org/10.1016/j.agry.2013.11.004>
- Schmidt, M.H., Lauer, A., Purtauf, T., Thies, C., Schaefer, M., Tschamtker, T., 2003. Relative importance of predators and parasitoids for cereal aphid control. *Proc. Biol. Sci.* 270, 1905–1909. <https://doi.org/10.1098/rspb.2003.2469>
- Senapathi, D., Goddard, M.A., Kunin, W.E., Baldock, K.C.R., 2017. Landscape impacts on pollinator communities in temperate systems: evidence and knowledge gaps. *Funct. Ecol.* 31, 26–37. <https://doi.org/10.1111/1365-2435.12809>
- Seree, L., 2022. Multifonctionnalité de systèmes de culture combinés à des bandes fleuries : Une approche interdisciplinaire pour relier la biodiversité et les services écosystémiques rendus (These de doctorat). université Paris-Saclay.
- Sérée, L., Barbottin, A., Chiron, F., Valantin-Morison, M., Gardarin, A., 2023. Within-field floral resources have the potential to increase parasitism rates in winter oilseed rape pests more than resources at field margins. *Agric. Ecosyst. Environ.* 344, 108288. <https://doi.org/10.1016/j.agee.2022.108288>
- Sérée, L., Chiron, F., Valantin-Morison, M., Barbottin, A., Gardarin, A., 2022. Flower strips, crop management and landscape composition effects on two aphid species and their natural enemies in faba bean. *Agric. Ecosyst. Environ.* 331, 107902. <https://doi.org/10.1016/j.agee.2022.107902>
- Shackelford, G., Steward, P.R., Benton, T.G., Kunin, W.E., Potts, S.G., Biesmeijer, J.C., Sait, S.M., 2013. Comparison of pollinators and natural enemies: a meta-analysis of landscape and local effects on abundance and richness in crops. *Biol. Rev.* 88, 1002–1021. <https://doi.org/10.1111/brev.12040>
- Shameer, K., Hardy, I.C., 2024. Host–parasitoid trophic webs in complex agricultural systems. *Curr. Opin. Insect Sci.* 65, 101253. <https://doi.org/10.1016/j.cois.2024.101253>
- Sharp, R., Chaplin-Kramer, R., Wood, S., Guerry, A., Tallis, H., Ricketts, T., Nelson, E., Ennaanay, D., Wolny, S., Olwero, N., Vigerstol, K., Derric Pennington, Mendoza, G., Aukema, J., Foster, J., Forrest, J., Cameron, D., Arkema, K., Lonsdorf, E., Kennedy, C., Verutes, G., Chong-Ki Kim, Guannel, G., Papenfus, M., Toft, J., Marsik, M.,

- Bernhardt, J., Griffin, R., Glowinski, K., Chaumont, N., Perelman, A., Lacayo, M., Mandle, L., Hamel, P., Vogl, A.L., Rogers, L., Bierbower, W., Denu, D., Douglass, J., 2018. InVEST User's Guide. [object Object]. <https://doi.org/10.13140/RG.2.2.32693.78567>
- Shi, X., Ma, C., de Kraker, J., Gong, S., Hodgson, J.A., Luo, S., van der Steen, J.J.M., Xiao, H., Wang, F., Tie, X., Chen, Z., Zou, Y., 2024. Influence of agricultural intensification on pollinator pesticide exposure, food acquisition and diversity. *J. Appl. Ecol.* 61, 1905–1917. <https://doi.org/10.1111/1365-2664.14701>
- Sibaja Leyton, M., Lattorff, H.M.G., Kiatoko, N., Requier, F., 2025. Climate effects on honey bees can be mitigated by beekeeping management in Kenya. *J. Environ. Manage.* 374, 123879. <https://doi.org/10.1016/j.jenvman.2024.123879>
- Sihag, R.C., 2018. Some Unresolved Issues of Measuring the Efficiency of Pollinators: Experimentally Testing and Assessing the Predictive Power of Different Methods. *Int. J. Ecol.* 2018, 3904973. <https://doi.org/10.1155/2018/3904973>
- Siopa, C., Carvalheiro, L.G., Castro, H., Loureiro, J., Castro, S., 2024. Animal-pollinated crops and cultivars—A quantitative assessment of pollinator dependence values and evaluation of methodological approaches. *J. Appl. Ecol.* 61, 1279–1288. <https://doi.org/10.1111/1365-2664.14634>
- Sirami, C., Gross, N., Baillod, A.B., Bertrand, C., Carrié, R., Hass, A., Henckel, L., Miguet, P., Vuillot, C., Alignier, A., Girard, J., Batáry, P., Clough, Y., Violle, C., Giralt, D., Bota, G., Badenhauer, I., Lefebvre, G., Gauffre, B., Vialatte, A., Calatayud, F., Gil-Tena, A., Tischendorf, L., Mitchell, S., Lindsay, K., Georges, R., Hilaire, S., Recasens, J., Solé-Senan, X.O., Robleño, I., Bosch, J., Barrientos, J.A., Ricarte, A., Marcos-Garcia, M.Á., Miñano, J., Mathevet, R., Gibon, A., Baudry, J., Balent, G., Poulin, B., Burel, F., Tschardtke, T., Bretagnolle, V., Siriwardena, G., Ouin, A., Brotons, L., Martin, J.-L., Fahrig, L., 2019. Increasing crop heterogeneity enhances multitrophic diversity across agricultural regions. *Proc. Natl. Acad. Sci.* 116, 16442–16447. <https://doi.org/10.1073/pnas.1906419116>
- Siviter, H., DeVore, J., Gray, L.K., Ivers, N.A., Lopez, E.A., Riddington, I.M., Stuligross, C., Jha, S., Muth, F., 2024. A novel pesticide has lethal consequences for an important pollinator. *Sci. Total Environ.* 952, 175935. <https://doi.org/10.1016/j.scitotenv.2024.175935>
- Stanley, D.A., Garratt, M.P.D., Wickens, J.B., Wickens, V.J., Potts, S.G., Raine, N.E., 2015a. Neonicotinoid pesticide exposure impairs crop pollination services provided by bumblebees. *Nature* 528, 548–550. <https://doi.org/10.1038/nature16167>
- Stanley, D.A., Gunning, D., Stout, J.C., 2013. Pollinators and pollination of oilseed rape crops (*Brassica napus* L.) in Ireland: ecological and economic incentives for pollinator conservation. *J. Insect Conserv.* 17, 1181–1189. <https://doi.org/10.1007/s10841-013-9599-z>
- Stanley, D.A., Smith, K.E., Raine, N.E., 2015b. Bumblebee learning and memory is impaired by chronic exposure to a neonicotinoid pesticide. *Sci. Rep.* 5, 16508. <https://doi.org/10.1038/srep16508>
- Stanley, D.A., Stout, J.C., 2014. Pollinator sharing between mass-flowering oilseed rape and co-flowering wild plants: implications for wild plant pollination. *Plant Ecol.* 215, 315–325. <https://doi.org/10.1007/s11258-014-0301-7>
- Stanley, J., Preetha, G., 2016. Pesticide Toxicity to Pollinators: Exposure, Toxicity and Risk Assessment Methodologies, in: Stanley, J., Preetha, G. (Eds.), *Pesticide Toxicity to*

- Non-Target Organisms: Exposure, Toxicity and Risk Assessment Methodologies. Springer Netherlands, Dordrecht, pp. 153–228. https://doi.org/10.1007/978-94-017-7752-0_3
- Stavert, J.R., Liñán-Cembrano, G., Beggs, J.R., Howlett, B.G., Pattemore, D.E., Bartomeus, I., 2016. Hairiness: the missing link between pollinators and pollination. *PeerJ* 4, e2779. <https://doi.org/10.7717/peerj.2779>
- Steffan-Dewenter, I., Münzenberg, U., Bürger, C., Thies, C., Tscharntke, T., 2002. Scale-Dependent Effects of Landscape Context on Three Pollinator Guilds. *Ecology* 83, 1421–1432. [https://doi.org/10.1890/0012-9658\(2002\)083\[1421:SDEOLC\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2002)083[1421:SDEOLC]2.0.CO;2)
- Steffan-Dewenter, I., Westphal, C., 2008. The Interplay of Pollinator Diversity, Pollination Services and Landscape Change. *J. Appl. Ecol.* 45, 737–741.
- Stein-Bachinger, K., Preißel, S., Kühne, S., Reckling, M., 2022. More diverse but less intensive farming enhances biodiversity. *Trends Ecol. Evol.* 37, 395–396. <https://doi.org/10.1016/j.tree.2022.01.008>
- Stenberg, J.A., 2017. A Conceptual Framework for Integrated Pest Management. *Trends Plant Sci.* 22, 759–769. <https://doi.org/10.1016/j.tplants.2017.06.010>
- Stephens, C.J., Schellhorn, N.A., Wood, G.M., Austin, A.D., 2006. Parasitic wasp assemblages associated with native and weedy plant species in an agricultural landscape. *Aust. J. Entomol.* 45, 176–184. <https://doi.org/10.1111/j.1440-6055.2006.00519.x>
- Sutter, L., Albrecht, M., Jeanneret, P., 2018a. Landscape greening and local creation of wildflower strips and hedgerows promote multiple ecosystem services. *J. Appl. Ecol.* 55, 612–620. <https://doi.org/10.1111/1365-2664.12977>
- Sutter, L., Amato, M., Jeanneret, P., Albrecht, M., 2018b. Overwintering of pollen beetles and their predators in oilseed rape and semi-natural habitats. *Agric. Ecosyst. Environ.* 265, 275–281. <https://doi.org/10.1016/j.agee.2018.06.030>
- Terres Inovia, 2019. Les atouts du colza [WWW Document]. Terres Inovia. URL <https://www.terresinovia.fr/-/les-atouts-du-colza> (accessed 7.28.25).
- Theodorou, P., Radzevičiūtė, R., Lentendu, G., Kahnt, B., Husemann, M., Bleidorn, C., Settele, J., Schweiger, O., Grosse, I., Wubet, T., Murray, T.E., Paxton, R.J., 2020. Urban areas as hotspots for bees and pollination but not a panacea for all insects. *Nat. Commun.* 11, 576. <https://doi.org/10.1038/s41467-020-14496-6>
- Thomann, M., Imbert, E., Devaux, C., Cheptou, P.-O., 2013. Flowering plants under global pollinator decline. *Trends Plant Sci.* 18, 353–359. <https://doi.org/10.1016/j.tplants.2013.04.002>
- Tian, Y., Xin, W., Lin, J., Ma, J., He, J., Wang, X., Xu, T., Tang, W., 2022. Auxin Coordinates Achene and Receptacle Development During Fruit Initiation in *Fragaria vesca*. *Front. Plant Sci.* 13. <https://doi.org/10.3389/fpls.2022.929831>
- Tibi, A., Martinet, V., Vialatte, A., Alignier, A., Angeon, V., Bedoussac, L., Bohan, D., Bougherara, D., Carpentier, A., Castagnéyrol, B., Cordeau, S., Courtois, P., Deguine, J.-P., Doelher, M., Enjalbert, J., Fabre, F., Femenia, F., Fréville, H., Goulet, F., Grateau, R., Grimonprez, B., Gross, N., Hannachi, M., Jeanneret, P., Labarthe, P., Launay, M., Lelievre, V., Lemarié, S., Martel, G., Masson, A.L., Navarrete, M., Plantegenest, M., Ravigné, V., Rusch, A., Suffert, F., Tapsoba, A., Thoyer, S.S., 2023. Protéger les cultures en augmentant la diversité végétale des espaces agricoles. Rapport scientifique de l'Expertise scientifique collective (report). INRAE. <https://doi.org/10.17180/q7wm-q442>

- Tibi A., Therond O., 2017. Evaluation des services écosystémiques rendus par les écosystèmes agricoles. Une contribution au programme EFESE.
- Timberlake, T.P., Tew, N.E., Memmott, J., 2024. Gardens reduce seasonal hunger gaps for farmland pollinators. *Proc. R. Soc. B Biol. Sci.* 291, 20241523. <https://doi.org/10.1098/rspb.2024.1523>
- Timberlake, T.P., Vaughan, I.P., Memmott, J., 2019. Phenology of farmland floral resources reveals seasonal gaps in nectar availability for bumblebees. *J. Appl. Ecol.* 56, 1585–1596. <https://doi.org/10.1111/1365-2664.13403>
- Toft, S., 2005. The quality of aphids as food for generalist predators: implications for natural control of aphids. *Eur. J. Entomol.* 102, 371–383. <https://doi.org/10.14411/eje.2005.054>
- Tscharntke, T., Grass, I., Wanger, T.C., Westphal, C., Batáry, P., 2022. Prioritise the most effective measures for biodiversity-friendly agriculture. *Trends Ecol. Evol.* 37, 397–398. <https://doi.org/10.1016/j.tree.2022.02.008>
- Tsiafouli, M.A., Thébault, E., Sgardelis, S.P., de Ruiter, P.C., van der Putten, W.H., Birkhofer, K., Hemerik, L., de Vries, F.T., Bardgett, R.D., Brady, M.V., Bjornlund, L., Jørgensen, H.B., Christensen, S., Hertefeldt, T.D., Hotes, S., Gera Hol, W. h., Frouz, J., Liiri, M., Mortimer, S.R., Setälä, H., Tzanopoulos, J., Uteseny, K., Pižl, V., Stary, J., Wolters, V., Hedlund, K., 2015. Intensive agriculture reduces soil biodiversity across Europe. *Glob. Change Biol.* 21, 973–985. <https://doi.org/10.1111/gcb.12752>
- Ullmann, K.S., Meisner, M.H., Williams, N.M., 2016. Impact of tillage on the crop pollinating, ground-nesting bee, *Peponapis pruinosa* in California. *Agric. Ecosyst. Environ.* 232, 240–246. <https://doi.org/10.1016/j.agee.2016.08.002>
- Urruty, N., Deveaud, T., Guyomard, H., Boiffin, J., 2016. Impacts of agricultural land use changes on pesticide use in French agriculture. *Eur. J. Agron.* 80, 113–123. <https://doi.org/10.1016/j.eja.2016.07.004>
- Vaissière, B., Freitas, B.M., Gemmill-Herren, B., 2011. Protocol to detect and assess pollination deficits in crops: a handbook for its use.
- Van Den Berge, S., Tessens, S., Baeten, L., Vanderschaeve, C., Verheyen, K., 2019. Contrasting vegetation change (1974–2015) in hedgerows and forests in an intensively used agricultural landscape. *Appl. Veg. Sci.* 22, 269–281. <https://doi.org/10.1111/avsc.12424>
- Van der Meersch, V., Billaud, O., San Cristobal, M., Vialatte, A., Porcher, E., 2022. Landscape floral resources provided by rapeseed correlate with next-year reproduction of cavity-nesting pollinators in a national participatory monitoring program. *Landsc. Ecol.* 37, 551–565. <https://doi.org/10.1007/s10980-021-01353-0>
- Van Reeth, C., Michel, N., Bockstaller, C., Caro, G., 2019. Influences of oilseed rape area and aggregation on pollinator abundance and reproductive success of a co-flowering wild plant. *Agric. Ecosyst. Environ.* 280, 35–42. <https://doi.org/10.1016/j.agee.2019.04.025>
- Vanbergen, A.J., 2014. Landscape alteration and habitat modification: impacts on plant–pollinator systems. *Curr. Opin. Insect Sci., Social insects/Global change biology* 5, 44–49. <https://doi.org/10.1016/j.cois.2014.09.004>
- Vanbergen, A.J., Initiative, the I.P., 2013. Threats to an ecosystem service: pressures on pollinators. *Front. Ecol. Environ.* 11, 251–259. <https://doi.org/10.1890/120126>

- Vázquez, D.P., Morris, W.F., Jordano, P., 2005. Interaction frequency as a surrogate for the total effect of animal mutualists on plants. *Ecol. Lett.* 8, 1088–1094. <https://doi.org/10.1111/j.1461-0248.2005.00810.x>
- Verocai, M., González-Barrios, P., Mazzilli, S.R., 2024. A comparative study of yield components and their trade-off in oilseed crops (*Brassica napus* L. and *Brassica carinata* A. Braun). *Eur. J. Agron.* 161, 127377. <https://doi.org/10.1016/j.eja.2024.127377>
- Verret, V., Gardarin, A., Makowski, D., Lorin, M., Cadoux, S., Butier, A., Valantin-Morison, M., 2017. Assessment of the benefits of frost-sensitive companion plants in winter rapeseed. *Eur. J. Agron.* 91, 93–103. <https://doi.org/10.1016/j.eja.2017.09.006>
- Vieira, M.C., Cianciaruso, M.V., Almeida-Neto, M., 2013. Plant-Pollinator Coextinctions and the Loss of Plant Functional and Phylogenetic Diversity. *PLOS ONE* 8, e81242. <https://doi.org/10.1371/journal.pone.0081242>
- Vucetich, J.A., Bruskotter, J.T., Nelson, M.P., 2015. Evaluating whether nature's intrinsic value is an axiom of or anathema to conservation. *Conserv. Biol.* 29, 321–332. <https://doi.org/10.1111/cobi.12464>
- Walters, K.F.A., Young, J.E.B., Kromp, B., Cox, P.D., 2003. Management of Oilseed Rape Pests, in: *Biocontrol of Oilseed Rape Pests*. John Wiley & Sons, Ltd, pp. 43–72. <https://doi.org/10.1002/9780470750988.ch3>
- Wan, N.-F., Fu, L., Dainese, M., Kiær, L.P., Hu, Y.-Q., Xin, F., Goulson, D., Woodcock, B.A., Vanbergen, A.J., Spurgeon, D.J., Shen, S., Scherber, C., 2025. Pesticides have negative effects on non-target organisms. *Nat. Commun.* 16, 1360. <https://doi.org/10.1038/s41467-025-56732-x>
- Wenzel, A., Grass, I., Belavadi, V.V., Tschardtke, T., 2020. How urbanization is driving pollinator diversity and pollination – A systematic review. *Biol. Conserv.* 241, 108321. <https://doi.org/10.1016/j.biocon.2019.108321>
- Westphal, C., Steffan-Dewenter, I., Tschardtke, T., 2003a. Mass flowering crops enhance pollinator densities at a landscape scale. *Ecol. Lett.* 6, 961–965. <https://doi.org/10.1046/j.1461-0248.2003.00523.x>
- Westphal, C., Steffan-Dewenter, I., Tschardtke, T., 2003b. Mass flowering crops enhance pollinator densities at a landscape scale. *Ecol. Lett.* 6, 961–965. <https://doi.org/10.1046/j.1461-0248.2003.00523.x>
- Whitehouse, A., Bowen-Jones, E., Amor, M., Banfield, N., Hadaway, P., Hetherington, P., 2025. THE 2024 REPORT - The Bugs Matter Citizen Science Survey.
- Wickham, H., 2016. *ggplot2, Use R!* Springer International Publishing, Cham. <https://doi.org/10.1007/978-3-319-24277-4>
- Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L.D., François, R., Grolemund, G., Hayes, A., Henry, L., Hester, J., Kuhn, M., Pedersen, T.L., Miller, E., Bache, S.M., Müller, K., Ooms, J., Robinson, D., Seidel, D.P., Spinu, V., Takahashi, K., Vaughan, D., Wilke, C., Woo, K., Yutani, H., 2019. Welcome to the Tidyverse. *J. Open Source Softw.* 4, 1686. <https://doi.org/10.21105/joss.01686>
- Wietzke, A., Westphal, C., Gras, P., Kraft, M., Pfohl, K., Karlovsky, P., Pawelzik, E., Tschardtke, T., Smit, I., 2018. Insect pollination as a key factor for strawberry physiology and marketable fruit quality. *Agric. Ecosyst. Environ.* 258, 197–204. <https://doi.org/10.1016/j.agee.2018.01.036>

- Williams, I.H., 2010. The Major Insect Pests of Oilseed Rape in Europe and Their Management: An Overview, in: Williams, I.H. (Ed.), *Biocontrol-Based Integrated Management of Oilseed Rape Pests*. Springer Netherlands, Dordrecht, pp. 1–43. https://doi.org/10.1007/978-90-481-3983-5_1
- Williams, N.M., Ward, K.L., Pope, N., Isaacs, R., Wilson, J., May, E.A., Ellis, J., Daniels, J., Pence, A., Ullmann, K., Peters, J., 2015. Native wildflower plantings support wild bee abundance and diversity in agricultural landscapes across the United States. *Ecol. Appl.* 25, 2119–2131. <https://doi.org/10.1890/14-1748.1>
- Willmer, P., 2011. *Pollination and Floral Ecology*. Princeton University Press.
- Winfree, R., Aguilar, R., Vázquez, D.P., LeBuhn, G., Aizen, M.A., 2009. A meta-analysis of bees' responses to anthropogenic disturbance. *Ecology* 90, 2068–2076. <https://doi.org/10.1890/08-1245.1>
- Woodcock, B.A., Bullock, J.M., Shore, R.F., Heard, M.S., Pereira, M.G., Redhead, J., Ridding, L., Dean, H., Sleep, D., Henrys, P., Peyton, J., Hulmes, S., Hulmes, L., Sárospataki, M., Saure, C., Edwards, M., Genersch, E., Knäbe, S., Pywell, R.F., 2017. Country-specific effects of neonicotinoid pesticides on honey bees and wild bees. *Science* 356, 1393–1395. <https://doi.org/10.1126/science.aaa1190>
- Woodcock, B.A., Garratt, M.P.D., Powney, G.D., Shaw, R.F., Osborne, J.L., Soroka, J., Lindström, S. a. M., Stanley, D., Ouvrard, P., Edwards, M.E., Jauker, F., McCracken, M.E., Zou, Y., Potts, S.G., Rundlöf, M., Noriega, J.A., Greenop, A., Smith, H.G., Bommarco, R., van der Werf, W., Stout, J.C., Steffan-Dewenter, I., Morandin, L., Bullock, J.M., Pywell, R.F., 2019. Meta-analysis reveals that pollinator functional diversity and abundance enhance crop pollination and yield. *Nat. Commun.* 10, 1481. <https://doi.org/10.1038/s41467-019-09393-6>
- Woodcock, B.A., Isaac, N.J.B., Bullock, J.M., Roy, D.B., Garthwaite, D.G., Crowe, A., Pywell, R.F., 2016. Impacts of neonicotinoid use on long-term population changes in wild bees in England. *Nat. Commun.* 7, 12459. <https://doi.org/10.1038/ncomms12459>
- Woodcock, T.S., Pekkola, L.J., Dawson, C., Gadallah, F.L., Kevan, P.G., 2014. Development of a Pollination Service Measurement (PSM) method using potted plant phytometry. *Environ. Monit. Assess.* 186, 5041–5057. <https://doi.org/10.1007/s10661-014-3758-x>
- Yvoz, S., Cordeau, S., Petit, S., 2022. Enhancing weed multifunctionality at a landscape scale: A simulation study. *Landsc. Urban Plan.* 228, 104589. <https://doi.org/10.1016/j.landurbplan.2022.104589>
- Yvoz, S., Petit, S., Biju-Duval, L., Cordeau, S., 2020. A framework to type crop management strategies within a production situation to improve the comprehension of weed communities. *Eur. J. Agron.* 115, 126009. <https://doi.org/10.1016/j.eja.2020.126009>
- Zaninotto, V., Raynaud, X., Gendreau, E., Kraepiel, Y., Motard, E., Babiar, O., Hansart, A., Hignard, C., Dajoz, I., 2020. Broader phenology of pollinator activity and higher plant reproductive success in an urban habitat compared to a rural one. *Ecol. Evol.* 10, 11607–11621. <https://doi.org/10.1002/ece3.6794>
- Zattara, E.E., Aizen, M.A., 2021. Worldwide occurrence records suggest a global decline in bee species richness. *One Earth* 4, 114–123. <https://doi.org/10.1016/j.oneear.2020.12.005>
- Zhao, Z., Shan, R., Sun, X., Sun, J., Wang, B., Wang, Z., 2023. Mapping and assessing supply and demand of crop pollination services in Shandong Province, China. *J. Clean. Prod.* 426, 139024. <https://doi.org/10.1016/j.jclepro.2023.139024>

- Zink, A., CaraDonna, P.J., Larsen, K., Iler, A.M., 2024. Pollination deficits increase with urbanization in Chicago. *Ecosphere* 15, e70100. <https://doi.org/10.1002/ecs2.70100>
- Zulian, G., Maes, J., Paracchini, M., 2013a. Linking Land Cover Data and Crop Yields for Mapping and Assessment of Pollination Services in Europe. *Land* 2, 472–492. <https://doi.org/10.3390/land2030472>
- Zulian, G., Maes, J., Paracchini, M., 2013b. Linking Land Cover Data and Crop Yields for Mapping and Assessment of Pollination Services in Europe. *Land* 2, 472–492. <https://doi.org/10.3390/land2030472>
- Zurbuchen, A., Landert, L., Klaiber, J., Müller, A., Hein, S., Dorn, S., 2010. Maximum foraging ranges in solitary bees: only few individuals have the capability to cover long foraging distances. *Biol. Conserv.* 143, 669–676. <https://doi.org/10.1016/j.biocon.2009.12.003>

REFERENCES

Appendix



Apis mellifera, in the Cévennes, 2021, © Thibault Gandara



Assessment of pollination services across farmed landscapes reveals negative impacts of pesticide use and habitat loss on pollination

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Introduction

Agricultural intensification:

- Leads to **habitat loss** and reduced floral diversity and abundance
- Exposes pollinators to pesticides (direct and indirect impacts)

Consequences for pollinators:

- Reduced pollinator diversity and abundance
- Possible negative feedback loop

Lack of pollinators ⇒ Possibly leading to a decrease in pollination services



Material and methods

Pollinometers

Design of the field experiment

3 strawberry plants with pollinator exclusion



3 strawberry plants with open pollination



Measurements after field pollination

Ripening of strawberries in a common garden and measurement of yield components (mass, height, width ...)

Measurement of effective pollination:

Pollination ensured by pollinators =

Open pollination - Exclusion



Objectives

Evaluate how to best measure pollination at the scale of an agricultural landscape, to identify its drivers

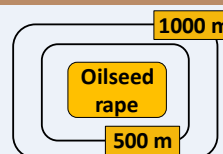
Two methods:

- **Pollination efficiency** ⇒ Pollinometer yield
- **Pollinator presence** ⇒ simplified surveys with morphogroups of pollinators.

Comparison of the two methods: Similar conclusions regarding the drivers?

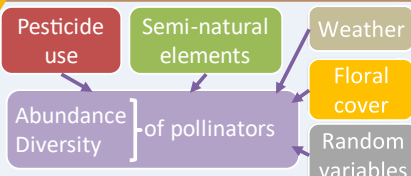
Morphogroup observations

Location of field observations



0 m : Oilseed rape field
500 and 1000 m : Weeds in the border of a cereal field

Model to study environmental correlates (glmm)



Comparison of two contrasting landscapes

CHARTRES

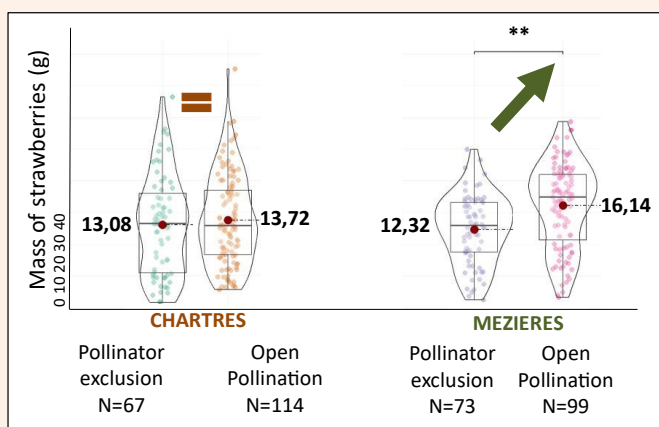
Conventional agriculture in Beauce with few semi-natural elements

MEZIERES

Areas mixing organic and conventional farming and more semi-natural elements

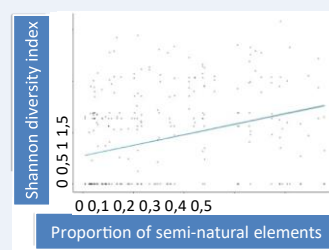
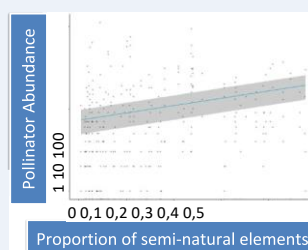
Results

Results of the model on the 4 different sectors

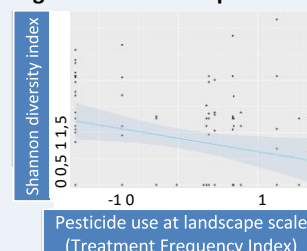
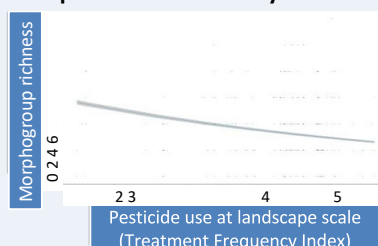


CHARTRES:
no effect of pollinator visits on strawberry mass

MEZIERES:
significant increase in strawberry mass



⇒ Semi-natural elements support a richer and more abundant pollinator community for intensive agricultural landscapes



⇒ Pesticide use impacts the diversity and abundance of pollinator species in agricultural landscapes negatively

Conclusion and perspectives

Intensively farmed landscapes appear to be less favorable for pollinators according to both methods:

- Areas with intensive agricultural practices are the least supportive of pollinator diversity and abundance.
- Consequently, agricultural intensification appears to strongly influence the spatial distribution of pollinators and, therefore, the pollination services within agricultural landscapes

Perspectives:

Pollinometers: Collaboration with other PhD students to estimate anthropogenic pressures on pollination. For future studies: select pollinometers that are more dependent on pollinators

Morphogroup observations: Extend this method in more complex and more contrasted agricultural landscapes to assess its relevance more widely



Une méthode accessible pour évaluer la pollinisation animale des cultures, déployable de la parcelle à la France entière

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Titre court : Evaluer la pollinisation animale des cultures

Résumé

La pollinisation animale, centrale pour la majorité des espèces cultivées, est susceptible de devenir limitante du fait du déclin des pollinisateurs sauvages comme domestiqués. Les outils existants pour mesurer la contribution des pollinisateurs au rendement des cultures sont difficilement transposables à de grandes surfaces, comme celle d'une exploitation agricole ou d'un territoire. Nous proposons un nouvel indicateur de la pollinisation animale. Cet indicateur est simple à produire car il ne nécessite que des données de dépendance des cultures aux pollinisateurs et de rendement des cultures sur un ensemble de parcelles. Nous montrons que, modulo quelques points de vigilance dans l'interprétation, cet indicateur permet de comparer des sites entre eux, d'identifier des zones de déficit de pollinisation animale, et de mettre en évidence les effets des pratiques agricoles et du paysage sur cette pollinisation.

Mots-clés : pollinisateurs, rendements, infrastructures agroécologiques, pratiques agricoles, exploitation agricole.

Abstract: A turn-key method for assessing animal pollination of crops, applicable from individual agricultural fields to France as a whole

Animal pollination, which is central to the yield of most crop species, is likely to become limiting due to the decline of both wild and domesticated pollinators. Existing tools for measuring the contribution of pollinators to crop yields are difficult to apply to large areas, such as farms or whole regions. We propose a new indicator of animal pollination. This indicator is simple to produce as it only requires data on crop dependence on pollinators, as well as crop yields across a set of fields. We show that, with a few points to bear in mind when interpreting the results, this indicator can be used to compare sites, identify areas with a deficit in animal pollination, and highlight the effects of farming practices and landscape on pollination.

Keywords: pollinators, crop yield, agroecological infrastructures, farming practices, farm



1. Introduction

Une majorité des plantes cultivées dépend au moins en partie des insectes ou d'autres animaux pour leur pollinisation (Ollerton et al. 2011), c'est-à-dire le transfert des grains de pollen entre les parties mâles et femelles des fleurs, permettant la production de graines et de fruits (Therond et al. 2017). Ceci rend les enjeux de pollinisation animale centraux dans le monde agricole, particulièrement dans un contexte où les pollinisateurs sont en déclin (Potts et al. 2010) et où les surfaces cultivées avec des espèces dépendantes des pollinisateurs sont en augmentation à l'échelle mondiale (Aizen et al. 2008). Si plusieurs études démontrent des changements majeurs dans l'abondance et/ou la diversité des pollinisateurs sauvages (Koh et al. 2016; par exemple Powney et al. 2019), ainsi que des problèmes d'effondrement des colonies d'abeille mellifère (Paudel et al. 2015), les conséquences en termes d'efficacité de la pollinisation des cultures comme des plantes sauvages restent incertaines. De façon générale, le service de pollinisation tend à être plus efficace en présence de pollinisateurs plus nombreux et plus diversifiés (Katumo et al. 2022), et donc l'érosion en cours devrait se traduire par une diminution de la pollinisation animale. De fait, plusieurs exemples locaux suggèrent que les rendements de certaines cultures sont limités par le déficit de pollinisation animale, par exemple pour le cassis dans le dijonnais (Mouterde 2024) ou encore le colza pour une culture plus répandue en France (Perrot et al. 2018). Cependant, la relation entre abondance ou diversité des pollinisateurs et pollinisation animale n'est pas univoque, et dans certains cas la pollinisation peut être maintenue à un niveau élevé malgré une diminution de la diversité des pollinisateurs (Ricketts et al. 2008), par exemple parce qu'un pollinisateur très efficace est toujours présent.

Les incertitudes autour d'une éventuelle érosion générale de l'efficacité de la pollinisation animale tiennent en partie au fait que la mesure de la contribution des pollinisateurs est fastidieuse et difficile à déployer sur des grandes surfaces, telles une exploitation agricole, un territoire, voire un pays entier, ou sur des durées de plusieurs années. Les méthodes d'estimation sont connues de longue date et éprouvées : elles reposent par exemple sur la comparaison de production de graines ou de fruits, de fleurs en pollinisation libre, accessible aux pollinisateurs, avec des fleurs ensachées, excluant donc les visites de pollinisateurs. La différence entre ces deux rendements renseigne sur la contribution des pollinisateurs. D'autres approches s'appuient sur la relation entre rendement des cultures et abondance ou diversité des pollinisateurs : une relation positive indique un déficit de pollinisation (Reilly et al. 2020; Turo et al. 2024). Ces méthodes sont cependant très lourdes à mettre en œuvre car elles nécessitent des manipulations longues et nombreuses, ou une connaissance des communautés de pollinisateurs présents, et ne sont donc utilisées que sur des surfaces, par exemple une ou quelques parcelles, et des durées réduites. Ce type d'approche a par exemple permis de démontrer le rôle du manque de pollinisateurs dans les faibles rendements du cassis ou une limitation par les pollinisateurs pour le tournesol (Chabert et al. 2022) ou le colza en France (Perrot et al. 2018), ou encore d'évaluer le service de pollinisation sur un territoire dans le projet Sebioref (Ouin et al. 2022), mais uniquement sur des surfaces restreintes et au prix d'un très fort investissement humain.

Pour évaluer la pollinisation animale sur de plus grands territoires et avec des moyens financiers et humains limités, les seules approches disponibles actuellement reposent sur des indicateurs de pollinisation potentielle modélisant l'abondance des pollinisateurs (Rouabah et al. 2024) selon les caractéristiques paysagères. En particulier, des indicateurs utilisant le modèle de Lonsdorf (2009) sont de plus en plus disponibles et appliqués (Zulian et al. 2013; Sharp et al. 2018; Bockstaller et al. 2021). Leur principe est de mobiliser des données d'occupation du sol, et parfois de climat, pour identifier les zones favorables à certains pollinisateurs sauvages, souvent des abeilles, en termes de disponibilité de ressources alimentaires, sites de nidification et conditions climatiques. Le modèle associe également un modèle de déplacement des pollinisateurs pour identifier les zones susceptibles d'être visitées à partir des sites de reproduction. Cet indicateur potentiel a été utilisé par exemple pour optimiser la distribution des cultures à floraison massive afin de maximiser la pollinisation animale (Desaegher et al. 2021). Cependant, il est assorti de plusieurs limites, liées principalement à sa nature indirecte : il ne mesure pas



la pollinisation effectivement réalisée, mais indique les endroits où des pollinisateurs sont susceptibles d'être présents en plus ou moins grand nombre. En particulier, dans son état actuel, il se focalise sur un seul type de pollinisateurs là où les cultures peuvent dépendre d'une grande diversité de pollinisateurs sauvages, comme les syrphes ou autres diptères (Rader et al. 2016) ou encore ne prend pas en compte l'effet de pratiques agricoles comme l'utilisation d'insecticides, aux effets démontrés sur la pollinisation (Stanley et al. 2015).

Dans cet article, nous présentons un nouvel indicateur de pollinisation animale, appelé "indicateur de pollinisation réalisée", qui s'appuie sur les données de rendement des cultures afin d'inférer la contribution des pollinisateurs en comparant les cultures dépendantes des pollinisateurs à celles qui ne le sont pas. Cet indicateur nécessite peu de données, assez facilement accessibles ou récoltables, et peut être calculé à différentes échelles spatiales, de la parcelle agricole (Gandara et al. 2025) à la France entière (Martin et al. 2019). Il pourrait être déployé massivement pour identifier les zones avec un déficit de pollinisation animale, mettre en évidence les effets de certaines pratiques agricoles sur l'efficacité de cette pollinisation, et suivre les variations du succès de pollinisation des cultures au cours du temps. Dans la suite, nous présentons d'abord la méthode de calcul de l'indicateur, suivie de quelques résultats principaux et nous terminons par des recommandations importantes pour l'utilisation et l'interprétation de l'indicateur.

2. Données et principe du calcul de l'indicateur de pollinisation réalisée

1.1 Données nécessaires

Le calcul de l'indicateur de pollinisation réalisée nécessite deux types de données agronomiques élémentaires : d'une part des données de rendement des cultures, à une résolution spatiale la plus fine possible, d'autre part, une information sur la dépendance du rendement de ces cultures à la pollinisation animale. Ces données élémentaires sont souvent déjà disponibles sur beaucoup de territoires.

Rendement des cultures

Comme nous sommes intéressés par une mesure de la pollinisation, nous travaillons préférentiellement avec des cultures dont le rendement dépend de la production de graines ou de fruits, résultant de la pollinisation des fleurs. Pour les premiers tests de l'indicateur, à deux échelles spatiales différentes, nous avons utilisé des données de rendement issues de deux sources : (1) celles fournies par le ministère de l'Agriculture et de la Souveraineté Alimentaire dans le cadre de la [Statistique Agricole Annuelle](#), qui recense chaque année le rendement moyen des cultures dans chaque département français (= un site). Pour cette approche nationale nous avons sélectionné 55 espèces cultivées dont les rendements dépendent de la production de graines ou de fruits, et nous avons extrait les rendements pour la période 2000-2010 ; (2) les données collectées sur la [plateforme d'observation paysagère de Fénay](#), composée de 140 parcelles commerciales de grandes cultures contiguës (environ 1000 ha) dans la plaine de Dijon. Chaque parcelle (= un site) est suivie chaque année depuis 2007 par l'unité de recherche Agroécologie (INRAE-Institut Agro-Université de Bourgogne), avec notamment une collecte des données de rendement et de pratiques. Pour cette deuxième zone d'étude nous avons sélectionné 14 espèces cultivées et les données de rendement sur la période 2007-2019.

Dépendance du rendement à la pollinisation animale

Pour chaque culture, la dépendance à la pollinisation animale est définie comme la diminution du rendement (exprimée en pourcentage du total) qui serait observée en l'absence de tout pollinisateur. Cet



indice varie de 0, pour les cultures non-dépendantes des pollinisateurs comme les céréales, à presque 100% pour des cultures qui ne sont pas du tout productives en l'absence de pollinisateurs comme les kiwis ou certaines courges. Ces valeurs ont été estimées par diverses études expérimentales, et synthétisées dans l'article de Klein et al. (2007), qui propose 5 classes : aucune dépendance (0%), et dépendances faible (5%), modeste (25%), forte (65%) et essentielle (95%). Cette synthèse mondiale fournit une seule valeur par espèce, et ignore l'existence de différences entre variétés pour la dépendance aux pollinisateurs, mais en première approche elle fournit une information utile pour la majorité des espèces cultivées en France. Récemment, Siopa et al. (2024) ont affiné cette quantification en proposant des valeurs continues de dépendance aux pollinisateurs, fondées sur la supplémentation en pollen.

1.2 Le calcul de l'indicateur

Standardisation des données de rendement

Comme nous allons le voir ci-dessous, l'indicateur de pollinisation réalisée met en relation les rendements des cultures avec leur dépendance aux pollinisateurs. Cependant, les rendements bruts des cultures sont par nature très différents d'une espèce à l'autre, dépendants notamment de la quantité d'eau dans la partie récoltée (exemple des concombres avec des rendements très élevés). Pour pouvoir comparer les rendements entre cultures, la première étape consiste donc en une standardisation, afin que toutes les cultures aient le même rendement moyen ($= 0$) et la même variabilité du rendement ($= 1$). Cette standardisation se fait **au sein de chaque culture**, à l'échelle de l'ensemble de la zone d'étude (Figures 1A et B). Dans ce cas, des valeurs standardisées négatives (respectivement positives) dans un site donné indique que les rendements y sont inférieurs (respectivement supérieurs) aux rendements moyens de cette culture dans la zone d'étude.

Mise en relation des données de rendement avec la dépendance des cultures aux pollinisateurs

La philosophie générale de calcul de l'indicateur est simple : elle repose sur l'hypothèse que, **toutes choses égales par ailleurs**, dans un site avec un déficit de pollinisateurs, le rendement standardisé des cultures dépendantes des pollinisateurs devrait être inférieur, en moyenne, au rendement standardisé des cultures non-dépendantes des pollinisateurs. La première partie de la phrase « toutes choses égales par ailleurs » est importante, et implique notamment une hypothèse sur les autres facteurs, nombreux, qui influencent le rendement des cultures (par exemple, caractéristiques des sols, conditions météorologiques, pratiques agricoles dans les parcelles, etc.) : ces facteurs sont considérés comme ayant un rôle équivalent, en moyenne, pour les cultures dépendantes et non-dépendantes des pollinisateurs, dans une zone donnée. C'est une hypothèse acceptable sous réserve que l'analyse soit faite sur un nombre suffisant d'espèces dans chaque catégorie de dépendance aux pollinisateurs (voir Discussion).

Cela étant posé, l'indicateur de pollinisation réalisée correspond à **la pente de la régression linéaire entre les rendements standardisés des cultures et la dépendance des cultures aux pollinisateurs** dans un site (Figure 1C). Dans le site 7, les rendements des cultures non-dépendantes des pollinisateurs sont autour de la moyenne (*i.e.*, 0) pour l'ensemble de la zone d'étude, ce qui indique que les conditions de culture sont relativement favorables. Cependant, les cultures dépendantes des pollinisateurs (dépendances de 0,65 et 0,95) ont des rendements inférieurs à la moyenne de la zone d'étude (rendements standardisés négatifs), malgré ces bonnes conditions de culture, ce qui suggère un déficit de pollinisation animale. Au contraire, dans le site 1, les rendements sont légèrement au-dessus de la moyenne de la zone d'étude pour toutes les cultures, quelle que soit leur dépendance aux pollinisateurs, ce qui suggère que la pollinisation animale est moins limitante dans ce site.

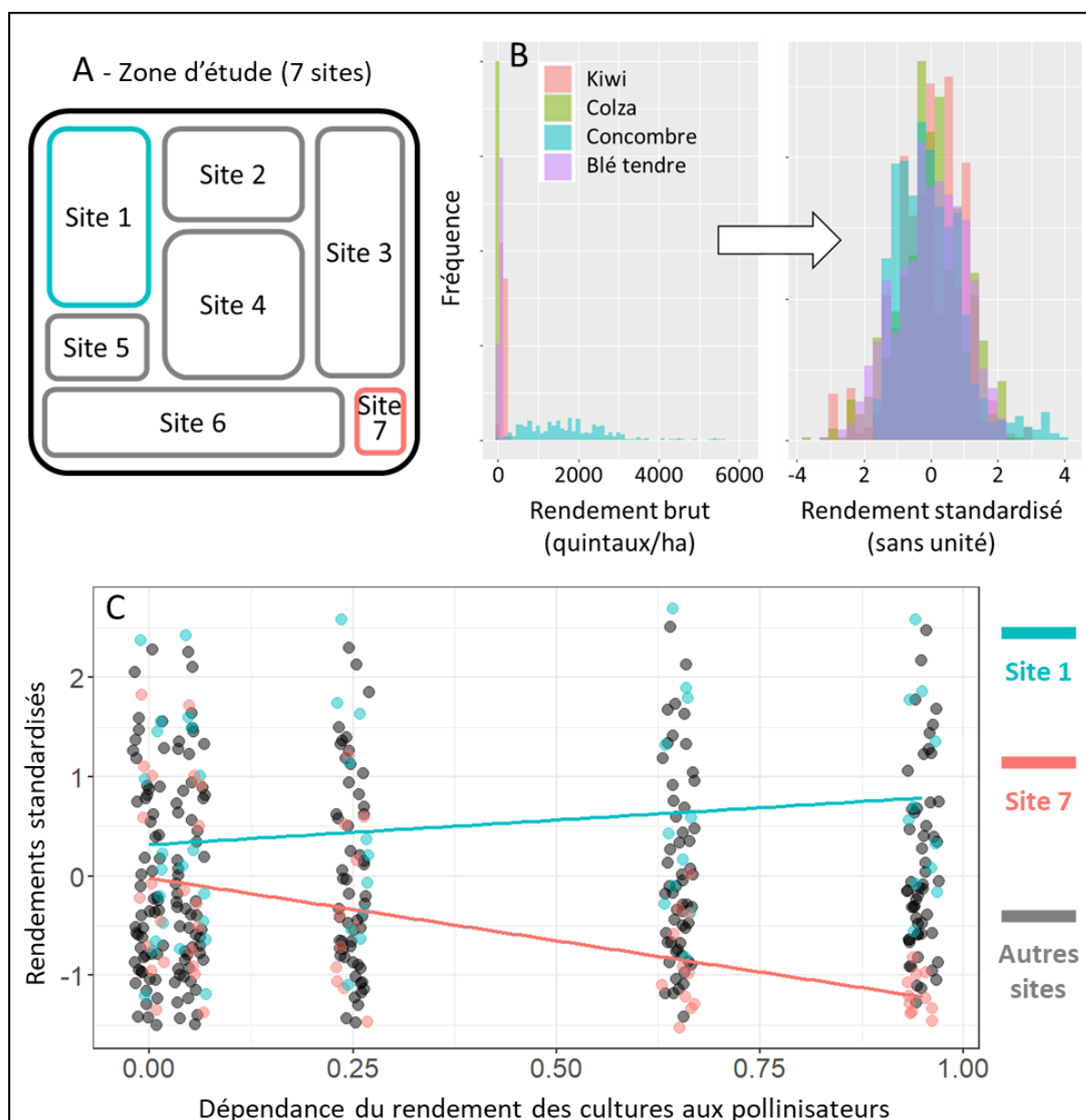


Figure 1 : Principes du calcul de l'indicateur de pollinisation réalisée. Cet indicateur est calculé à l'échelle d'une zone géographique (A), découpée en sites. Cette zone peut être la France, et les sites sont par exemple les départements, ou une zone plus restreinte, comme le site expérimental de Fénay, et les sites sont des parcelles ou des groupes de parcelles. Dans l'exemple théorique proposé ici, la zone est découpée en 7 sites (B). Les données de rendements de chaque culture sont standardisées à l'échelle de l'ensemble de la zone d'étude (C). Exemple de régression pour deux sites avec des limitations en pollen différentes. Le graphique montre la distribution des rendements standardisés (moyenne = 0 et variance = 1 pour chaque culture à l'échelle de la zone d'étude) dans un exemple théorique, en fonction des 5 classes de dépendance aux pollinisateurs de Klein et al. (2007). Chaque point correspond à une donnée de rendement pour une espèce cultivée, un site et une année (si des données pluriannuelles sont disponibles). Dans la représentation graphique, les points sont légèrement déplacés autour de la valeur de dépendance aux pollinisateurs, pour une meilleure lisibilité. Deux sites sont mis en exergue avec des couleurs différentes et la droite de régression permettant le calcul de l'indicateur (voir texte). A noter que le calcul de l'indicateur requiert des données de rendement pour des cultures avec des niveaux de dépendance différents au sein de chaque site, que ces sites soient des parcelles agricoles ou des regroupements de parcelles à des résolutions spatiales plus grossières.



Résolution spatiale et stratégies de spatialisation de l'indicateur

Les utilisateurs de l'indicateur seront souvent intéressés par une résolution spatiale la plus fine possible ; celle-ci est dépendante de deux facteurs : d'une part la résolution spatiale des données, en deçà de laquelle il n'est pas possible de descendre, d'autre part les répétitions disponibles pour les données de rendement. En effet, le calcul de l'indicateur requiert des données de rendement issues de différents sites, chacun comportant des cultures à niveaux de dépendance variables, que ce soit sur une parcelle en rotation ou sur un ensemble de parcelles. Comme l'indicateur repose sur le calcul d'une régression linéaire par site entre les rendements standardisés et la dépendance des cultures aux pollinisateurs, il faut suffisamment de données de rendement pour des cultures de dépendances variées pour une estimation fiable de la pente de la régression. Si l'on dispose de données pluriannuelles avec des séries temporelles suffisamment longues (en pratique supérieures à 10 ans), les répétitions temporelles peuvent être utilisées, à condition qu'il y ait eu sur chaque site une rotation des cultures permettant de disposer de données pour des cultures avec des dépendances contrastées aux pollinisateurs. En revanche, en l'absence de données temporelles, ou pour des séries temporelles trop courtes, les répétitions peuvent être obtenues en regroupant les unités d'observations de base (par exemple des parcelles) dans l'espace, avec une résolution spatiale d'autant plus grossière qu'un site regroupe beaucoup d'unités d'observation. Plusieurs options de regroupement spatial, avec des résolutions spatiales différentes, sont présentées dans Gandara et al. (2025).

1.3 Relation de l'indicateur de pollinisation réalisée avec d'autres indicateurs de pollinisation et avec des variables environnementales

Pour tester notre indicateur, nous avons examiné sa corrélation avec les indicateurs de pollinisation potentielle, fournissant une information sur les zones potentiellement abondantes en pollinisateurs à partir de modèles de déplacement des pollinisateurs et d'une cartographie d'occupation des sols pour évaluer les ressources disponibles : la carte produite par Zulian et al. (2013) dans le cas de l'étude à l'échelle de la France entière et une cartographie produite par nos soins pour l'analyse des données de la plateforme paysagère de Fénay, à partir du modèle InVEST (Sharp et al. 2018). Pour cette dernière analyse, nous avons également pu examiner la relation entre l'indicateur de pollinisation réalisée et l'utilisation de pesticides dans les parcelles, mesuré comme l'Indice de Fréquence de Traitement cumulé sur les 13 années d'étude.

3. Résultats : une cartographie des zones présentant des déficits de pollinisation, disponible à différentes échelles spatiales

Dans cette partie, nous présentons les grandes lignes des variations spatiales de l'indicateur de pollinisation à deux échelles : celle de la France, à partir des données de la Statistique Agricole Annuelle, et celle d'un paysage agricole, à partir des données de la zone expérimentale de Fénay. Des résultats plus détaillés sont disponibles dans Martin et al. (2019) et Gandara et al. (2025), respectivement.

1.1 A l'échelle nationale, un gradient latitudinal de pollinisation conforme aux connaissances sur l'écologie des pollinisateurs

Le calcul de l'indicateur de pollinisation réalisée à la résolution des départements français, grâce aux données de la Statistique Agricole Annuelle pour 55 espèces cultivées dont le rendement dépend de la production de graines ou de fruits, montre des disparités fortes entre départements, avec notamment un gradient latitudinal associé à des déficits de pollinisation plus forts dans le nord de la France (Figure 2A). On note notamment des déficits particulièrement marqués dans le Bassin parisien. Au contraire, la situation semble moins problématique autour du bassin méditerranéen. L'indicateur de pollinisation réalisée est par ailleurs remarquablement corrélé avec l'indicateur de pollinisation potentielle de Zulian et

al. (Figure 2B, coefficient de corrélation de Spearman $\rho = 0.65$, $P < 0.001$), ce qui suggère que l'utilisation de données d'occupation des sols et de climat peut fournir en première approche une bonne estimation de la pollinisation. Cependant, la corrélation n'est pas parfaite non plus, et les différences résiduelles sont probablement révélatrices d'autres facteurs influençant la pollinisation réalisée, qui ne sont pas pris en compte dans le modèle de Zulian et al. (2013) : diversité des pollinisateurs au-delà des abeilles sauvages, rôle des pollinisateurs gérés, notamment l'abeille mellifère, impact des pratiques agricoles. L'échelle nationale n'est cependant pas la plus pertinente pour tenter de séparer les effets relatifs de ces variables, car le gradient de pollinisation nord-sud est associé à plusieurs autres gradients nord-sud confondus : l'agriculture française est plus intensive au nord qu'au sud, les infrastructures agroécologiques y sont plus rares et le climat moins favorable pour une partie des pollinisateurs, notamment les abeilles sauvages. Des échelles spatiales plus fines, par exemple celle d'un paysage, permettent d'aller plus loin dans la compréhension des mécanismes qui influencent la pollinisation des cultures.

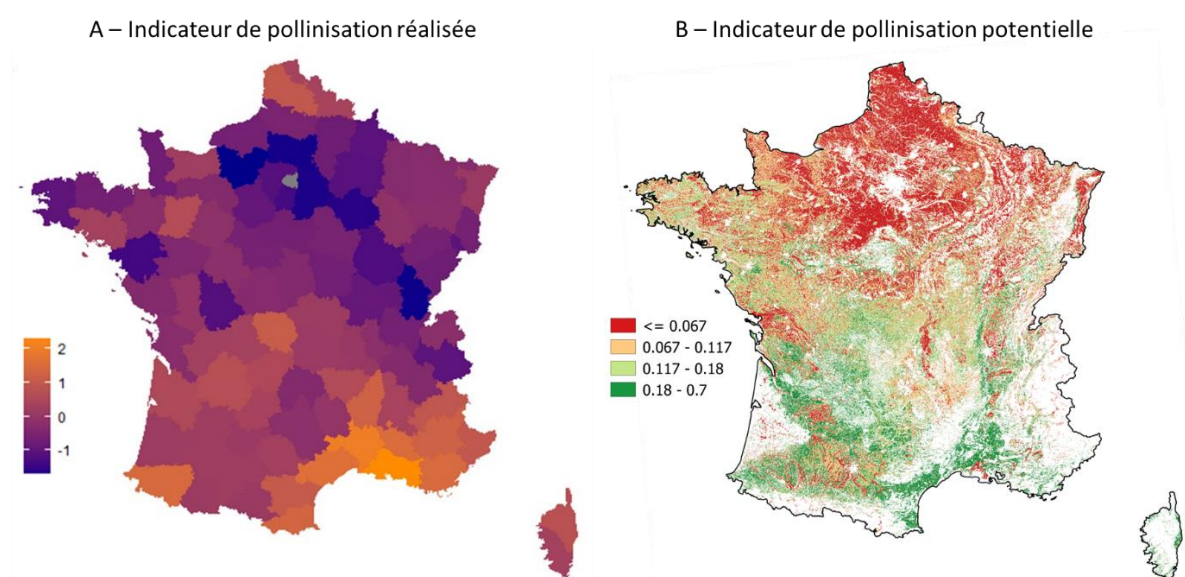


Figure 2 : comparaison de la variabilité spatiale de notre indicateur de pollinisation réalisée en France (A), à la résolution spatiale des départements, avec la variation de l'indice de pollinisation potentielle (B) de Zulian et al. (2013). Dans les deux cas, les valeurs de l'indicateur n'ont pas d'unité. En (A), les couleurs de l'orange vers le bleu indiquent des déficits de pollinisation de plus en plus marqués. En (B), les couleurs du vert vers le rouge indiquent des déficits de pollinisation de plus en plus marqués. La cartographie de l'indicateur de pollinisation potentielle a été retravaillée pour la France dans le cadre de l'EFES (Therond et al. 2017), en ne se focalisant que sur les espaces agricoles. Les pixels en blanc correspondent donc à d'autres occupations du sol.

1.2 A l'échelle d'un paysage agricole, l'indicateur de pollinisation réalisée révèle les effets des infrastructures agroécologiques et l'utilisation d'insecticides dans les parcelles

Dans la plateforme paysagère de Fénay, les indicateurs de pollinisation potentielle et réalisée sont encore bien corrélés (Figure 3) mais toujours avec des différences. La corrélation positive entre les deux indicateurs est liée au rôle central, et bien connu, des éléments semi-naturels -inclus dans le modèle utilisé pour l'indicateur de pollinisation potentielle-, qui favorisent l'abondance et la diversité des pollinisateurs (Kennedy et al. 2013). Les différences, en revanche, peuvent être partiellement expliquées par une qualité variable, non caractérisée, des éléments semi-naturels et par le rôle des pratiques dans les parcelles, pratiques qui ne sont pas incluses dans le modèle de pollinisation potentielle. En effet, quand l'indicateur est calculé à la résolution spatiale de la parcelle, nous observons une relation négative entre la pollinisation réalisée et l'indice de fréquence de traitement en insecticides (Gandara et al. 2025).

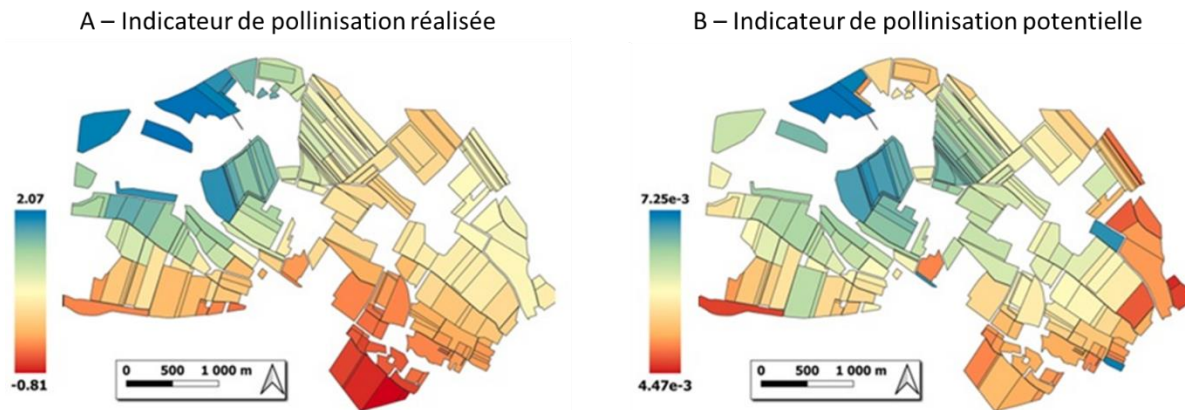


Figure 3 : comparaison de la variance spatiale de l'indicateur de pollinisation réalisée dans la plateforme paysagère de Fénay (A), à la résolution spatiale des parcelles, avec la variation de l'indice de pollinisation potentielle (B) calculé avec l'outil InVEST (Sharp et al. 2018). Dans les deux cas, les couleurs du bleu vers le rouge indiquent des déficits de pollinisation de plus en plus marqués, et les valeurs de l'indicateur n'ont pas d'unité. Figure tirée de Gandara et al. (2025).

4. Discussion : quelques précautions dans le calcul et l'interprétation de l'indicateur de pollinisation réalisée

L'indicateur de pollinisation réalisée est un outil prometteur, qui peut être calculé à partir de données relativement disponibles, et qui va au-delà des indicateurs de pollinisation existants : en effet, cet indicateur basé sur les rendements renseigne la pollinisation réalisée, contrairement aux indicateurs potentiels basés sur la présence prédite de pollinisateurs. A ce titre, il permet de prendre en compte la pollinisation assurée par l'ensemble des pollinisateurs des cultures et d'inclure toutes les variables environnementales influençant cette pollinisation, notamment l'effet des pratiques agricoles qui ne sont souvent pas considérées dans les modèles existants. Cependant, plusieurs précautions doivent être prises pour une bonne utilisation et interprétation de l'indicateur.

1.3 L'indicateur de pollinisation réalisée est relatif, et ne permet pas une estimation dans l'absolu des déficits de pollinisation

Par son mode de calcul, qui inclut une standardisation des rendements de chaque culture à l'échelle de la zone d'étude dans son ensemble, l'indicateur informe sur les classements des sites les uns par rapport aux autres, mais ne dit rien sur les pertes de rendement absolues causées par un déficit de pollinisation. Par construction, les rendements standardisés varient entre -2 et +2 et sont centrés sur 0, cela pour tous les niveaux de dépendance. Ainsi, une relation négative entre ces rendements et la dépendance aux pollinisateurs dans certains sites implique, en miroir, une relation positive dans d'autres. Les relations négatives signalent clairement un déficit de pollinisation (les cultures dépendantes présentent des rendements inférieurs à la moyenne nationale). L'interprétation des relations positives est moins directe : si un déficit de pollinisation touche toute la zone d'étude, même les sites à relation positive restent en déficit, mais dans une moindre mesure que les sites à relation négative (leurs cultures dépendantes ont les meilleurs rendements relatifs). A noter cependant qu'en l'absence de déficit, l'indicateur ne détecte aucun signal : les pentes des relations restent proches de zéro pour tous les sites. L'indicateur de pollinisation réalisée met donc en évidence des déficits dès lors que les pentes sont variables d'un site à l'autre, et classe les sites selon la sévérité du déficit ou inversement selon la contribution des pollinisateurs au rendement des cultures qui en sont dépendantes. Pour connaître l'effet absolu du déficit de pollinisation sur les rendements, il est indispensable d'utiliser les techniques éprouvées de supplémentation en pollen, pour estimer à quel point les rendements peuvent être augmentés par un apport de pollen illimité.



1.4 L'indicateur de pollinisation réalisée nécessite plusieurs cultures par niveau de dépendance aux pollinisateurs

L'interprétation de l'indicateur repose sur une hypothèse centrale : à part l'efficacité de la pollinisation animale, tous les facteurs influençant le rendement, qui sont nombreux (caractéristiques des sols, conditions météorologiques, pratiques agricoles, etc.) ont en moyenne le même effet sur les espèces cultivées quelle que soit leur dépendance aux pollinisateurs. C'est ce qui est sous-entendu dans l'affirmation « toutes choses égales par ailleurs ». Pour que cette hypothèse soit vérifiée le mieux possible, il est indispensable que chaque catégorie de dépendance aux pollinisateurs soit représentée par le plus grand nombre d'espèces cultivées possible. Prenons un exemple caricatural où l'indicateur serait calculé avec seulement deux espèces : une céréale A, avec une dépendance de 0 pour les pollinisateurs, et une courge B, avec une dépendance de 95 % pour les pollinisateurs. Par ailleurs, la céréale est très résistante à la sécheresse mais supporte peu l'humidité (maladies fongiques) alors que la courge a de forts besoins en eau. Avec un tel jeu de données, les rendements standardisés de la céréale sont élevés dans les sites les plus secs et faibles dans les sites très arrosés, et c'est le contraire pour les rendements de la courge. La relation entre rendements standardisés et dépendance aux pollinisateurs est donc négative dans les sites secs et positive dans les sites arrosés, et ce **même si la pollinisation animale n'est limitante nulle part**. Dans ce cas précis, les effets du climat et de la dépendance à la pollinisation sont confondus et l'indicateur ne fonctionne pas : il conclut à un déficit de pollinisation animale dans les sites secs, alors que ce n'est qu'une question de préférence climatique. En revanche, avec plusieurs espèces cultivées fonctionnellement contrastées dans chaque classe de dépendance aux pollinisateurs, on attend qu'il n'y ait pas de corrélation entre dépendance aux pollinisateurs et préférences climatiques, édaphiques, ou aux pratiques agricoles. Un corollaire de cette propriété est que l'indicateur ne fournit pas une mesure du déficit de pollinisation pour une culture isolément, seulement pour des sites dans une zone donnée, sur l'ensemble des cultures incluses dans le calcul. Par ailleurs, si toutes les cultures dépendantes des pollinisateurs sont bien pollinisées par un seul type de pollinisateurs (l'abeille domestique par exemple), l'indicateur peut passer à côté d'un déficit de pollinisation par les autres pollinisateurs (pollinisateurs sauvages par exemple).

1.5 Le choix de la résolution spatiale dépend des attentes des utilisateurs

Selon la finesse des données de rendement disponibles, l'indicateur peut être calculé à différentes résolutions spatiales, y compris jusqu'à celle de la parcelle agricole si l'on dispose d'une série temporelle suffisamment longue pour chaque parcelle. Le choix de la meilleure résolution spatiale dépend des questions que l'on souhaite aborder avec l'indicateur. Pour comprendre l'effets des pratiques dans la parcelle sur la pollinisation, la résolution spatiale de la parcelle est assez logiquement la plus pertinente, d'autant que la typologie des pratiques peut varier rapidement d'une parcelle à l'autre dans un territoire agricole. En revanche, pour visualiser la configuration spatiale de l'efficacité de la pollinisation dans un territoire ou paysage agricole, des résolutions plus grossières peuvent être plus efficaces, car elles permettent d'une part de moyenniser des effets de pratiques intra-parcelle parfois contrastés, et d'autre part d'augmenter la précision de l'indicateur en augmentant le nombre de données utilisées pour calculer la pente de la relation entre rendements standardisés et dépendance aux pollinisateurs. Les lecteurs et lectrices intéressés trouveront plus de détails dans l'article de Gandara et al. (2025).

1.6 L'indicateur peut aussi être utilisé pour un suivi des variations temporelles de l'efficacité de la pollinisation

Le présent article s'est concentré sur l'étude des variations spatiales de l'efficacité de la pollinisation, mais l'indicateur peut aussi être appliqué avec un découpage des données dans le temps, plutôt que dans l'espace. L'indicateur classera alors les intervalles de temps, par exemple les années, entre moments avec un fort déficit de pollinisation et moments avec une meilleure pollinisation. Une perspective



naturelle de cet indicateur est donc d'être testé pour suivre les changements temporels de la pollinisation en France.

5. Conclusions

L'indicateur de pollinisation réalisée, fondé sur les données de rendement des cultures et leur dépendance aux pollinisateurs, est un outil prometteur pour identifier des zones où la pollinisation animale est la plus limitante, et ainsi soit adapter son assolement, à court terme, pour installer les cultures très dépendantes des pollinisateurs dans les zones les plus favorables, soit repenser à plus long terme un territoire agricole pour promouvoir des aménagements et pratiques favorables aux pollinisateurs là où ils n'assurent plus leur rôle de pollinisation. Cet indicateur apporte une plus-value par rapport aux outils existants qui en restent à la pollinisation potentielle, car il permet de prendre en compte tous les pollinisateurs et tous les facteurs qui les influencent, notamment les pratiques dans les parcelles. Nous souhaitons continuer à le déployer dans une gamme de contextes agricoles variées, et les personnes connaissant des territoires où des données de rendement des cultures sont disponibles sont chaleureusement invitées à nous contacter.

Ethique

Les auteurs déclarent que les expérimentations ont été réalisées en conformité avec les réglementations nationales applicables.

Déclaration sur la disponibilité des données et des modèles

Les données qui étayent les résultats évoqués dans cet article sont accessibles sur demande auprès de l'auteur de correspondance de l'article.

Déclaration relative à l'Intelligence artificielle générative et aux technologies assistées par l'Intelligence artificielle dans le processus de rédaction.

Les auteurs n'ont pas utilisé de technologies assistées par intelligence artificielle dans le processus de rédaction.

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Contributions des auteurs

EP a rédigé la première version de l'article. Tous les auteurs ont relu et amélioré la rédaction.

Déclaration d'intérêt

Les auteurs déclarent ne pas travailler, ne pas conseiller, ne pas posséder de parts, ne pas recevoir de fonds d'une organisation qui pourrait tirer profit de cet article, et ne déclarent aucune autre affiliation que celles citées en début d'article.

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Références bibliographiques :

- Aizen, M. A., L. A. Garibaldi, S. A. Cunningham, and A. M. Klein. 2008. Long-term global trends in crop yield and production reveal no current pollination shortage but increasing pollinator dependency. *Current Biology* 18: 1572–1575. <https://doi.org/10.1016/j.cub.2008.08.066>.
- Bockstaller, C., C. Sirami, D. Sheeren, O. Keichinger, L. Arnaud, A. Favreau, F. Angevin, et al. 2021. Contribution of remote sensing to the calculation of agri-environmental indicators for the CAP, farmers and stakeholders Apports de la télédétection au calcul d'indicateurs agri-environnementaux au service de la PAC, des agriculteurs et porteurs d'enjeu. *Innovations agronomiques*. INRAE. <https://doi.org/10.15454/NS4W-A314>.
- Chabert, S., R. E. Mallinger, C. Senechal, A. Fougeroux, O. Geist, V. Guillemard, S. Leylaverne, C. Malard, J. Pousse, and B. E. Vaissiere. 2022. Importance of maternal resources in pollen limitation studies with pollinator gradients: A case study with sunflower. *Agriculture Ecosystems & Environment* 330. Amsterdam: Elsevier: 107887. <https://doi.org/10.1016/j.agee.2022.107887>.
- Desaegher, J., D. Sheeren, and A. Ouin. 2021. Optimising spatial distribution of mass-flowering patches at the landscape scale to increase crop pollination. *Journal of Applied Ecology* 58. Hoboken: Wiley: 1876–1887. <https://doi.org/10.1111/1365-2664.13949>.
- Gandara, T., A. Gardarin, J. Desaegher, S. Petit, E. Porcher, and A. Michelot-Antalik. 2025. A crop yield-based pollination index reveals the impacts of land cover and pesticide use on realized pollination at a landscape scale. *Agriculture Ecosystems & Environment* 392. Amsterdam: Elsevier: 109747. <https://doi.org/10.1016/j.agee.2025.109747>.
- Katumo, D. M., H. Liang, A. C. Ochola, M. Lv, Q.-F. Wang, and C.-F. Yang. 2022. Pollinator diversity benefits natural and agricultural ecosystems, environmental health, and human welfare. *Plant Diversity* 44. Beijing: Keai Publishing Ltd: 429–435. <https://doi.org/10.1016/j.pld.2022.01.005>.
- Kennedy, C. M., E. Lonsdorf, M. C. Neel, N. M. Williams, T. H. Ricketts, R. Winfree, R. Bommarco, et al. 2013. A global quantitative synthesis of local and landscape effects on wild bee pollinators in agroecosystems. *Ecology Letters* 16: 584–599. <https://doi.org/10.1111/ele.12082>.
- Klein, A.-M., B. E. Vaissiere, J. H. Cane, I. Steffan-Dewenter, S. A. Cunningham, C. Kremen, and T. Tscharntke. 2007. Importance of pollinators in changing landscapes for world crops. *Proceedings of the Royal Society B-Biological Sciences* 274: 303–313. <https://doi.org/10.1098/rspb.2006.3721>.
- Koh, I., E. V. Lonsdorf, N. M. Williams, C. Brittain, R. Isaacs, J. Gibbs, and T. H. Ricketts. 2016. Modeling the status, trends, and impacts of wild bee abundance in the United States. *Proceedings of the National Academy of Sciences of the United States of America* 113: 140–5. <https://doi.org/10.1073/pnas.1517685113>.
- Lonsdorf, E., C. Kremen, T. Ricketts, R. Winfree, N. Williams, and S. Greenleaf. 2009. Modelling pollination services across agricultural landscapes. *Annals of Botany* 103: 1589–1600. <https://doi.org/10.1093/aob/mcp069>.
- Martin, G., C. Fontaine, F. Accatino, and E. Porcher. 2019. New indices for rapid assessment of pollination services based on crop yield data: France as a case study. *Ecological Indicators* 101: 355–363. <https://doi.org/10.1016/j.ecolind.2019.01.022>.
- Mouterde, P. 2024. Pourquoi l'effondrement de la biodiversité entraîne des baisses de rendements agricoles, October 16.
- Ollerton, J., R. Winfree, and S. Tarrant. 2011. How many flowering plants are pollinated by animals? *Oikos* 120: 321–326. <https://doi.org/10.1111/j.1600-0706.2010.18644.x>.



- Ouin, A., É. Andrieu, G. Balent, R. Carrié, J.-P. Choisis, J.-F. Dejoux, J.-P. del Corso, et al. 2022. PSDR4 Sebioref - Une approche paysagère et territorialisée des services écosystémiques et des valeurs attachées pour guider les décideurs publics. *Innovations Agronomiques*. March 25.
- Paudel, Y. P., R. Mackereth, R. Hanley, and W. Qin. 2015. Honey Bees (*Apis mellifera* L.) and Pollination Issues: Current status, impacts and potential drivers of decline. *Journal of Agricultural Science* 7: p93. <https://doi.org/10.5539/jas.v7n6p93>.
- Perrot, T., S. Gaba, M. Roncoroni, J.-L. Gautier, and V. Bretagnolle. 2018. Bees increase oilseed rape yield under real field conditions. *Agriculture Ecosystems & Environment* 266. Amsterdam: Elsevier: 39–48. <https://doi.org/10.1016/j.agee.2018.07.020>.
- Potts, S. G., J. C. Biesmeijer, C. Kremen, P. Neumann, O. Schweiger, and W. E. Kunin. 2010. Global pollinator declines: trends, impacts and drivers. *Trends in Ecology & Evolution* 25: 345–353. <https://doi.org/10.1016/j.tree.2010.01.007>.
- Powney, G. D., C. Carvell, M. Edwards, R. K. A. Morris, H. E. Roy, B. A. Woodcock, and N. J. B. Isaac. 2019. Widespread losses of pollinating insects in Britain. *Nature Communications* 10. London: Nature Publishing Group: 1018. <https://doi.org/10.1038/s41467-019-08974-9>.
- Rader, R. A., I. B. Bartomeus, L. A. Garibaldi, M. P. D. Garratt, B. G. Howlett, R. G. Winfree, S. A. Cunningham, et al. 2016. Non-bee insects are important contributors to global crop pollination. *Proceedings of the National Academy of Sciences of the United States of America* 113: 146–151. <https://doi.org/10.1073/pnas.1517092112>.
- Reilly, J. R., D. R. Artz, D. Biddinger, K. Bobiwash, N. K. Boyle, C. Brittain, J. Brokaw, et al. 2020. Crop production in the USA is frequently limited by a lack of pollinators. *Proceedings of the Royal Society B-Biological Sciences* 287. London: Royal Soc: 20200922. <https://doi.org/10.1098/rspb.2020.0922>.
- Ricketts, T. H., J. Regetz, I. Steffan-Dewenter, S. A. Cunningham, C. Kremen, A. Bogdanski, B. Gemmill-Herren, et al. 2008. Landscape effects on crop pollination services: are there general patterns? *Ecology Letters* 11: 499–515. <https://doi.org/10.1111/j.1461-0248.2008.01157.x>.
- Rouabah, A., C. Rabolin-Meinrad, C. Gay, and O. Therond. 2024. Models of bee responses to land use and land cover changes in agricultural landscapes – a review and research agenda. *Biological Reviews* 99: 2003–2021. <https://doi.org/10.1111/brv.13109>.
- Sharp, R., R. Chaplin-Kramer, S. Wood, A. Guerry, H. Tallis, T. Ricketts, E. Nelson, et al. 2018. *INVEST User's Guide*. The Natural Capital Project, Stanford University, University of Minnesota, The Nature Conservancy, and World Wildlife Fund. <https://doi.org/10.13140/RG.2.2.32693.78567>.
- Siopa, C., L. G. Carneiro, H. Castro, J. Loureiro, and S. Castro. 2024. Animal-pollinated crops and cultivars-A quantitative assessment of pollinator dependence values and evaluation of methodological approaches. *Journal of Applied Ecology* 61. Hoboken: Wiley: 1279–1288. <https://doi.org/10.1111/1365-2664.14634>.
- Stanley, D. A., M. P. D. Garratt, J. B. Wickens, V. J. Wickens, S. G. Potts, and N. E. Raine. 2015. Neonicotinoid pesticide exposure impairs crop pollination services provided by bumblebees. *Nature* 528: 548–+. <https://doi.org/10.1038/nature16167>.
- Therond, O., M. Tichit, A. Tibi, F. Accatino, L. Biju-Duval, and et al. 2017. Volet “écosystèmes agricoles” de l’Evaluation Française des Ecosystèmes et des Services Ecosystémiques. INRA. <https://doi.org/10.15454/PRMV-WC85>.
- Turo, K. J., J. R. Reilly, T. P. M. Fijen, A. Magrath, and R. Winfree. 2024. Insufficient pollinator visitation often limits yield in crop systems worldwide. *Nature Ecology & Evolution*. Berlin: Nature Portfolio. <https://doi.org/10.1038/s41559-024-02460-2>.
- Zulian, G., J. Maes, and M. Paracchini. 2013. Linking Land Cover Data and Crop Yields for Mapping and Assessment of Pollination Services in Europe. *Land* 2: 472–492. <https://doi.org/10.3390/land2030472>.



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