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D10.6

Landscape effects on pest populations and assemblages

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1. Summary

This report summarises the findings of a modelling approach taken to explore the effect of landscape structure and the deployment of field scale management strategies on pest population dynamics with the aim of contributing to the design of landscapes management strategies for pest suppression. Using the AgBioscape modelling system developed in WP10 of PURE, we have built models to explore the effect of landscape structure on pest population dynamics, and in particular the deployment of (1) field-scale management strategies at the landscape scale, and (2) non-crop habitats for the support of biocontrol agents. Two applications were developed to address these aspects.

A model of the coleopteran maize pest, *Diabrotica virgifera virgifera*, was used to explore, design and test strategies for the control of *Diabrotica* taking into account the influences of spatial processes and landscape scale effects. Focussing on the potential of crop rotation to control *Diabrotica*, simulation experiments were conducted to determine the performance of a mandatory fixed rotation strategy in comparison with an adaptive rotation strategy. The results support the EC recommendation in favour of crop rotation as a control measure and establish that, in general terms a 3 year rotation is likely to be effective in a wide range of maize cropping systems. The results also predict that a fixed rotation strategy is sub-optimal and can be improved by the adoption of an adaptive strategy in which break crops are applied in response to pest populations exceeding an action threshold. The adaptive strategy achieves control with less rotation and also suppresses the spread of rotation resistance in the *Diabrotica* population. However, the adaptive strategy results in an uneven distribution of risk across the landscape.

A non-specific host-parasitoid model was developed to explore the effectiveness of conservation biocontrol when local habitat management strategies are scaled up to the landscape scale. The results demonstrate that the spatial population dynamics that determine the response of the parasitoids to the landscape are critically dependent on the influence of habitat quality on local populations. The potential to manipulate natural enemy populations at the landscape scale through the management of habitat quality at the patch scale was exemplified by simulating two alternative scenarios. A classical approach to conservation biocontrol in which poor survival of adult parasitoids on the crop is countered by the introduction of resource rich habitats effectively stabilised local populations of natural enemies that would otherwise not persist. However, despite a positive response to the landscape composition of conservation habitat, this strategy was not very effective in supporting biocontrol at the landscape scale. Much larger parasitoid populations were supported by increasing adult survival on crop habitats, suggesting that measures to supplement crops with food resources may be a more effective conservation biocontrol strategy.

This study has demonstrated the potential importance of landscape effects for the regulation of crop pest populations; indicating that the deployment of crops and pest control measures at the landscape scale could be used to achieve better pest control outcomes, while understanding the spatial processes that underlie the landscape scale dynamics of natural enemy populations can be used to design effective biocontrol strategies. Furthermore, the study establishes the value of modelling approaches in the design and testing of landscape scale strategies to enhance sustainable pest control as part of an IPM approach.

2. Objectives

The objectives of WP10 have been to explore the ecological processes that underpin the response of pests to changes in habitat and to design ecological engineering strategies based on the management of habitat to achieve pest suppression. At the landscape scale, WP10 has deployed empirical and theoretical approaches to explore the response of pests to the dynamic habitat mosaic that is presented by farmed landscapes. The empirical study of three contrasting cropping systems and pedo-climatic regions found the abundance of pest or natural enemy populations to be sensitive to habitat and management conditions at a range of spatial scales and inferred that the majority of pests should be amenable to regulation by ecological engineering strategies as long as the appropriate management of these habitats can be established. The results also indicated that cropped habitats and their management provide a flexible and effective route to achieving this and should be considered alongside the semi-natural habitat amendment strategies (Deliverable 10.2). Building on these findings a modelling approach has been taken to explore the effect of landscape structure and the deployment of field scale management strategies on pest population dynamics with the aim of contributing to the design of landscapes management strategies for the pest suppression. A modelling system, AgBioscape (formerly named AgriBioScape), has been develop in WP10 for the simulation of dynamic interactions between the composition and configuration of farming landscapes and populations of natural and semi-natural species that inhabit them, including crop pests (Deliverable 10.4).

Using the AgBioscape system we have developed several models to explore the effect of landscape structure on pest population dynamics, and in particular the deployment of (1) field-scale management strategies at the landscape scale, and (2) non-crop habitats for the support of biocontrol agents.

3. Deliverable procedure

AgBioscape

The AgBioscape modelling system couples discrete time population models with an explicit representation of the farmed landscape using two primary software modules: the land-use mosaic generator and population process module. The land-use mosaic generator works by continually subdividing a 2-dimensional space to produce a network of rectangular land parcels, the size, shape and clustering of which can be controlled. After generating a mosaic of fields, a series of land uses is assigned to each, allowing users to specify how the landscape changes over time in response to crop rotation or other land use changes. The population process module uses a matrix population model approach to simulate the population dynamics of local populations. Local populations are arranged on regular 2-dimensional grids and overlaid on the land-use mosaic. Each grid-cell holds a numerical vector representing the stage structure of a local population, while transition matrices are used to specify the demographic changes in stage structure that occur over time as a function of intra- and inter-specific interactions, as well as the prevailing habitat and environmental conditions that are derived from the land-use mosaic. Local populations are linked by dispersal which is modelled empirically using dispersal kernels. These can be extended to represent complex dispersal processes by combining kernels, either in single or multi-stage dispersal events, or by the inclusion of attraction or repulsion responses to represent active dispersal. Full details of the AgBioscape modelling system are given in the Deliverable 10.4 report.

Applications

Landscape scale effects on the control of Diabrotica virgifera virgifera by crop rotation

Diabrotica vigifera vigifera (Coleoptera: Chrysomelidae), henceforth *Diabrotica*, initially invaded Europe in the 1990s and has spread to become a substantial problem for maize production in central Europe (Meinke et al. 2009). *Diabrotica* is now endemic in some regions with the potential to spread throughout the maize growing regions of Europe resulting in a predicted annual loss of *ca.* 500 M€ (Wesseler & Fall 2010). Following the failure to eradicate *Diabrotica* or prevent its further spread, the European Commission withdrew *Diabrotica* from the list of regulated harmful organisms with quarantine status. In place of regulations associated with this previous status the EC has adopted recommendations of measures for control *Diabrotica* (Commission Recommendation 2014/63/EU). These recommendations support non-chemical control in line with EC policy in favour of Integrated Pest Management. In particular the recommendations state a preference for the use of crop rotation which is known to be effective in controlling *Diabrotica* and provides additional agronomic benefits. However, the continuous production of maize is often favoured by farmers because of the absence of a suitable economic alternative crop and other constraints that undermine the use of rotations. Furthermore the reduction in maize cropping associated with the introduction of rotation may have knock-on effects leading to wider and undesirable social impacts (Anon 2009).

Existing knowledge supports the use of rotation to control *Diabrotica*, however, management strategies that maximise the length of maize rotation while maintaining control have yet to be established. In this application we develop a spatially explicit model of a maize cropping system to identify the optimal rotation strategy, achieving *Diabrotica* control while maximising the area of maize grown within the landscape. The model is then extended by incorporating a rotation resistant strain of *Diabrotica* to explore the spread of rotation resistance and the impact on rotation based control of *Diabrotica*.

We assume a landscape dominated by a simple maize cropping system in which maize producing fields, possibly in rotation with a break crop, and a non-crop habitat constitute the full range of habitat types. Based on the current conditions within Europe, we initially assume that *Diabrotica* is a strict host specialist and can only persist on maize. Adult *Diabrotica* exhibit low survival on break-crops and non-crop habitats and also a high probability of dispersing from these habitats. Subsequently we consider the introduction of rotation resistance to the *Diabrotica* population. This is expressed in terms of increased survival and reduced dispersal associated with the break crop. This response is modelled on the situation in the USA where the ability to feed on soybean is thought to be the basis for the development of rotation resistance (Curzi et al. 2012).

Simulating 25km^2 landscapes over a duration of 50 years, experiments were conducted to determine the potential of crop rotation to control *Diabrotica*, maintaining population densities below thresholds known to cause crop damage (Baufield & Enzian, 2005) Throughout we compare the performance of a mandatory fixed rotation strategy with an adaptive strategy in which a break-crop must be introduced into a rotation if the density of *Diabrotica* adults exceeds a critical threshold within the field during the preceding year.

A detailed description of the *Diabrotica* model is given in PURE Deliverable 10.4

Effect of habitat deployment on conservation biocontrol

Both crop management and habitat composition have been shown to affect the abundance and composition of parasitoid communities in arable ecosystems (e.g. Jonsson et al. 2012; Mates et al. 2012; see also Macfadyen et al. 2009). Furthermore, intensive agricultural practices are expected to negatively affect hymenoptera parasitoids, which are particularly sensitive to pesticides (Thomson and Hoffmann 2006). Therefore, the presence of semi-natural habitats at a local or landscape scale should promote parasitoid populations (Thies and Tscharntke 1999; Landis et al. 2000). In addition, flowering habitats provide complementary resources to the parasitoids, notably pollen and nectar, which frequently increase longevity and fecundity in female wasps, in particular for synovigenic species that produce and/or mature their eggs after emergence (Schmale et al. 2001). On the basis of this knowledge it is reasonable to assume that the conservation of parasitoids through the management of habitats within cropping landscapes offers the potential for top-down regulation of pest populations. However, the effectiveness of habitat based conservation strategies demands that natural enemies are conserved in sufficient numbers, that their presence is spatio-temporally synchronized with the targeted pest, and that their ability to attack the pest is not undermined by trophic interactions in the form of alternative prey, or by competition, predation or hyper-parasitism (e.g. Xue et al. 2012; Martin et al. 2013). In the case of parasitoids, the potential to predict the influence of these factors and the subsequent outcome may not be easy. For example, the response of parasitoids to crop and other habitats depends on their biology, particularly their dispersal ability, as well as the distribution of habitats within the landscape, while parasitoid abundance and parasitism rates are also likely to be determined by pest abundance, perhaps independent of habitat (Costamagna et al. 2004; Thies et al. 2005; Jonsson et al. 2012).

Here we have developed a spatially explicit host-parasitoid model to explore the effectiveness of conservation biocontrol when local habitat management strategies are scaled up to the landscape scale. Initial simulations take into account alternatives for the introduction of conservation habitats and explore the conditions under which pest control is enhanced in a simple host-parasitoid system.

A simple crop – pest – parasitoid system was modelled based on a cereal cropping system, cereal aphid pest and a parasitic wasp as natural enemy of the cereal aphid. For the aphid and parasitoid populations parameterisation of the life-history models was made with reference to a wide range of published studies but without particular reference to specific species.

Initial non-spatial simulations were run to examine the behaviour of the host-parasitoid system on isolated habitat patches and to establish the sensitivity of populations to the host and parasitoid life-history parameters. Using these results the criteria for beneficial and non-beneficial habitats were established for use in the simulation of conservation biocontrol scenarios on the basis of two qualitatively distinct habitats: crop (non-beneficial) and conservation (beneficial) habitats.

Following the local sensitivity analyses a series of spatial simulations were performed to examine and demonstrate 1) the local effects of conservation habitats, 2) spatial effects in the absence of conservation habitats, and 3) scaling up local conservation biocontrol effects to the landscape scale.

A detailed description of the host-parasitoid model is given in PURE Deliverable 10.4

4. Results

Landscape scale effects on the control of Diabrotica by crop rotation

Fixed rotation strategy

The simplest approach to rotation management is to apply a mandatory rotation of fixed length to all maize producing fields within a landscape. For the most part, *Diabrotica* populations have an annual life-cycle which can be successfully broken by the introduction of a single year of non-maize cropping into the rotation. Therefore, optimisation of the fixed rotation strategy should focus on the length of the rotation, i.e. the number of maize years between breaks. Simulations of maize cropping systems show the impact of rotation on the density of *Diabrotica* populations (Fig. 1). These results indicate that a 3 year rotation (2 years maize: 1 year break) is sufficient to eradicate *Diabrotica* from isolated fields (Fig. 1).

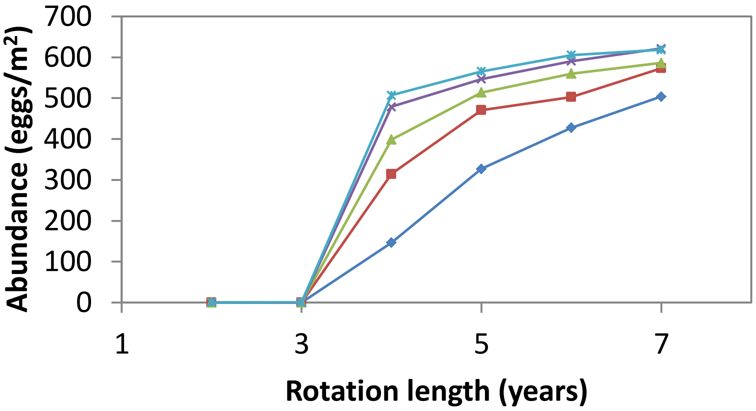


Fig. 1. Long-term average density of Diabrotica populations on isolated fields subjected to rotations of varying length, i.e. 3 years (2 years maize: 1 year break) to 7 years (6 years maize:1 year break). Results are given for field sizes from 2-10 ha (2 ha blue cross, 4 ha purple cross, 6 ha green triangle, 8 ha red square, 10 ha blue diamond).

Where rotations are synchronised within a landscape the optimal duration of the rotation is largely determined by the local, field scale dynamics of *Diabrotica*. However, here we assume that the periodicity in maize production would be unacceptable to the supply chain. Under these circumstances we can expect the effectiveness of rotation to be influenced by spatial processes. The effect of this can be seen in Fig. 2 which shows the average density of *Diabrotica* in landscapes subject to fixed 3 year rotations. In landscapes where maize cropping accounts for less than 40% of the land use, the degree of isolation between fields is sufficient for rotation to be effective. However, as the area given over to maize production increases *Diabrotica* control diminishes so that population densities come to substantially exceed the crop damage threshold in the long term (Fig. 2)

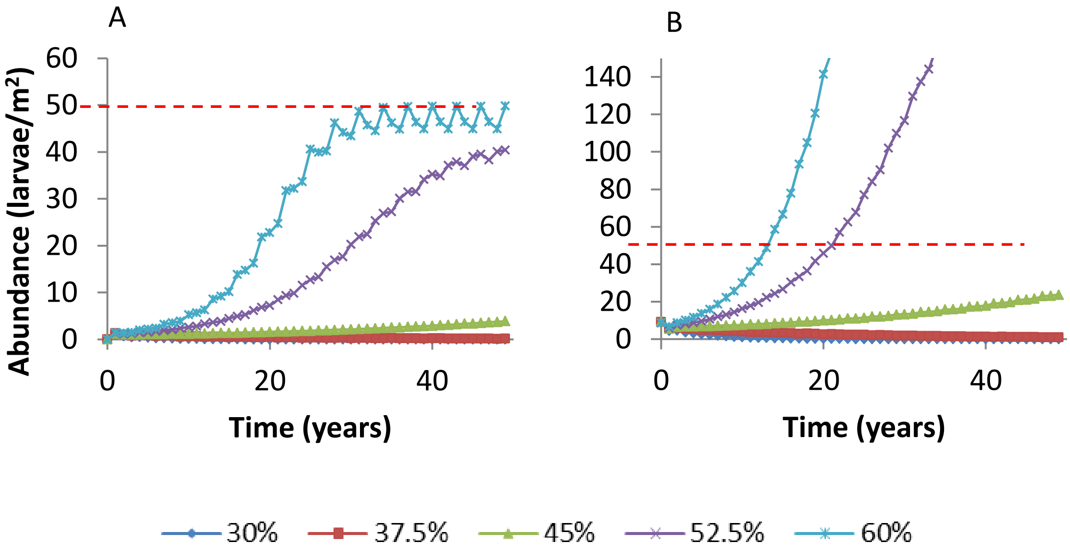


Fig. 2 Simulation time-series showing the change in average density of Diabrotica on (A) first and (B) second year maize fields in landscapes with fixed 3 year maize rotation (2 year maize : 1 year break). Area of landscape under maize rotation varies from 30 to 60%.

Adaptive rotation strategy

As an alternative to the mandatory fixed rotation, we have considered the use of an adaptive rotation strategy. In this case we assume that maize fields are monitored each year for adult *Diabrotica*, 2 weeks after first emergence, and a break-crop introduced in the subsequent year if density exceeds an action threshold of 5 adults plant^{-1}. The results show the adaptive strategy to be more effective than the fixed 3 year rotation strategy. In landscapes dominated by maize cropping (> 50% maize rotation) the *Diabrotica* population is controlled to levels below (Fig 3A) or around (Fig. 3B) the level at which plants are damaged. In landscapes with less maize production *Diabrotica* is controlled well below the damage threshold while also allowing a third year of maize to be grown on some occasions (Fig 3C). A feature of this strategy, however, is that both the density of *Diabrotica* and the frequency of break crops become patchily distributed in the landscape (Fig. 4). Although these patches are dynamic and move about the landscape, this occurs over decades so that the benefits of the control strategy are not evenly shared across the landscape in the short and medium term.

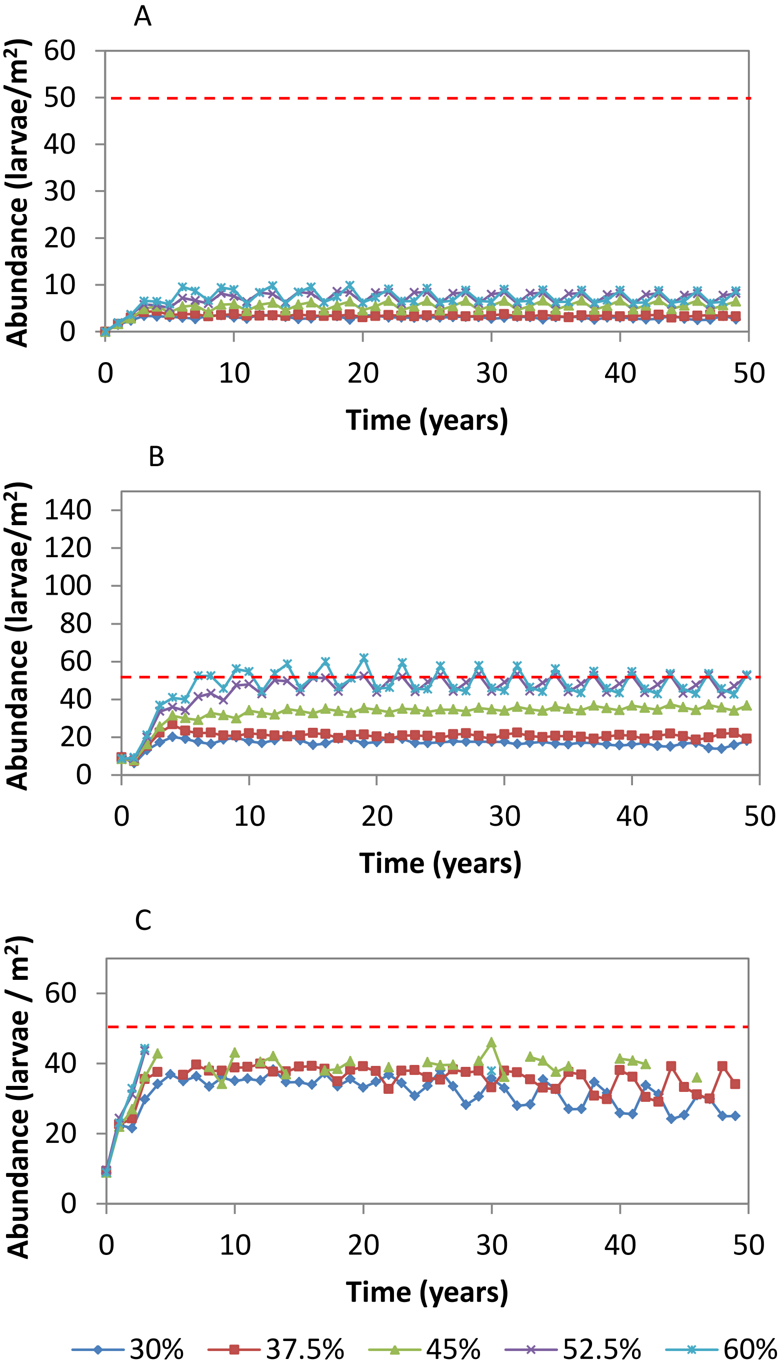
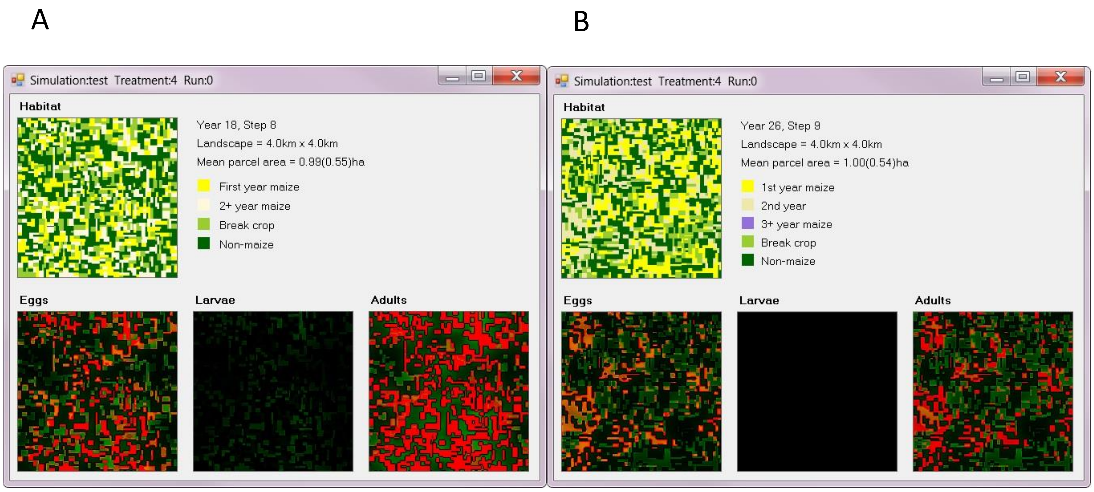


Fig. 3 Simulation time-series showing the change in average density of Diabrotica on (A) first, (B) second and (C) third or more year maize fields in landscapes with an adaptive rotation strategy. Area of landscape under maize rotation varies from 30 to 60%.



Year 18, Step 8
Landscape = 4.0km x 4.0km
Mean parcel area = 0.99(0.55)ha

Year 26, Step 9
Landscape = 4.0km x 4.0km
Mean parcel area = 1.00(0.54)ha

Fig. 4 Screen shots from the AgBioscape model of Diabrotica showing the cropping pattern (top left panel) and distribution of Diabrotica by life-history stage (bottom three panels) at two similar time points (years 18 and 20) in 16km^2 landscapes with 60% maize production using a fixed 3 year (A) or adaptive (B) rotation strategy. Intermediate densities of Diabrotica are indicated in green and high densities in red.

Rotation resistance

In some states of the USA the evolution of a rotation resistant strain of *Diabrotica* has the potential to undermine rotation based control strategies (Levine & Oloumi-Sadeghi 1996). There is currently no evidence of the development of rotation resistance in Europe; however, it is valuable to consider what influence the development of such a strain might have on the effectiveness of the rotation based control being recommended by the EC.

Assuming starting densities for *Diabrotica* under equilibrium conditions for landscapes with a fixed 3 year rotation strategy, a small population of rotation resistant *Diabrotica* was introduced at random across the landscape. In most cases the rotation resistant strain came to dominate the population leading ultimately to the failure of the control strategy (Fig. 5 & 6). Only where a relatively small proportion of the landscape, i.e. ≤ 40%, is dedicated to maize production in landscapes with an average field size of 10 ha, is the control sufficiently effective to eradicate *Diabrotica* before the spread of the resistant strain takes place (Fig 6 B). In all other cases rotation resistance came to dominate the *Diabrotica* populations within 20 and 40 years (Fig. 5 & 6).

Repeating the simulations with the adaptive rotation strategy leads to qualitatively similar results. However, the adaptive strategy again outperformed the fixed strategy by substantially reducing the rate of spread of the rotation resistant strain, at least over the first 50 years.

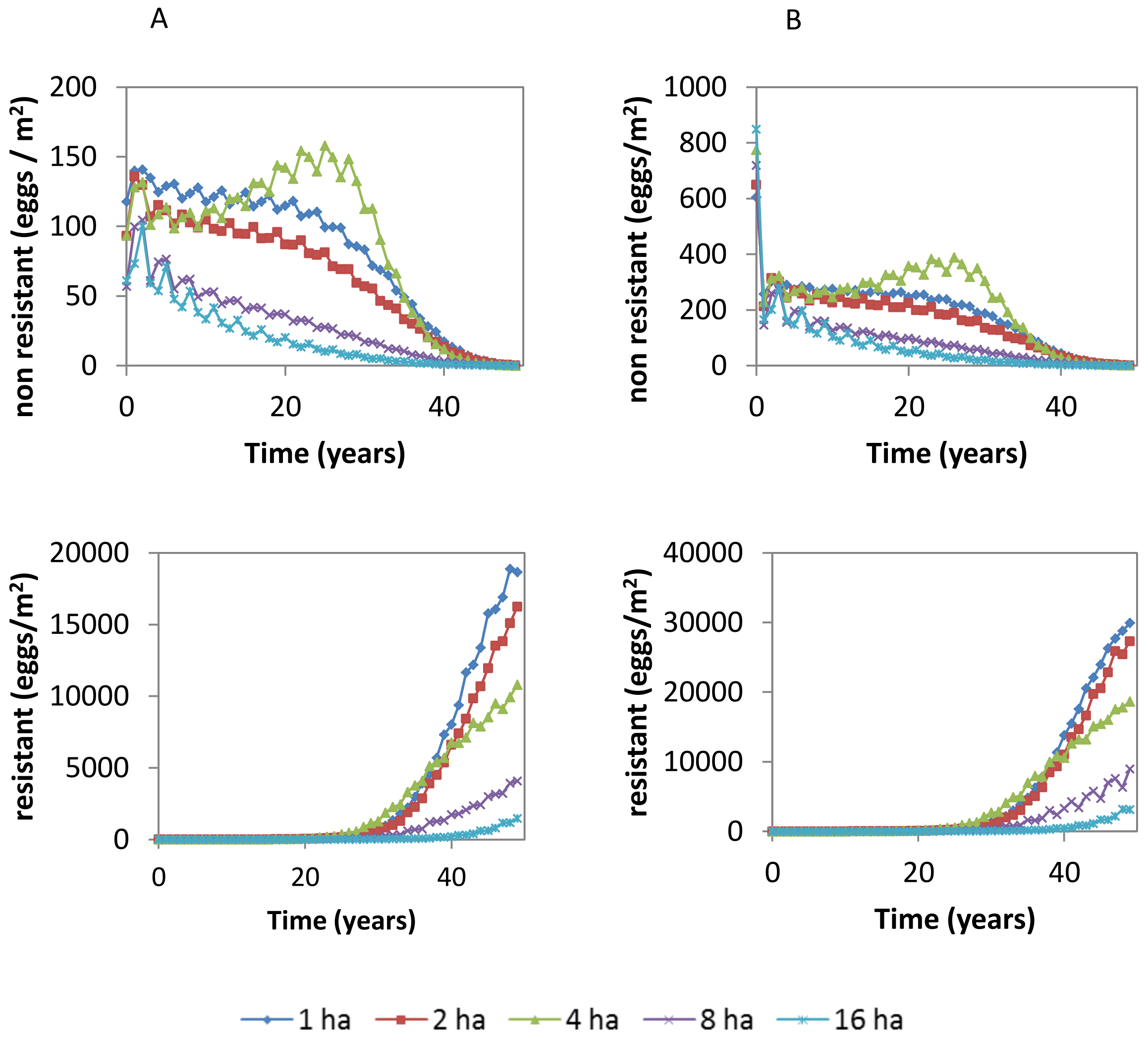


Fig. 5. Simulation time-series showing the dynamics of rotation resistance in Diabrotica populations in response to the deployment of a fixed 3year rotation (2 year maize: 1 year soybean) on (A) first year and (B) second year maize crops in landscapes composed of 60% maize rotation and average field sizes from 1 to 16 ha.

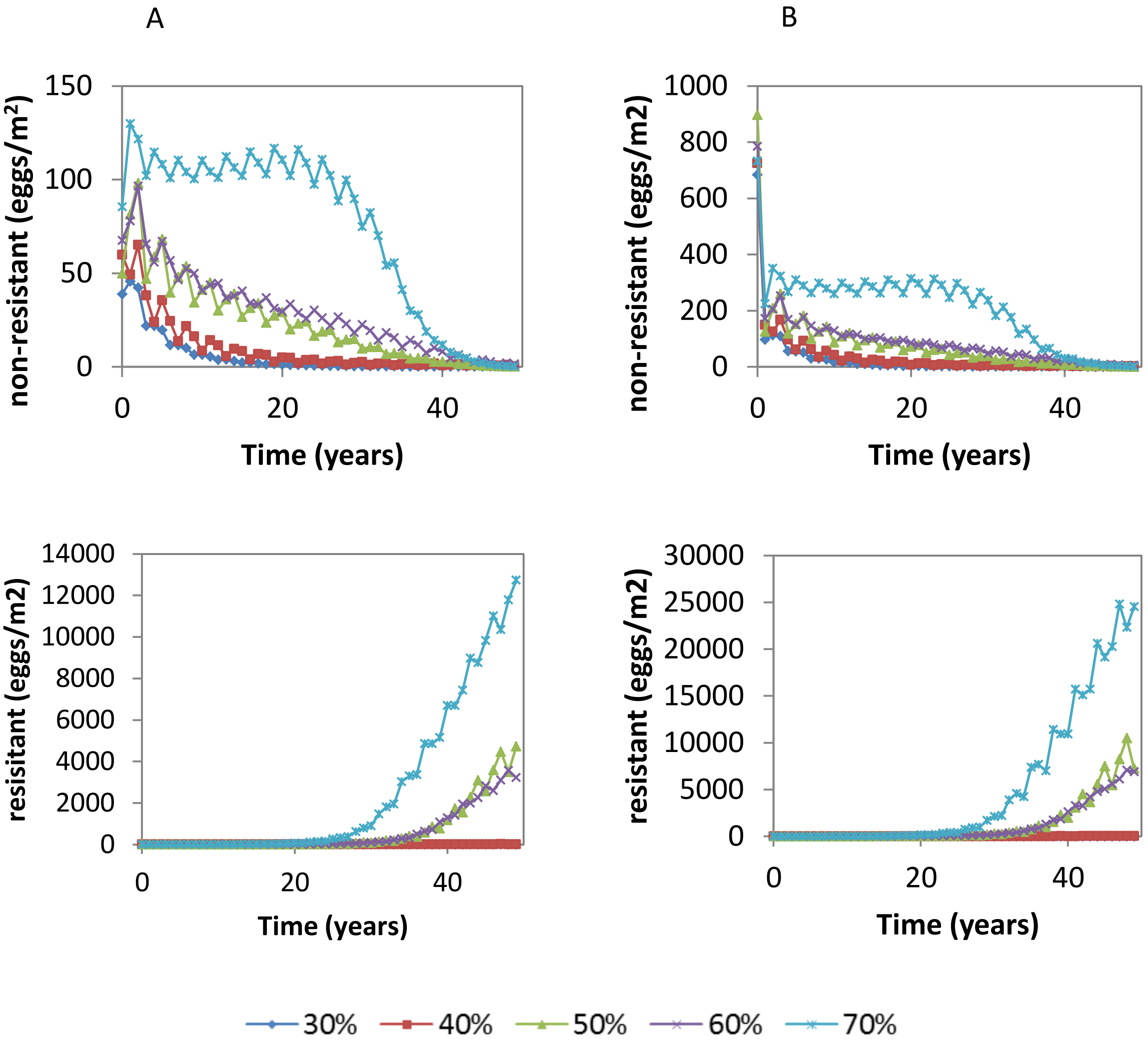


Fig. 6. Simulation time-series showing the spread of rotation resistant and decline of non–resistant strains of Diabrotica in response to the deployment of a fixed 3year rotation (2 year maize: 1 year soybean) on (A) first year and (B) second year maize crops in landscapes of differing composition from 30 to 70% maize rotation with an average field size of 10 ha.

Effect of habitat deployment on conservation biocontrol

Local dynamics

The population dynamics of isolated patches showed that stability (persistence) of the aphid-parasitoid system was possible though only over a restricted range of parameter values. The inclusion of the egg stage in the stage-structure of the aphids plays an important role in stabilising the aphid and consequently parasitoid populations by providing a demographic refuge from parasitism that is critical in permitting the aphid populations to persist overwinter, a capacity which is lost as overwinter survival of eggs is reduced. These results are in accord with previous theoretical studies that have shown that stages invulnerable to parasitism act to stabilise host-parasitoid dynamics (Murdoch et al. 1987).

Even in the presence of an invulnerable aphid stage, the system exhibited frequent instability. The persistence of the parasitoid populations was highly sensitive to density independent survival of adult parasitoids, with persistence only occurring in a narrow range of values. When survival fell below the narrow range of stabilising survival values, the seasonal growth rate of the parasitoid populations was frequently insufficient to maintain an overwintering population (e.g. Fig. 7A). When adult parasitoid survival exceeded the stabilising range, high parasitoid population numbers drove the aphid population to, or near to, extinction resulting in parasitoid extinction (Fig. 7C).

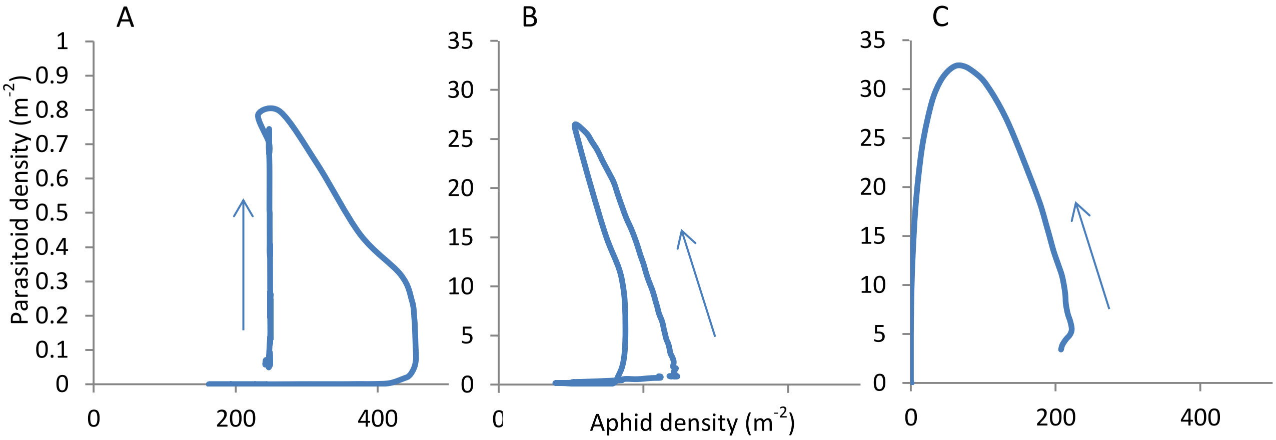


Fig 7. Phase planes showing the seasonal dynamics for example years during which parasitoid extinction occurred. (A) Low parasitoid survival leading to instability, (B) intermediate parasitoid survival leading to stability, (C) high parasitoid survival leading to instability. Arrows indicate direction of seasonal changes in aphid and parasitoid density from mid-May.

These behaviours were used as the basis for conservation biocontrol scenarios. The influence of habitat on the dynamics of local populations, i.e. habitat quality, is captured by making one or more of the parameters of the population transition matrices a function of habitat type. A number of options exist for this including the direct effect on vital rates (e.g. reproduction, survival, emergence, etc.) or indirectly via local carrying capacity and subsequent density dependent effects on the vital rates. In the absence of specific information on which to base the representation of habitat quality with respect to the aphid and parasitoid species, a simple dichotomous approach was adopted. In the first scenario it is assumed that crop habitats are characterised by insufficient floral resources to maintain sufficient levels of adult parasitoid survival, thereby leading to low-survival instability in crop monocultures (e.g. Fig. 7A). Targeting the survival of adult parasitoids through the provision of additional floral resources is a recognised strategy for conservation biocontrol (Bianchi & Wackers 2008; Vattala et al. 2006). Consequently to simulate CBC strategies we assumed that conservation habitats were characterised by low aphid survival, i.e. lower than that experienced on the crop, but high parasitoid survival leading to unstable local population dynamics of the sort exemplified in Fig 7C.

Coupled crop-conservation patch dynamics

To assess the performance of this CBC scenario it is first necessary to demonstrate the local effect of CBC, i.e. the positive impact on parasitoid populations, and parasitism rates in crop habitats through the introduction of neighbouring conservation habitat. To do this a two patch system was simulated in which single crop and conservation habitat patches were coupled by host and parasitoid dispersal. To demonstrate the effectiveness of local CBC the persistence and abundance of both parasitoid and host populations were compared against coupled crop patches.

Dispersal was permitted to take place throughout the year and was set to levels resulting in average inter-patch dispersal rates equivalent to 2.5% for parasitoids and 1% for aphids per day during March to September and 0% during the winter months. Under these conditions the aphid-parasitoid system was stabilised. In fact, stability was achieved in all cases where adult parasitoid survival exceeded the interval at which populations on isolated conservation habitat patches were stable and below the equivalent interval for on crop habitats.

Spill-over

To assess the spatial extent to which the introduction of conservation habitat may influence surrounding crop habitats a small linear landscape of 20 patches was simulated. Nineteen of the patches were cereal crop habitat and for the remaining patch, conservation habitat was positioned at an intermediate location within the one-dimensional landscape. Aphids experience reduced survival on the conservation habitat leading to a bottom-up suppressive effect on the aphid populations (Fig 8A, blue line). In the presence of parasitoids, parasitism leads to an additional, top-down, reduction in aphid density in the conservation habitat. A spill-over of the parasitoid population from the conservation habitat leads to a reduction in aphid density in the adjacent crop patches with the extent of the spill-over determined by the degree of parasitoid dispersal (Fig 8A & B). Within the zone-of-influence the aphid-parasitoid system is stabilised while parasitoid populations become extinct in those crop patches outside the zone-of-influence.

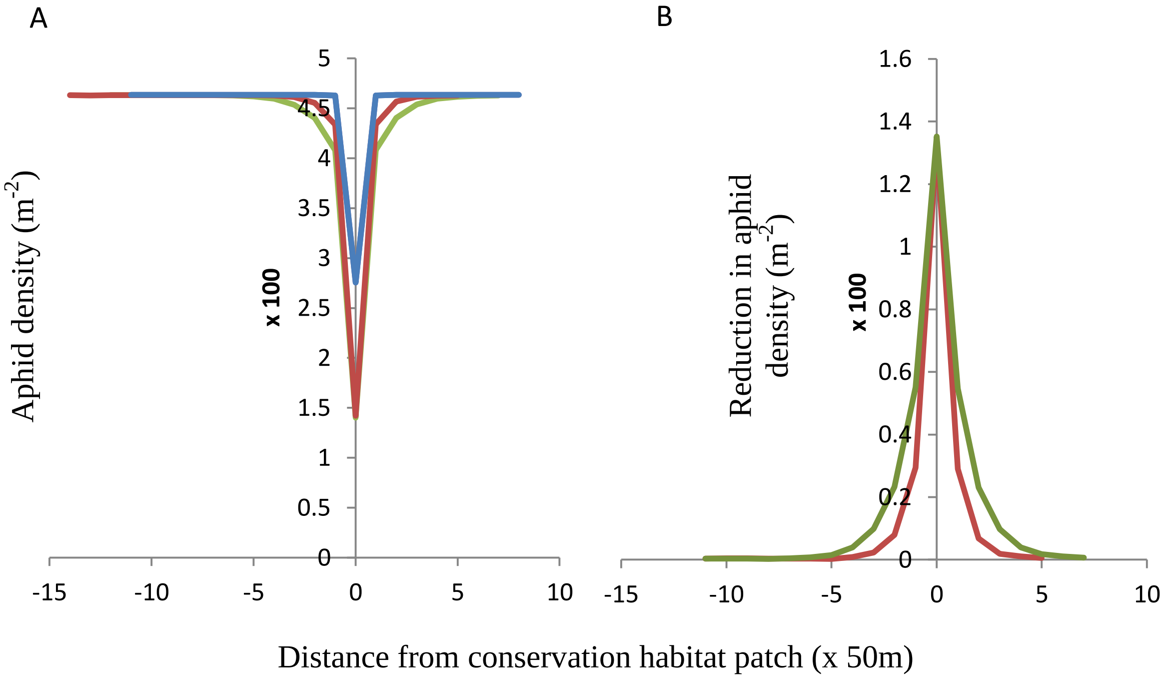


Fig. 8. Fifty year simulation of aphid populations in 20 contiguous habitat patches arranged in a one-dimensional landscape. (A) single 50m^2 patch of conservation habitat was located at an intermediate position (zero on the x-axis) between a total of nineteen similarly sized patches of crop habitat. (A) shows average aphid density in the absence (blue) and presence of parasitoids. (B) Reduction in average aphid population density due to parasitism. Parasitoid dispersal (patch emigration rates) was set at 5% (red) and 15% (green).

Landscape dynamics

On the basis of the preceding results a positive pest suppressive effect of a conservation biocontrol strategy in which conservation habitats are introduced into the cropped landscape is predicted. This was observed for a wide range of conditions and is exemplified by the results in Table 1. The results are consistent with the analysis of the one-dimensional landscapes showing the stabilising effect of introducing conservation habitats into the landscape of crop monoculture. The conservation effect is enhanced as the proportion of conservation habitat is increased from 5 to 25 %. The effect of patch size on the effectiveness of conservation habitat deployment was not consistent, though at low levels of conservation habitat (5%) local extinction seems to be substantially higher. This suggests a greater degree of isolation between crop and conservation habitats leading to a proportion of *de facto* crop monoculture. It should also be noted that even under the most favourable conditions simulated here the biocontrol effect was minimal with an average reduction of 6% in aphid density on the crop.

Table 1. Average densities for aphid and parasitoid populations over 50 year simulations on 2km x 2km landscapes under differing conservation biocontrol scenarios. The crop monoculture provides a negative control against which the biocontrol scenarios were compared. In the conservation habitat scenarios the landscapes were comprised of 95% or 75% continuous cereal cropping with 5% or 25 % respectively given over to permanent conservation habitat patches. For both conservation habitat landscapes the conservation habitat patches were configured as 50m x 50m and 100m x 100m patches. The conservation habitat patches were randomly position in the landscape in all cases. The crop + resource supplement scenario assumes a continuous crop monoculture in which adult parasitoid survival is increased to levels at and above the value shown to confer stability on isolated crop patches.(95% confidence intervals are given in brackets, based on 3 simulations)

Conservation biocontrol landscape scenario			Parasitoid density (m^{-2})		Aphid density (m^{-2})		Extinction fraction[1] (%)	Biocontrol effect[2] (%)
			Crop	Cons.	Crop	Cons.		
Crop monoculture			0.00	NA	464.46	NA	100	NA
Conservation habitat	5%	50m	0.43 (±0.06)	4.26 (±0.64)	460.62 (±0.36)	229.34 (±7.98)	41.25	0.83 (±0.07)
	25%	50m	3.57 (±0.15)	8.03 (±0.03)	438.87 (±0.95)	161.95 (±1.54)	0.00	5.51 (±0.21)
	5%	100m	0.80 (±0.299)	7.26 (±0.68)	458.45 (±1.71)	153.72 (±1.44)	1.00	1.29 (±0.37)
	25%	100m	2.91 (±0.66)	6.98 (±0.67)	444.51 (±3.52)	146.53 (±3.61)	0.00	4.29 (±0.76)
Crop + supplement	0.7		13.74	NA	344.81	NA	0	25.76
	0.725		14.79	NA	358.44	NA	0	22.83
	0.75		13.36	NA	359.71	NA	0	22.55

[1] Extinction fraction estimated as the average percentage of local populations with zero density at year 50. [2] Biocontrol effect estimated as the percentage reduction in aphid density in comparison with the Crop monoculture scenario

In other simulations we observed that landscapes made up of habitat monocultures support stable aphid-parasitoid populations if the survival of adult parasitoids exceeds the locally stable interval as described above (see section "Local dynamics"), there is variation between local populations in the initial densities, and the dispersal is sufficiently low relative to the extent of the landscape to prevent synchronisation of the populations. The stabilising effect of these conditions on host-parasitoid models has been observed before (Briggs et al. 2004) and can be ascribed to source-sink dynamics that results from asynchrony between local populations (Fig. 9). This phenomenon raises the possibility of using a resource supplement to raise parasitoid survival in crop habitats as an alternative to the use of conservation habitat patches as the basis for conservation biocontrol strategies. Simulations show this scenario to be more effective, reducing aphid population densities by 26%, although the extent is dependent on the extent to which the survival of adult parasitoids can be increased. This stabilising mechanism requires a number of populations to be coupled; however, simulations have shown the effect to operate in landscapes with a cropped area of just 20% under both perennial crop and crop rotation scenarios.

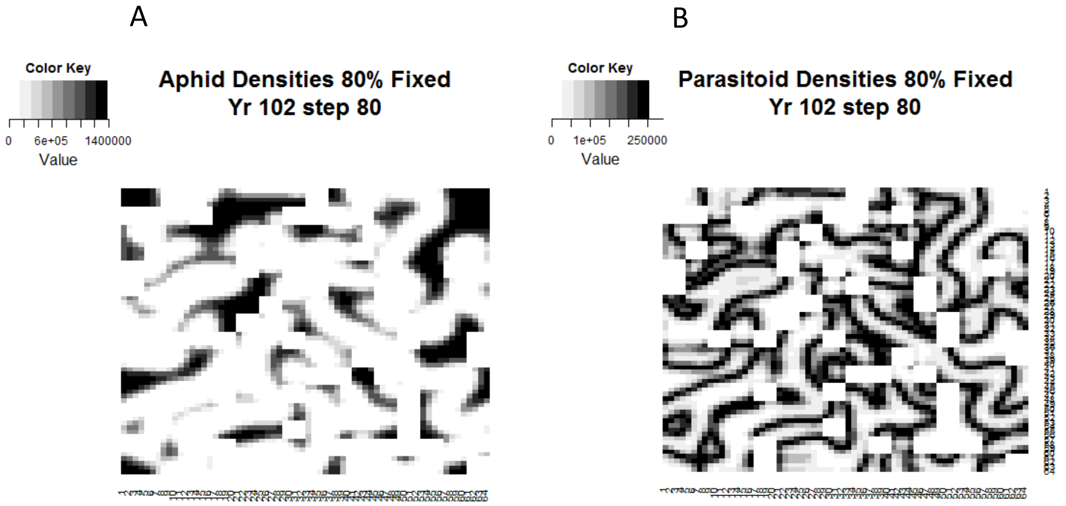


Fig. 9. Heat maps showing the distribution of (A) aphids and (B) parasitoids across a landscape comprised of 80% crop monoculture and 20% other non-crop habitat (empty squares). This landscape provides 3 conditions which together allow the parasitoid population to persist, i.e. adult parasitoid survival exceeding the locally stable interval, heterogeneity in initial population densities, and limited dispersal relative to the extent of the landscape. The formation of spatial structures in population densities is characteristic of these systems.

5. Conclusions

The AgBioscape *Diabrotica* model is an effective tool with which to explore, design and test strategies for the control of *Diabrotica* taking into account the influences of spatial processes and landscape scale effects. The results support the EC recommendation in favour of crop rotation as a control measure and establish that, in general terms a 3 year rotation is likely to be effective in a wide range of maize cropping systems. However, the results also predict that a fixed rotation strategy is sub-optimal and can be improved by the adoption of an adaptive strategy in which break crops are applied in response to pest populations exceeding an action threshold. This strategy results in an effective 3 year rotation were otherwise control was not achieved. For those landscapes where control was achieved with a fixed rotation strategy, the adaptive strategy can maintain this control while maintaining higher levels of maize production. The adaptive strategy also outperformed the fixed strategy in its ability to supress the spread of rotation resistance. However, an uneven distribution of risk across the landscape is associated with the adaptive control strategy.

The model has been used to explore other aspects of *Diabrotica* control including the combination optimal deployment of foliar sprays and the influence of monitoring error and free loading on the outcome. These will be reported along with additional research which will consider the use of combined control strategies and the value of spatial and area-wide data on setting action thresholds. In addition to providing specific insight into the control of *Diabrotica* this study clearly demonstrates the value of incorporating landscape scale considerations into the design of bottom-up pest control strategies. By taking a spatially explicit approach novel insight into the performance of potential control strategies can be gained and used in the design of more effective control strategies.

The study of biocontrol provides a very different example with which to test the landscape approach to understanding and designing pest control strategies. In this case the landscape effects act on the top-down regulation of pest populations by interacting with the dynamics of the pest-natural enemy system. The non-specific host-parasitoid system considered here allows a general exploration of the landscape effects associated with pest biocontrol by specialist parasitoid natural enemies. The results demonstrate that the spatial population dynamics determining the response of the parasitoid population to landscape are critically dependent on the influence of habitat quality on local populations. This offers the potential to manipulate natural enemy populations at the landscape scale through the management of habitat quality at the patch scale. This is exemplified by the two scenarios considered in this study. The first is consistent with a classical view of conservation biocontrol in which poor survival of adult parasitoids on the crop is countered by the introduction of resource rich habitats into the landscape. Assuming these habitats are maintained in the long-term this strategy appears robust being capable of stabilising local populations of natural enemies that would otherwise not persist without being overly sensitive to the levels of parasitoid survival that are achieved on the crop or conservation habitats. However, this classical conservation biocontrol strategy was found not to be very effective in supporting biocontrol at the landscape scale; despite making favourable assumptions about the quality and extent of the conservation habitat and the dispersal ability of the parasitoid only produced a 6% reduction in the crop pest population density. Much larger parasitoid populations were supported by increasing adult survival on crop habitats suggesting that strategies for providing a resource supplement to crops may be a more effective conservation biocontrol strategy.

Together the applications considered in this simulation study indicate the potential importance of landscape effects for the regulation of crop pest populations. We have shown how the deployment of crops and pest control measures at the landscape scale might be used to achieve better pest control outcomes and that understanding the spatial processes that underlie the landscape scale dynamics of natural enemy populations can be used to design effective biocontrol strategies.

These results are wholly consistent with the empirical findings of PURE that have shown landscape scale patterns of crop, crop management and semi-natural habitat to influence a wide range of crop-pest systems. The results presented here go further by establishing the value and potential to use modelling approaches to design and test landscape scale strategies to enhance sustainable pest control as part of an IPM approach.

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