



PURE

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1 Summary

Here we report on the development and verification of AgriBioScape¹ (AB-Scape), a modelling system 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.

AB-Scape embodies a generic modelling approach that couples a discrete time approach to modelling population dynamics with a landscape simulation model that simulates both landscape structure and composition, including the dynamics of crop sequences and other landuse changes

The AB-Scape approach has been justified on the basis of the characteristics of crop production systems, the landscapes and the pest and beneficial taxa that inhabit them.

As computer simulation models, application specific versions of AB-Scape are implemented in the object oriented programming language C#.

Verification of the AB-Scape approach was pursued through the development of two models that allowed attributes of key importance to the functioning of spatially explicit models and their application to pest regulation scenarios to be tested.

A model of *Diabrotica virgifera virgifera* (western corn rootworm - WCR) populations inhabiting maize dominated landscapes was developed. The behaviour of the model was found to be consistent with the known patterns of WCR infestation and in particular the model successfully captured the colonization behaviour of WCR and the effects of this on pest abundance and management.

A generic aphid-parasitoid system was modelled and coupled to a landscape simulation of a UK wheat based cropping system with the objective of verifying the potential of AB-Scape to represent multi-trophic systems. The simulations of aphid density and parasitism were highly consistent with both field and modelling results reported elsewhere indicating that the approach used for specifying parasitoid (predator)-prey interactions and the spatio-temporal synchronisation of species was successful.

In conclusion the development of AB-Scape has achieved the objective of Deliverable 10.4, providing an implemented and tested modelling framework capable of representing a wide range of pests, crops and landscapes. AB-Scape provides a suitable platform for the further development and analysis of models towards the objective of designing pest-suppressive landscapes.

2 Objectives

The objective of this study was to develop a model that was capable of simulating the dynamic interactions between pest populations and the composition and configuration of farming landscapes. The work has been pursued in support of the wider objective of identifying landscape characteristics important in the regulation of pests and also to explore the ecological processes that underpin the response of pests to changes in habitat and the design of ecological engineering strategies based on the management of habitat to achieve pest suppression.

3 Deliverable procedure

3.1 Introduction

Simplification of agricultural landscapes through the loss of semi-natural habitats and the reduction in crop diversity has been a feature of agricultural intensification (e.g. Robinson & Sutherland 2002, Meeus 1993, Kadlecova et al. 2012, Ihse 1995). However, spatial and temporal variation in crop management such as the choice of crop type and variety, tillage practices and pesticide application means a degree of heterogeneity is retained even in the simplest of cropping systems. Furthermore, most agricultural landscapes have retained some boundaries and there remain areas of land inaccessible to machinery which allows non-crop habitats to persist, while at a larger scale, cropped land is often interspersed with land of other types such as forestry, grazed land and urban areas. Furthermore the reintroduction of habitat heterogeneity is a feature of agri-environment schemes which commonly support the introduction of uncropped vegetation, for example in the form of margins and hedgerows. As a consequence current spatial trends do not necessarily show an association between elements of landscape complexity and farming intensity (Persson et al 2010).

The movement and dispersal of organisms across the resulting mosaic is the rule rather than the exception (Mazzi & Dorn 2012, Benvenuti 2007, Petit et al 2013), leading to sensitivity in naturally occurring populations to the agricultural landscape, its composition and configuration. The effect of this is demonstrable with a wide range of taxa including weeds (Petit et al. 2011, Kovacs-Hostyanszki et al. 2011, Gaba et al. 2010), insects (Chaplin-Kramer et al 2011, Veres et al. 2013), and other taxa (mammals, birds) showing responses in both diversity and abundance to a variety of landscape characteristics. We infer from these and other, similar results that landscapes may be designed and managed with the objective of promoting both the diversity and abundance of a wide range of taxa, the ecosystem services they provide and ecosystem functions more generally, for example the regulation of pest populations. Though the importance of landscape scale effects have been highlighted and new studies have begun to unravel some of the detail that points to underlying mechanisms (e.g. Jonsson et al. 2012, Martin et al. 2013) these empirical approaches face practical limitations as a result of the large spatial and temporal scale of these effects and could not in the foreseeable future provide a way to design and test landscape management strategies. As a consequence, modelling provides an essential approach to the further development of this topic (Birch et al. 2011).

An appropriate modelling strategy has a number of important advantages including the ability to:

- Consider systems on a spatial and temporal scale beyond the practical limits of any empirical study.
- Apply to a wide range of landscapes, cropping systems, and taxa.

- Simulate novel landscapes and landscape management strategies for which no examples currently exist.
- Address the complex multi-trophic systems and the potential trade-offs between species and between ecosystem services.
- Provide results within a short-time frame.

To deliver these advantages demands that the modelling approach fulfils certain criteria. In particular the model should be sufficiently flexible to be able to represent a wide range of landscapes, crop production systems, and plant and animals species, including multi-trophic combinations. With these capabilities a modelling approach may be applied to a very wide range of issues sensitive to the landscape. These include those of relevance to the development of IPM strategies such as area-wide IPM, multi-pest control strategies, the role of agri-environment schemes in IPM, and the design of pest suppressive landscapes through the spatio-temporal deployment of habitats and their management. Here we report on the development and implementation of a modelling framework, AgriBioScape, capable of achieving these goals. Fulfilment of the deliverable has been achieved through the completion of three interdependent processes:

1. Theoretical model development.
2. Development of software for model implementation.
3. Verification of the modelling approach and testing of the model software through the development, parameterisation and simulation of example crop-pest systems.

These are described in the remainder of this report.

3.2 Theoretical model development

3.2.1 Model requirements and overview

In developing a model it is necessary to consider the structure and function of the system or systems to be modelled in order to identify the features of potential importance in determining the behaviour of the systems which should therefore be included in the model. Here we summarise the key features of crop production systems from a landscape ecology perspective and in doing so set out the general requirements of the model.

Crop production landscapes comprise 3 land elements: crop producing, semi-natural habitats, urban or peri-urban land. The crop producing areas consist of land parcels (e.g. fields and orchards) on which one or potentially many crop types are grown and which are subject to a range of management interventions that can have a profound effect on the abiotic conditions of a field. In addition to field heterogeneity, conditions may also vary with a field due for example to the presence of multiple crops (e.g. intercrops), crop and non-crop vegetation (e.g. grass margins), and variation in crop management (conservation headlands). Annual cropping systems also exhibit profound temporal variation in conditions as a result of seasonal cultivation while annual and perennial systems can experience abrupt changes in conditions due to the application of management treatments such as tillage and pesticide treatments. Within the cropped landscapes non-cropped habitats are often present, interspersed between the fields and orchards. These are frequently associated with boundaries between fields but are also present where land is of marginal production quality, inaccessible, or has been abandoned. In addition to these small grained features of non-cropped habitat, more expansive areas may be present such as areas of woodland and forest, heathland, coastal and riparian areas, and the domestic, commercial and industrial components of urban and peri-urban zones. The structural aspects of cropped landscapes such as field size and shape are also

important, determining the extent of boundary associated habitats and also the scale at which crop based heterogeneity occurs.

Finally, the temporal variation in landscape composition and structure that results from crop rotation and the seasonal patterns of crop cultivation is a marked feature of cropped landscapes and one of potential importance in dictating the dynamics of resident populations (DeWoody et al. 2005, Mertens et al. 2002).

Agricultural landscapes are inhabited by a wide range of taxa; microbes, vascular plants, molluscs, arthropods, mammals, and birds all play important roles as pests, pathogens or beneficial organisms. Individual organisms of any species typically disperse to a sufficient extent that populations are sensitive to spatio-temporal patterns in the biotic and abiotic conditions that result from the landscape heterogeneity describe above.

The extent to which the landscape heterogeneity influences the organisms inhabiting these areas is species or functionally specific. For a highly specialised crop pest the landscape may appear as a set of habitable islands distributed amongst an uninhabitable matrix. In this case the system could be conceptualised as a metapopulation (Hanski 1994) and a metapopulation model approach adopted in which nearly all the landscape heterogeneity is discounted. However, to accommodate more complex situations where species exhibit more general habitat preferences or multi-species scenarios in which species exhibit differences in habitat preference, it is necessary to account for a potentially much wider range of heterogeneity in the composition, configuration, structure and management of habitats. This requires a spatially explicit modelling approach capable of representing complex landscapes and the dynamics of populations inhabiting these (Fahrig and Merriam 1994, Wiens et al. 1993, Wiegand et al. 1999).

In pursuing a spatially explicit approach, we assume the organisms inhabiting the system belong to a single regional population that is comprised of multiple local populations, defined spatially both in their location and extent. In defining local populations we assume that they cover an area that is at sufficiently small to permit the population to fully mixed and that this may vary between species according to the size and mobility of individuals. Many species inhabiting agricultural ecosystems have complex life-cycles with age or stage related differences in their response to abiotic conditions. In cropping systems the organisms are exposed to abrupt changes in the environment, often invoking discrete demographic events. The temporarily discrete stage specific conditions that this invokes are well represented by a stage/age structured matrix projection approach (e.g. Caswell 2001) to modelling the local population dynamics. By allowing vital rates to be a function of local population densities, intra and interspecific predatory and competitive interactions can also be captured in this approach. Similarly, by making vital rates functionally dependent on habitat type the population and landscape models are coupled.

In addition to demographic processes that take place at a local level, regional populations and their dynamics are sensitive to dispersal and its effect on local immigration and emigration (Kool et al. 2013). Consequently modelling dispersal and the connectivity between local populations is an essential aspect of the model. The mode of dispersal varies substantially between organisms. Dispersal may be passive where organisms do not possess motile or sensory functions or may be effectively so where these are overwhelmed by external forces such as wind. In other cases dispersal may be active, enabling individuals to locate themselves within the landscapes on the basis of habitat preferences.

3.2.2 Model description

The system to be modelled comprises the landscape, represented by spatio-temporal distribution of vegetation or habitat types, and a population of one or more species of animal and plant. The model is made spatially explicit by resolving the state variables: habitat quality

and the size of each population into a number of contiguous cells of a 2-dimensional lattice with a separate lattice for habitat quality and for each population (Fig. 1). The habitat quality lattice is obtained by discretising a landscape habitat map simulated by a landscape simulation model. The resolution of the grids may vary between habitat and species and between species. In this way the state of the system at any given time is defined by the 2-dimensional set of values for each state. A discrete time approach is taken in which the state of the system evolves according to a set of Markov Chains that determine the dynamics of land use (i.e. type of vegetation or habitat) and plant or animal populations.

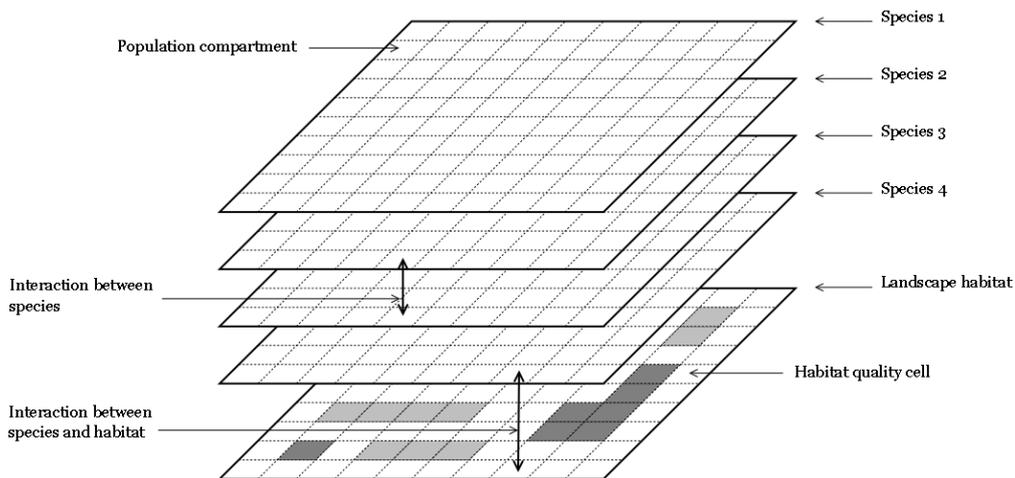


Figure 1. Diagram showing the multiple lattice structures used in AB-Scape that are used to resolve the spatial variation in habitat, and population states and examples of the links between each lattice.

3.2.2.1 Landscape model

In simulating the landscape 2 aspects are considered, 1) structure and 2) land use. Structurally the landscape is made up of 2 dimensional land parcels and the boundaries between them. The land parcels may have different land uses being either cropped areas such as fields or orchards, i.e. crop parcels, or areas that are comprised of any one of a number of non-cropped habitats, e.g. woodland or other semi-natural habitats. As expected the boundary elements occur at the interface between adjacent land parcels each of which may have habitat types assigned to them. In addition, distinct areas within parcels can be specified allowing margins, strips and patches to be represented.

To simulate the landscape structure a rectangle representing the landscape is specified including its height, width, and the total number of land parcels contained, $N_{lp\text{total}}$. The initial landscape rectangle is then split recursively until the desired number of land parcels is produced (Fig. 2). In the basic algorithm each splitting of a rectangular land parcel produces two, not necessarily equal sized, daughter rectangles. At each split the allocation of final land parcels associated to a parent rectangle to each of the daughter rectangles is determined by the value L_{split} where $L_{split} = L + r(1 - 2L_{min})$. Here, r is a random number with a uniform distribution on the interval $[0, 1]$ and L_{min} is the minimum proportion of the land parcels that can be allocated. The number of land parcels assigned to the two daughter rectangles is given by $N_{lp\text{daughter}1} = \lceil L_{split}N_{lp\text{parent}} \rceil$ and $N_{lp\text{daughter}2} = \lceil (1 - L_{split})N_{lp\text{parent}} \rceil$. The splitting process is repeated for each rectangle until $N_{lp} = 1$ (Fig 2).

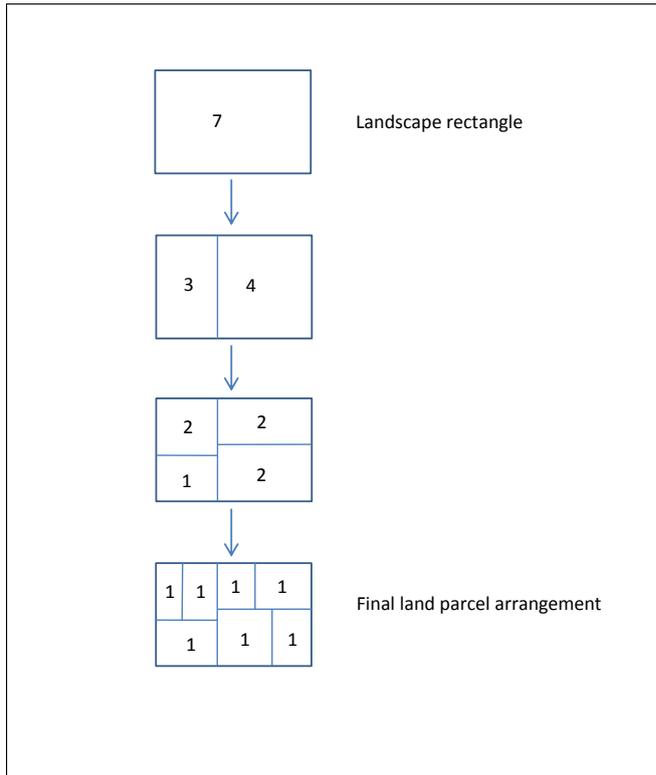


Figure 2. Diagram showing the recursive partitioning of the landscape into a target number of land parcels, $N_{lptotal}$. In this example $N_{lptotal} = 7$. The integer values indicate the number of land parcels, N_{lp} , to be generated from each rectangle. See text for explanation of the algorithm used to determine N_{lp} for each rectangle.

The mean size of the land parcels is determined by the total number of land parcels within the landscape, $N_{lptotal}$, while the size distribution and clustering of the parcels is determined by the parameter L_{min} which controls the degree of asymmetry in the distribution of land parcels between daughter rectangles.

In locating the position of a split the algorithm first determines whether to split the parent rectangle horizontally or vertically with the orientation being determined according to a random sample from a single Bernoulli trial with probability $P_{vertical}$ where,

$$P_{vertical} = \frac{w - 2s_{min}}{w + h - 4s_{min}}$$

If a rectangle's width is greater than its height then the split is more likely to be vertical, and similarly if the rectangle's height is greater than its width then it is more likely to be split horizontally. The orientation is also influenced by the parameter s_{min} , a real number on the interval $[0, 0.5]$. After determining the orientation of the split, the algorithm sets the size of the resulting two daughter rectangles by determining the relative position of the split, s_{split} (see Fig. 3),

$$s_{split} = s_{min} + r(1 - 2s_{min}).$$

Here, r is a random number with a uniform distribution on the interval $[0, 1]$ resulting in the split falling on the intervals $[w \times s_{min}, w \times (1 - s_{min})]$ or $[h \times s_{min}, h \times (1 - s_{min})]$. In determining the relative size of the daughter land parcels the parameter s_{min} influences the variation in land parcel area.

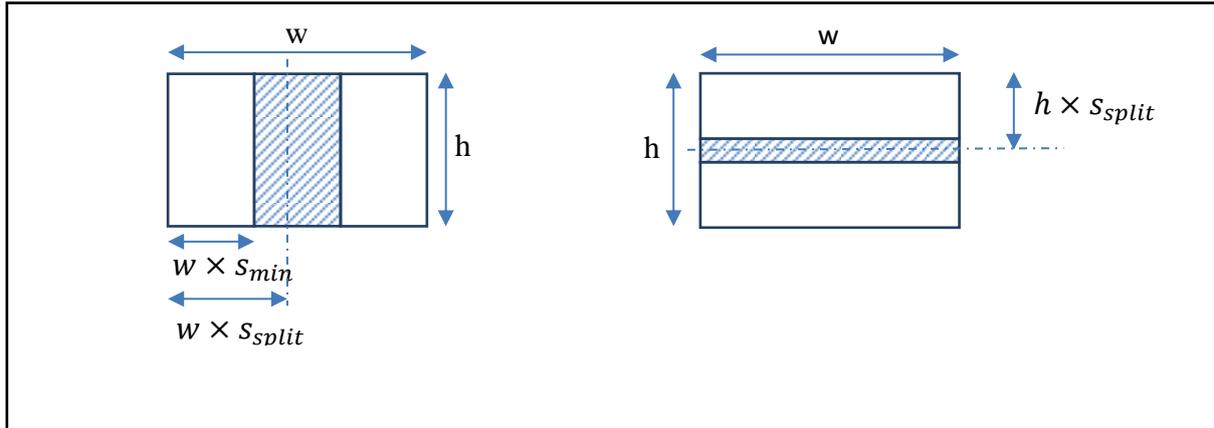


Figure 3. The position at which a vertical or horizontal split is made in a parent land parcel to produce two daughter parcels falls on the intervals $[w \times s_{min}, w \times (1 - s_{min})]$ or $[h \times s_{min}, h \times (1 - s_{min})]$ thereby setting the minimum parcel area of $(w \times s_{min})$ or $(h \times s_{min})$ for any given split.

At each split, the presence of a boundary habitat is allocated to both sides of the split at random on the basis of a single Bernoulli trial with the probability $P_{boundary}$. This information is inherited by daughter rectangles through subsequent splits. Only one boundary habitat type is permitted within a landscape.

In general, the composition of the landscape is simulated by specifying a habitat type for each of the land parcels. Because of crop rotation and other forms of land use change it is necessary to account for temporal changes in habitat type assigned to a land parcel. This is done by specifying habitat sequences. These can be of variable length and each element of the basic sequence has a duration of one year. When a habitat sequence is specified that is shorter than the duration of a simulation the sequence is repeated. In this way crop rotations may be specified. A number of alternatives exist for modelling habitat sequences. In simulations developed so far we have considered 2 main types of land use, semi-natural habitats such as woodland, and arable fields. In the case of semi-natural areas we have assumed these to be of fixed habitat type while crop rotations have been modelled as a first-order Markov chain following the approach set out in previous crop rotation models such as LandsFACTS (Castellazzi et al. 2008). In this case the state of the crop sequence for given field at time t , i.e. the crop being cultivated at that time, is represented by a binary state vector $c(t)$ and the transition from one crop to another in the subsequent year is represented by a stochastic transition matrix, the elements of which are the probability of transition from this crop type to another. With a first-order Markov chain it is possible to represent repeat crops by distinguishing between crops of the same species based on the number of consecutive years cropping, e.g. year 1 wheat, year 2 wheat, etc. However, representing rules that stipulate time intervals between the cultivation of the same crop type cannot easily be represented without recourse to higher order Markov chains (Castellazzi et al. 2008). To allow for differences in the management of crops during the winter the annual crop sequences may be extended by the addition of a seasonally biennial component that alternates between summer and winter. The summer states are defined solely by the crop or land use type as described above, whereas the winter states are defined by crop type, as before, but with the addition of two further states “stubble” and “bare ground”.

For each landscape to be simulated a set of habitat sequences of the type described above is defined and assigned randomly to each land parcel according to a multinomial distribution,

the probabilities of which determine the proportion of habitat types within the landscape and hence set the general pattern of landscape composition.

Once the arable fields have been identified a number of within field habitat elements may also be specified. Those currently implemented are consistent with Land Managers Options of the Scottish Rural Development Programme under Axis 2 of the European Commission Regulation (EC 1698/2005) and include features such as areas of unharvested crop, uncropped margins, and conservation headlands, all of which are elements common to many agri-environment schemes. For each arable field an uncropped margin of width m_{width} and habitat type $m_{habitat}$ or conservation headland of width h_{width} was added at random to all four interior edges of the land parcel, and an area p_{dimen}^2 and habitat $p_{habitat}$ was added to the north-west corner of a land parcel. In each case their addition was random following Bernoulli distribution with probabilities P_{margin} , $P_{headland}$, P_{patch} respectively.

Finally, once the landscape has been simulated it is made spatially discrete by overlaying a 2-dimensional lattice of grid squares onto the simulated landscape and mapping the habitat types of the underlying land parcels, boundaries and within field elements onto the lattice (landscape habitat lattice of Fig. 1). To do this the land parcels over which a square of the lattice lies are identified and the predominant habitat type by area assigned to the square. Any grid square bisected by a boundary habitat as defined during the splitting process is assumed to be of that habitat type.

3.2.2.2 Local population model

To analyse the dynamics of local populations, a matrix projection approach was taken, representing the stage- or age-specific demographics of the species to be modelled. The matrix projection models are constructed as per Caswell (2001), and the general framework of the model is described as follows,

$$\mathbf{n}(t + 1) = \mathbf{A}[\boldsymbol{\theta}, \mathbf{n}(t)] \mathbf{n}(t) + \mathbf{m}(t),$$

where the state vector $\mathbf{n}(t)$ is the density of individuals (m^{-2}) in each of the stage or age classes at time t , $\mathbf{n}(t + 1)$ is the state vector at the next time step (i.e. $t + 1$), and \mathbf{A} is the population projection matrix which depends on p parameters represented by the $p \times 1$ vector $\boldsymbol{\theta}$. The effect of immigration as a result of dispersal from other local populations is captured in the model by the addition of the vector $\mathbf{m}(t)$ the elements give the stage or age specific density on entering the population from other local populations.

By default the time steps, t , are taken to be yearly, matching both the annual cropping cycle of arable systems and the life-cycle of many arable species. However, to account for species with shorter generation times, and for periodic environmental variation it is possible to decompose the annual transition matrix into the product of a number of matrices that project the population between phases within the year. As an example, in the case of periodic seasonal variation the transition matrix \mathbf{A} might be represented by two seasonal transition matrices, i.e.

$$\mathbf{A} = \mathbf{S}\mathbf{W},$$

where \mathbf{S} and \mathbf{W} are the transition matrices corresponding to over-summer (spring to autumn) and over-winter (autumn to spring) transitions respectively. In another example we have further decomposed the over-summer transitions of an insect pest into a series of m phases defined by the monitoring and application of insecticide, i.e.

$$\mathbf{A} = \mathbf{B}_m \dots \mathbf{B}_2 \mathbf{B}_1 \mathbf{W}.$$

To model trophic interactions the matrix population models of the interacting species are coupled, making one or more of the demographic transitions a function of the interacting species' density. The form of this relationship can be chosen to represent the specific nature of these interactions, accounting for functional responses or ratio dependence and their effects on survival and reproduction. Where interacting species are included in a single simulation the duration and timing of transitions are synchronised in order to ensure that time lags are not inadvertently introduced into the interaction between species.

The influence of habitat on the dynamics of local populations is captured by making one or more of the parameters of the 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 current implementations of the model, pesticide applications are the only management activities included in addition to those represented by the crop rotation and over-winter crop treatment. Pesticide applications may be modelled in a variety of ways depending on the specific aspects of the crop system and pest being simulated. In general terms the lethal effects of pesticide applications are represented by the supplementary reduction in survival of sensitive stages during those transitions that take place during the phase of pesticide application and activity. In cases where the timing of the pesticide application does not coincide with a transition between existing life-cycle phases it may be necessary to include an additional post-application phase to allow the timing of the pesticide application to be correctly specified; where multiple pesticide applications are made, this may necessitate the introduction of multiple phases and transitions. It is also possible to make the application of pesticide dependent on pest densities and to affect non-pest species to represent complex effects of spraying such as non-target effects, threshold based spraying strategies, and regional monitoring and spraying strategies. Though currently representing pesticide management, this approach may be adopted to represent any disturbance associated with a crop management practice including tillage and harvesting.

3.2.2.3 Dispersal models

Dispersal is assumed to take place on one or more occasion during a species life-cycle. The dispersal events may take place in synchrony with existing transitions. If dispersal is not in synchrony, additional transitions are included to allow the dispersal to take place at the appropriate time, or times in the case of multiple dispersal events. For each dispersal event a stage or age specific proportion of a local population disperse. Passive dispersal is modelled using a 2-dimensional dispersal kernel appropriate for the species and stage being considered. To represent habitat selection associated with active dispersal the passive dispersal processes is supplemented by a second process in which the passively dispersed individuals landing in unsuitable habitat are relocated to the nearest suitable area if one exists within a prescribed search radius. If suitable habitat does not exist the individuals remain in the unsuitable habitat and do not relocate.

3.2.2.4 Stochasticity

The approaches used to simulate of the landscape is not inherently stochastic, however, in the current implementations of the model the algorithms for generating landscape structure and habitat sequences contain stochastic elements leading to spatial variation in landscape structures and spatio-temporal variation in habitat types. Simulating the landscapes in this way results in random variation in habitat over time; this, with the inclusion of functions linking the vital rates of species with habitat type as described above (section 3.2.2.2), leads to environmental stochasticity in the population dynamics. The spatial component of the random environmental variation does not contribute to environmental stochasticity in the accepted

sense but does mean that the landscapes vary with each simulation and requires the behaviour of the model to be averaged over a number of simulations.

In addition to environmental stochasticity the model accounts for demographic stochasticity, i.e. random variation arising from the application of probabilistic vital rates to finite populations using the approach set out by Caswell (2001).

3.3 Model implementation and software

In the implementation of the modelling approach computationally efficient methods are required to enable the software to run spatially explicit simulations involving multi-species interacting and dispersing over large numbers of local populations on a standard desktop PC. In addition the software needs to be able to accommodate new applications that may arise. The software should therefore be easy to maintain and change which, in turn, requires that the source code of the software is accessible. An object-oriented design approach was used to satisfy these requirements and the software written in the object oriented programming language C#. The C# programming language is approved as a standard by Ecma (ECMA-334) and ISO (ISO/IEC 23270:2006).

The software system consists of two main components or modules; a landscape simulation module, and population module. The landscape simulation module and the population module communicate with each other through the “habitat quality lattice” data structure. The population module consists of three sub-modules; the life cycle processes sub-module, the dispersal sub-module and the management sub-module (Fig. 4). The sub-modules interact with each other through the “species population lattices” data structure (Fig 1).

The software is designed to be configured using a number of XML (eXtensible Markup Language) files. An XML file is a simple text file that can be easily created and edited using standard computer applications. XML is a markup language that defines a set of rules for encoding data in a format that is readable by both human and computer software.

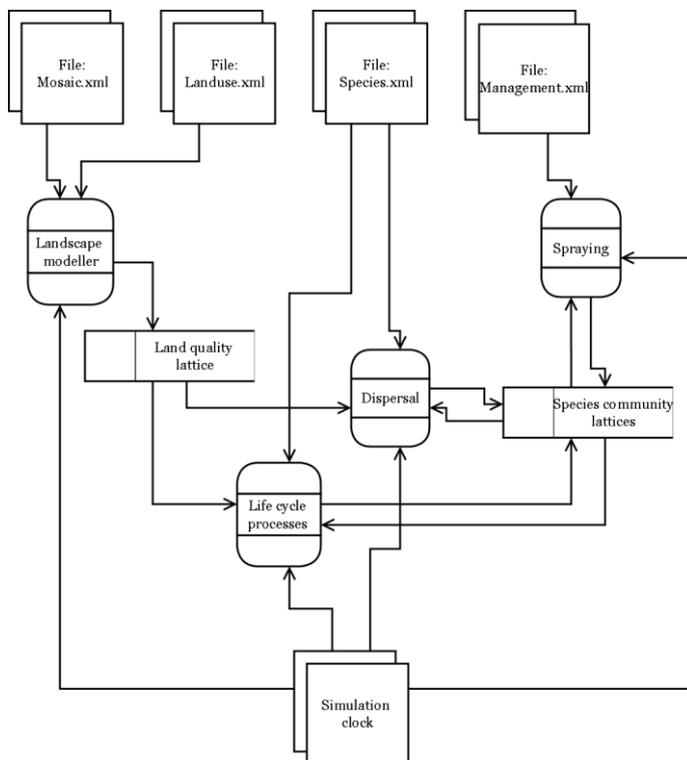


Figure 4. Software design: Data flow diagram showing the flow of data between sub-modules of the programme and the interface with the XML input files that are used to configure the programme.

3.4 Example applications and model verification

The application of AB-Scape to the simulation of a wide range of taxa, landscapes, and cropping systems has been a primary goal in its development. To determine the success of the approach requires the performance of system specific models to be tested. The relative ease with which AB-Scape models can be developed has been explored through the development of a number of prototype models including a multi-species model of arable weed communities, a single species crop-pest model, and a multi-trophic model. In addition AB-Scape has been used to simulate a range of crop landscapes from simple maize dominated landscapes to complex landscapes combining cereal rotations with areas of semi-natural habitats and the inclusion of agri-environment habitat prescriptions. Verification of the approach was pursued through the development of two models that allowed some basic attributes considered to be of key importance to the functioning of a spatially explicit model and its application to a pest regulation scenario. These models were of western corn root worm infesting a maize cropping system and a multi-trophic model based on an aphid-wheat system. In the case of the western corn rootworm model a comparison with empirical data on the distribution of root worm between neighbouring maize fields allowed the dispersal processes to be tested. In the second example, a comparison was made of the progression of aphid population size and mummification rates to assess the models capacity to capture the spatio-temporal synchronisation of pest and natural enemy populations. The choice of examples on which to base the model verification exercise is a deviation from those proposed in the project Description of Works (DOW). This decision was based on the suitability of the systems and the availability of data for comparison of specific aspects of the modelling approach.

3.4.1.1 Modelling western corn rootworm (*Diabrotica virgifera virgifera* LeConte) and in maize cropping systems.

3.4.1.1.1 Introduction

The western corn rootworm (WCR), *Diabrotica virgifera virgifera* LeConte (Coleoptera: Chrysomelidae), is a major pest of maize crops in America and Europe. Though thought to have originated in Mexico, it has spread through the US corn-belt. Accidentally introduced into Europe during the last 30 years (Meinke et al. 2009), WCR 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€ (Wessler & Fall 2010).

The actual and potential economic losses associated WCR infestation in maize demand the development of management strategies to control crop damage in endemic areas and to limit the spread of WCR into unaffected areas (Boriani et al. 2006). The sustainability of these strategies is a concern with development of resistance to Bt maize (Gassmann et al. 2011), rotation resistance and resistance to insecticides (Parimi et al. 2006). Modelling studies have played an important role in research into these topics, with a large number of spatial and non-spatial models developed to explore the population dynamics of WCR, the evolution of resistance, and its geographic spread (Szalai et al. 2014).

The WCR-maize system is relatively simple; the cropping system is such that the landscapes are typically dominated by maize which is grown continuously or as the dominant crop within simple rotations of maize plus a break-crop. The trophic ecology of the system is also simple, particularly in Europe where maize provides the sole host of WCR and it has no known natural enemies. Here we have taken advantage of this and the preceding experimental and modelling studies to rapidly develop and parameterise a model of WCR in the maize cropping systems of central Europe. This was used to test in general terms the ease with which a model could be developed in AB-Scape and to test the performance of the resulting model by making qualitative comparisons with the well-known behaviour of the system.

3.4.1.1.2 Model description

Landscape model

Assuming complete host specificity for WCR it is possible to represent the crop production landscape in relatively simple terms, considering only three field types: continuous maize, maize rotations, and non-maize cropping (Fig. 5). In compositional terms the landscapes were then allowed to vary according to 1) the proportion of the landscape given over to maize production, 2) the ratio of continuous to rotation maize cropped fields and 3) the length of maize rotations. Structurally, the landscape was varied in terms of the average field area and the separation distance between neighbouring fields.

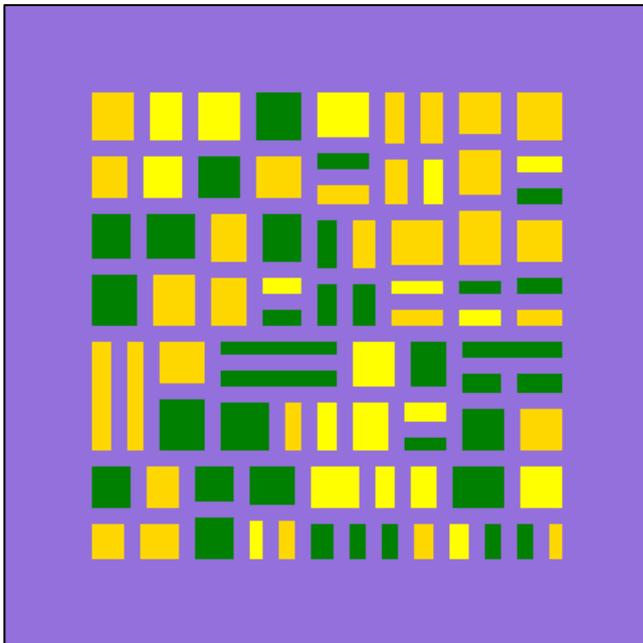


Figure 5. Example of simulated maize cropping landscape showing arable fields set within a non-arable mosaic (purple). Three classes of field were identified: continuous maize (yellow), maize rotation (orange), and non-maize (green).

Local population model

WCR is univoltine. In temperate regions oviposition takes place from July to September with eggs entering diapause and over-wintering in the soil (Meinke et al. 2009). The larvae hatch in spring and feed almost exclusively on maize roots (Moeser & Vidal 2005) passing through three larval instars. The larvae pupate in late spring and early summer with adults emerging around a month later, dependent on sex and temperature, (Meinke et al. 2009). On emergence, adult females ascend nearby maize plants where they are located by adult males and mating takes place (Spencer et al. 2009). In Europe, and the US where rotation-resistant WCR is not present, the females then continue to feed almost exclusively on maize with dispersal taking place within and between fields. The life-cycle is then completed with oviposition taking place at these feeding sites (Spencer et al. 2009).

To represent this life-cycle a stage-classified model was specified. Three stages were identified:

n_1	Egg
n_2	Larvae
n_3	Adult

The life-cycle was decomposed into 6 phases (Table 1). Adult phases were further separated into a series of steps to accommodate a series of dispersal events, ten in total. The transitions between steps within a phase were identical.

Table 1. Description of the life-cycle phases of WCR and the transition matrices used to project the population between the phases.

Phase	Duration (months)	Step	Transition	Matrix
1	7.5	1	Post-harvest to early spring	$\begin{bmatrix} s_{1egg} & 0 & 0 \\ 0 & 0 & 0 \\ 0 & 0 & 0 \end{bmatrix}$
2	1	2	Spring hatching	$\begin{bmatrix} s_{2egg} & 0 & 0 \\ h_{larvae} & 0 & 0 \\ 0 & 0 & 0 \end{bmatrix}$
3	1	3	Larval survival	$\begin{bmatrix} s_{3egg} & 0 & 0 \\ 0 & s_{3larvae} & 0 \\ 0 & 0 & 0 \end{bmatrix}$
4	0.5	4,5	Adult emergence and dispersal	$\begin{bmatrix} s_{4egg} & 0 & 0 \\ 0 & s_{4larvae}(1-p_{4adult}) & 0 \\ 0 & p_{4adult} & (1-d)s_{4adult} \end{bmatrix} + \begin{bmatrix} 0 \\ 0 \\ m \end{bmatrix}$
5	1	6-10	Adult emergence, dispersal and ovipositioning	$\begin{bmatrix} s_{5egg} & 0 & f \\ 0 & s_{5larvae}(1-p_{5adult}) & 0 \\ 0 & p_{5adult} & (1-d)(1-i)s_{5adult} \end{bmatrix} + \begin{bmatrix} 0 \\ 0 \\ m \end{bmatrix}$
6	1	10-14	Dispersal and ovipositioning	$\begin{bmatrix} s_{6egg} & 0 & f \\ 0 & 0 & 0 \\ 0 & p_{6adult} & (1-d)(1-i)s_{6adult} \end{bmatrix} + \begin{bmatrix} 0 \\ 0 \\ m \end{bmatrix}$

The vital rates included in the transition matrices are egg survival during phases 1 to 6. Here, $s_{1egg} = 0.44$, $s_{2egg} = 0.18$, $s_{3egg} = 0.015$, while the few eggs remaining after phase 3 go on to survive a second winter, i.e. s_{4egg} to $s_{6egg} = 1$. Larval survival during phase 3 to 5 is given by $s_{3larvae}$, $s_{4larvae}$, and $s_{5larvae}$; and adult survival during phases 4, 5 and 6 by s_{4adult} , s_{5adult} , s_{6adult} . Larval survival in each phase is density dependent, being a function of larval density at time (t , $step$) which defines the year, i.e. t , and the step within year, i.e. $step$, and is sensitive to habitat quality associated with the crop and non-crop vegetation, e.g.

$$s_{3larvae} = \left(0.06 - \frac{0.06}{e^{\left(\frac{10750-n_2(t,step)}{2150}\right)}} \right) \times q_{larvae}(c(t)),$$

where,

$$q_{larvae}(\mathbf{c}(t)) = \begin{cases} 1 & c(t) = \text{first year maize} \\ 1 & c(t) = \text{second and subsequent years maize} \\ 0 & c(t) = \text{break crop} \\ 0 & c(t) = \text{non - crop} \end{cases}$$

Habitat quality also affects survival (Elliot et al. 1990) which, in the absence of insecticide treatment, is defined and parameterised as follows:

$$s_{4adult} = \begin{cases} 0.95, & c(t) = \text{first year maize} \\ 0.95, & c(t) = \text{second and subsequent years maize} \\ 0.8, & c(t) = \text{break crop} \\ 0.8, & c(t) = \text{non - crop} \end{cases},$$

$$s_{5adult} = \begin{cases} 0.95, & c(t) = \text{first year maize} \\ 0.95, & c(t) = \text{second and subsequent years maize} \\ 0.8, & c(t) = \text{break crop} \\ 0.8, & c(t) = \text{non - crop} \end{cases},$$

$$s_{6adult} = 0.7.$$

We also assume that the maize crops are subject to management in the form of insecticide applications. These take place during phases 5 and 6 conditional on the density of adult populations exceeding an action threshold of 5 m⁻² and are effective immediately, remaining so for two weeks giving a weekly adult mortality rate i , where

$$i(n_3(t, step), \mathbf{c}(t)) = \begin{cases} 0.67 & c(t) = \text{maize AND } [n_3(t, step) \geq \text{action threshold OR } n_3(t, (step - 1)) \geq \text{action threshold}] \\ 0 & c(t) \neq \text{maize OR } [n_3(t, step) < \text{action threshold AND } n_3(t, step - 1) < \text{action threshold}] \end{cases}$$

The pupation of the larvae and subsequent emergence of adult beetles (p_{4adult} , p_{5adult} , and p_{6adult}) takes place during phases 4-6. The number of adults emerging peaks midway through the 6 weeks of phases 4 and 5, according to

$$p_{4adult} = 0.08(step - 2)^{1.4},$$

with all remaining larvae reaching adulthood at the onset of phase 6.

Adults reproduce over the 8 steps of phase 5 and 6 to give a maximum per capita lifetime reproductive output of $8 \times f$. Here $f = 60$ giving a maximum lifetime reproductive output of 480. Finally, a proportion of adults, d , leave the population through emigration which takes place at each of the 10 steps that comprise phases 4, 5, and 6; while a number of adults enter the population through immigration, m , from other local populations on the basis of dispersal models as described below.

Dispersal model

Dispersal takes place in ten discrete events, one at each step of phases 4, 5 and 6 (Table 1). On each dispersal event the majority (99%) of dispersing individuals are assumed to be making short range foraging movements with the remaining 1% making long range movements. An exponential dispersal kernel is used to model the short range foraging while a uniform kernel is applied in the case of long range dispersal as follows:

Short range dispersal: Exponential

$$p(r|\theta) = \begin{cases} \frac{K}{\lambda \left(e^{\frac{r}{\lambda}} \right)}, & r \leq r_{max1} \\ 0, & r > r_{max1} \end{cases}$$

where $p(r|\theta)$ is the probability of a dispersal event to radial distance r along a bearing θ , and λ is the median dispersal distance, $r_{max1} = 1000$, and $\lambda = 200$.

Long range dispersal: Uniform

$$p(r|\theta) = \begin{cases} K, & r \leq r_{max2} \\ 0, & r > r_{max2} \end{cases}$$

where $r_{max2} = 6000$.

Both short and long range dispersal are also assumed to consist of active and passive elements as described in section 3.2.2.3 with 95% of the dispersing individuals pursuing active dispersal and the other 5% passive dispersal, for both short and long range movements.

3.4.1.2 Verification

The following results were based in simulation of 10km x 10km landscapes and population lattices with grid dimensions of 50m x 50m. Fifty percent of fields within the landscape were assumed to be supporting maize either continuously cropped or in rotation with a break crop. All fields were subject to an IPM based pesticide treatment strategy as described in section 3.4.1.1.2.

Examination of the dynamics of local WCR populations indicates that the behaviour of the model is consistent with the known patterns of WCR infestation (Szalai et al. 2011). The adults are absent in the break crop but present in increasing numbers in the periods of continuous maize crops (Fig. 6). First year maize experience net-immigration while subsequent crops are net exporters of WCR. Though third year maize populations do not achieve notably higher adult densities than second year maize this is because of insecticide application triggered by the action threshold being crossed (Fig. 6).

As a result of the high level of host specificity exhibited by larval WCR in Europe means they are not able to persist in non-maize crop. As a consequence crop rotation is known to be one of the most effective forms of control in Europe (Szell et al. 2005). The dramatic effect of rotation on WCR abundance is captured by the model. For example simulations of WCR populations in landscapes described in section 3.4.1.1.2 but with varying length of maize rotations, show a dramatic increase in the density of WCR in response to an increasing rotation length (Fig. 7)

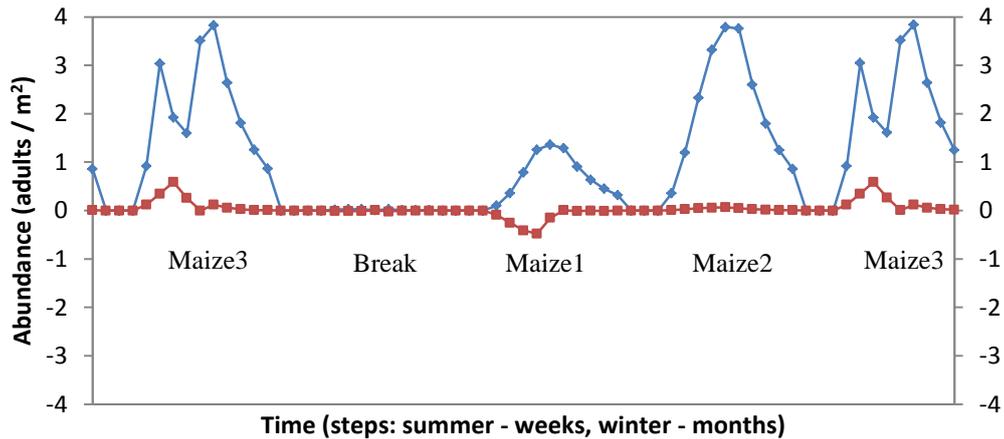


Figure 6. An example of the variation in adult WCR density (diamonds) and net migration (squares) in a single local population situated within a field subject to a maize rotation with break crop (Break), first (Maize1), second (Maize2) and third (Maize3) year maize crops.

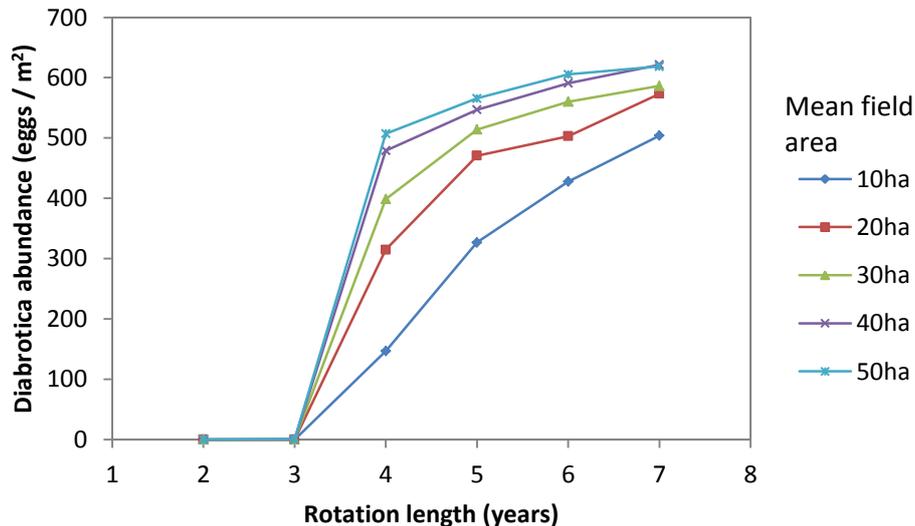


Figure 7. The response of the regional (whole landscape) density of WCR populations (eggs m^{-2}) to increasing rotation length where the number of years continuous maize cropping is given by rotation length – 1. Simulations were repeated for landscapes of varying average field size.

The importance of rotation is also evident in the ratio of adult abundance which has been found to be approximately 4 times higher in second and subsequent year maize than first-year crops (Sivcev et al. 2009; Szalai et al. 2011); a feature also evident in the model simulations (Fig. 6).

It follows from this that the colonisation first-year maize crops by adult WCR is a key ecological process in determining the persistence and spread of WCR populations in areas where rotation is practiced (Szalai et al. 2011). Pursuing the distinction between first year and subsequent or continuous maize fields it is possible to examine the colonisation behaviour of WCR. In a detailed study of WCR in Hungary, Szalai et al. (2011) demonstrated a significant linear relationship exists between the abundance of adults in first-year maize fields and average adult abundance of adjacent fields that were subject to continuous maize cropping.

This relationship, which was found to be robust, explained approximately 60% of the variation in the abundance of adults in first-year maize fields and as such suggests a predominant role for short-range dispersal in the dynamics of WCR populations. Again, the model is able to capture this important feature of the system with an accurate estimation of the relationship between the relative abundance of first-year and adjacent continuous maize fields, the coefficient of the linear model fitted to the simulated data was 0.19 (Fig. 8) which compares favourably with the equivalent value of 0.17 reported by Szalai et al. (2011) as does the 54% of variance in adult abundance in first-year fields that is explained by the relationship.

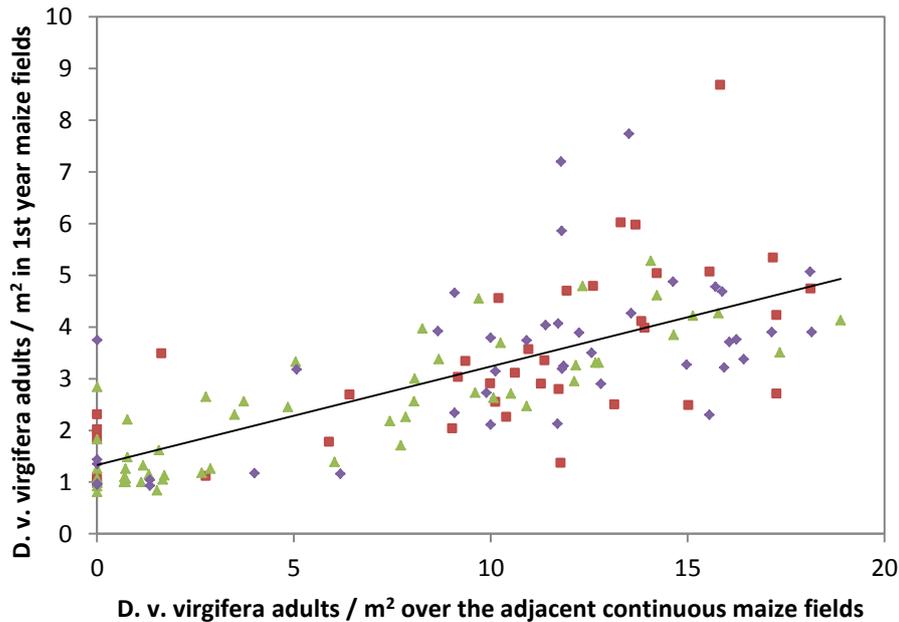


Figure 8. The density of adult WCR in first year maize fields in comparison with the density of adults in neighbouring fields that are continuously cropped with maize. Fitted line: $y = 0.1909x + 1.3276$.

Finally, as a consequence of these findings it has been suggested that the patterns of maize cropping within the landscape, such as field separation distance, is likely to play an important role in the area-wide management of WCR populations (Beckler et al. 2004, Szalai et al. 2011). Simulation results show that the behaviour of the model is consistent with this expectation and, furthermore is capable of provide more detailed insight into this, and other, aspects of the WCR – maize system (Fig. 9).

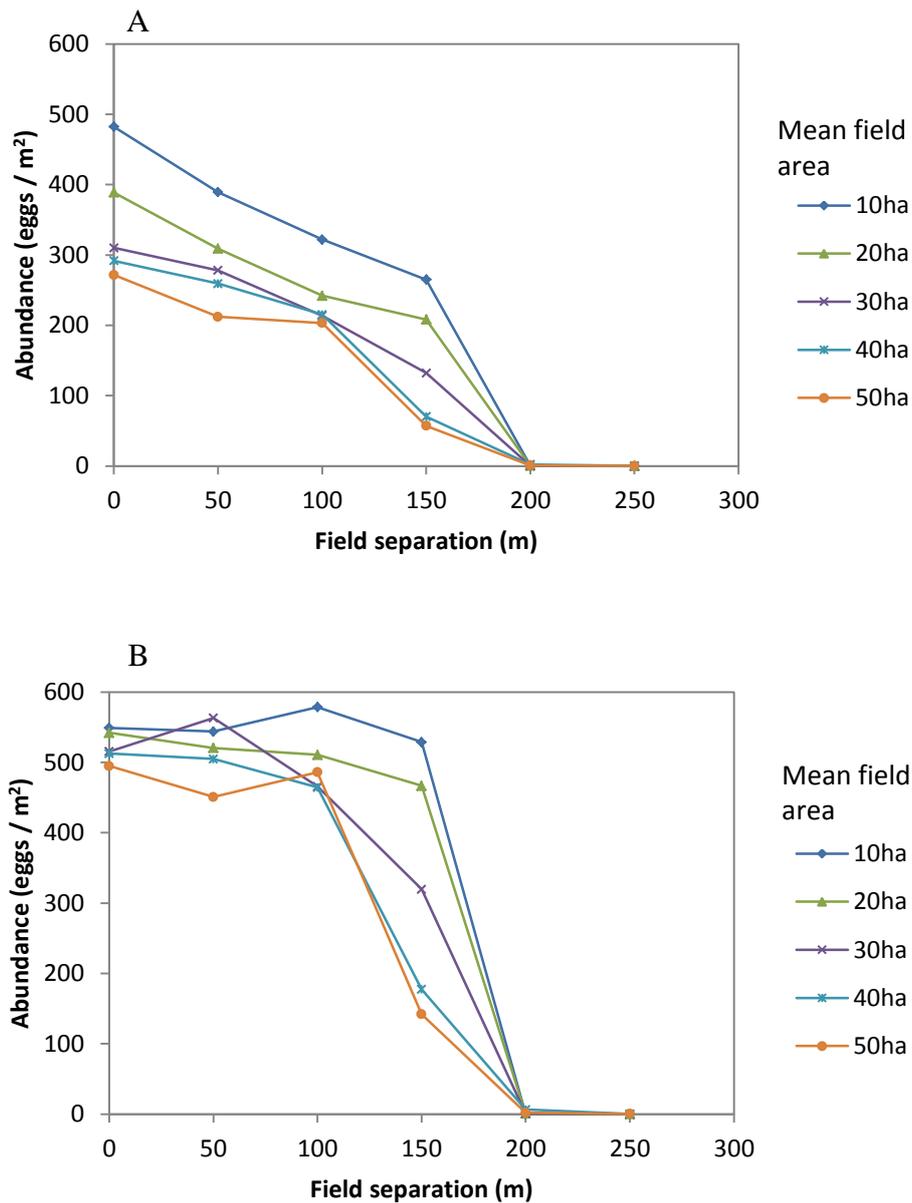


Figure 9. The response WCR egg density in (A) first-year and (B) continuous maize crops to an increase in the separation distance between all fields within a landscape.

3.4.2 Biological control of insect pests in a wheat cropping system

3.4.2.1 Introduction

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 Tschardtke 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). Furthermore, hedgerows are known to shelter very abundant and diverse communities of hymenoptera parasitoids and may provide refuge to their populations during pesticide treatments.

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 distractions in the form of alternative prey, or intra-guild 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 scale at which parasitoids respond to these local and landscape factors depends on their biology, particularly their dispersal ability, as well as the structure of landscape heterogeneity, while the link between parasitoid abundance and parasitism rates may depend on both pest and parasitoid abundance (Costamagna et al. 2004; Thies et al. 2005; Jonsson et al. 2012).

Modelling approaches are particularly useful in these circumstances and the design and testing of landscape scale conservation biological control strategies is one of the primary applications to be pursued with the AB-Scape modelling approach. Here we describe a generic tri-trophic model developed to test the potential of AB-Scape to represent multi-trophic systems, and specifically the specification of predator-prey interactions and the spatio-temporal synchronisation of interacting species.

3.4.2.2 Model description

A generic aphid-parasitoid system was constructed and coupled to a landscape simulation of a UK wheat based cropping system. The population models were based on the pea aphid – *Aphidius ervi* components of the model developed by Snyder and Ives (2003), hereafter referred to as S&I. As a result the parameterisation of the model may not be representative of conditions in the UK wheat system, however, it has the benefit of providing simulated and empirical data against which the AB-Scape results could be compared (Snyder and Ives, 2003). In line with the results of S&I we restrict the model to the simulation of populations during the summer when aphids complete a parthenogenetic life-cycle on crops.

Landscape model

For the purpose of this study we considered the landscape to be comprised of arable fields each subject to a cereal-based rotation that, in addition to wheat, includes a broad-leaf break-crop and grass ley. As simulations are restricted to summer months only, crop sequences were not modelled.

Local population models

The pea aphid and by analogy the generic monoecious aphid considered here undergoes a relatively simple life-cycle. Overwintering as eggs on crops or non-crop vegetation, the eggs hatch in spring. After one or two generations winged forms develop, migrating to crops where they initiate colonies through parthenogenesis giving rise to live young that pass through four larval stages before developing into adults in a process taking approximately 10 days. In the autumn the aphids migrate to their overwintering sites where the life-cycle is completed.

For the purpose of comparison with the results of S&I we consider only the parthenogenetic phase of the life-cycle. Following S&I, a stage-classified model was specified in which five life-cycle stages were identified:

n_{a1}	Instar 1
n_{a2}	Instar 2
n_{a3}	Instar 3
n_{a4}	Instar 4
n_{a5}	Adult

The dynamics of the aphid populations are determined by the survival of each stage, including the effect of parasitism and the reproductive output of the adults. Updating the aphid population every 2 days in line with the duration of each instar gives rise to a Leslie matrix \mathbf{L}_a of the form,

$$\mathbf{L}_a = \begin{bmatrix} 0 & 0 & 0 & 0 & f \\ s_1 & 0 & 0 & 0 & 0 \\ 0 & s_2 & 0 & 0 & 0 \\ 0 & 0 & s_3 & 0 & 0 \\ 0 & 0 & 0 & s_4 & s_5 \end{bmatrix}$$

For the sake of simplicity survival is considered to be the same for all stages, i.e. for $i = 1, 2, 3, 4, 5$,

$$s_i = s_a \times \frac{1}{(1 + k(\sum_{j=1}^6 n_{aj}(t) + \sum_{j=1}^4 n_{pj}(t)))} \times e^{-ar_i n_{ps}(t)/1 + ga(\sum_{j=1}^6 n_{aj}(t) + \sum_{j=1}^4 n_{pj}(t))}$$

where the parameters are as described in table 2. Here aphid survival is considered to be the product of density-independent survival (s_a), density-dependent survival as a function of parasitized ($\sum_{j=1}^4 n_{pj}(t)$) and non-parasitized larvae ($\sum_{j=1}^6 n_{aj}(t)$), and the rate of parasitism, $e^{-ar_i n_{ps}(t)/1 + ga(\sum_{j=1}^6 n_{aj}(t) + \sum_{j=1}^4 n_{pj}(t))}$.

AB-Scape does not currently support delayed density dependence, though its inclusion would be relatively straight forward. Therefore, we do not include the delayed density dependence specified by S&I.

Table 2. Parameters and parameter values for the aphid population dynamic model.

Parameter	Description	Value
f	Fecundity	8
a	parasitoid searching efficiency	1.46
$r_{[1,2,3,4,5]}$	relative searching efficiency	[0.12,0.27,0.39,0.16 0.06]
g	type of functional response	0.0011
s_a	density-independent aphid survival	0.94
k	density-dependent aphid survival coefficient	0.0016

The life-cycle of the parasitoid, *Aphidius ervi*, begins when an adult female lays an egg within an aphid. The egg develops passing through a series of larval instars. The parasitized aphid remains alive during the initial development of the parasitoid, but eventually succumbs and dies as the larvae develop. Once larval development is complete the parasitoid emerges to form an aphid mummy in which it pupates. Following pupation the adult parasitoids emerges and the life-cycle is complete.

As with the aphid, a stage-classified model was specified to represent the parasitoids life-cycle. Eight stages were identified:

n_{p1}	Egg
n_{p2}	Instar 1
n_{p3}	Instar 2
n_{p4}	Instar 3
n_{p5}	Mummy 1
n_{p6}	Mummy 2
n_{p7}	Mummy 3
n_{p8}	Adult

The duration of each stage was assumed to be 2 days allowing the parasitoids population to be updated in synchrony with the aphid population using the Leslie matrix \mathbf{L}_p , and the immigration vector $\mathbf{m}(t)$, i.e.

$$\mathbf{L}_p = \begin{bmatrix} 0 & 0 & 0 & 0 & 0 & 0 & 0 & f \\ s_1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & s_2 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & s_3 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & s_4 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & s_5 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & s_6 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & s_7 & (1-d)s_8 \end{bmatrix} + \begin{bmatrix} 0 \\ 0 \\ 0 \\ 0 \\ 0 \\ 0 \\ 0 \\ m_8 \end{bmatrix}$$

Here the survival of the parasitoids is stage dependent. For the egg and larval stages it is assume that the survival of the parasitoid is entirely dependent on the survival of its aphid host, i.e. for the parasitized aphids ($i = 1, 2, 3, 4$)

$$s_i = s_a \times \frac{1}{\left(1+k\left(\sum_{j=1}^6 n_{aj}(t)+\sum_{j=1}^4 n_{pj}(t)\right)\right)}$$

For subsequent stages the survival rates, s_5, s_6, s_7, s_8 are assumed to be constant and density independent.

The rate of egg production, f , over the 2 day transition period is given by the total number of aphids parasitized in that time,

$$f = \sum_{i=2}^5 n_{ai}(t) \left(1 - e^{-ar_i n_{ps}(t)/1+ga\left(\sum_{j=1}^6 n_{aj}(t)+\sum_{j=1}^4 n_{pj}(t)\right)}\right).$$

Parameters for the parasitoid population model are described in table 3.

Table 3. Parameters and parameter values for the parasitoid population dynamic model.

Parameter	Description	Value
a	parasitoid searching efficiency	1.46
g	type of functional response	0.0011
$r_{[1,2,3,4,5]}$	relative searching efficiency	[0.12,0.27,0.39,0.16 0.06]
k	density-dependent aphid survival coefficient	0.0016
s_a	density-independent aphid survival	0.94
s_5, s_6, s_7	mummy-stage parasitoid survival	0.62
s_8	adult parasitoid survival	0.8

Dispersal model

During the summer when aphids complete a parthenogenetic life-cycle on crops are relatively immobile and we assume there is no migration between local populations. However, adult parasitoids are expected to move within the landscapes seeking out new hosts with the proportions d leaving a local population and m_8 entering it. We assume that the movements of the dispersing individuals are relatively short range and so adequately represented by an exponential dispersal kernel, i.e.

$$p(r|\theta) = \begin{cases} \frac{K}{\lambda \left(e^{\frac{r}{\lambda}} \right)}, & r \leq r_{max1} \\ 0, & r > r_{max1} \end{cases}$$

where $p(r|\theta)$ is the probability of a dispersal event to radial distance r along a bearing θ , and λ is the median dispersal distance, $r_{max1} = 100$, and $\lambda = 20$.

3.4.2.3 Verification

Simulations were carried out on a 5km x 5km landscape with a mean field size of 12.5 ha and population lattices with grid dimensions of 50m x 50m. Sixty percent of fields were assumed to be under wheat with 20% break-crop and 20% grass ley.

The simulated local population densities were expressed as the number of aphids per stem assuming a fixed crop density. The results show an initial increase in aphid density followed by a decline which is associated with rising rates of parasitism (Fig. 10 A). This simulation was conducted in the absence of parasitoid movement in line with the model of Snyder and Ives (2003) and the field trials that were conducted as small scale caged experiments. The results were highly consistent with both experimental and modelling results reported by S&I (see S&I figures 5 and 6). This suggests that implementation of the aphid-parasitoid model in AB-Scape, and in particular the approach used for synchronising the aphid and parasitoids populations was successful. It also suggests that the departures from S&I model, such as the exclusion of a delay in aphid density dependence, are not of particular importance in this system.

The opportunity was then taken to repeat the simulations but with the inclusion of parasitoid dispersal. In the short-term, i.e. in the first twenty days, parasitoids dispersal did not have a substantial impact of aphid dynamics or parasitism rate though overall aphid density was noticeably reduced (Fig. 10 B). Extending the simulations beyond the 20 days reported by S&I the influence of parasitoid movement and the introduction of spatial processes on the dynamics of local populations become evident (Fig 11).

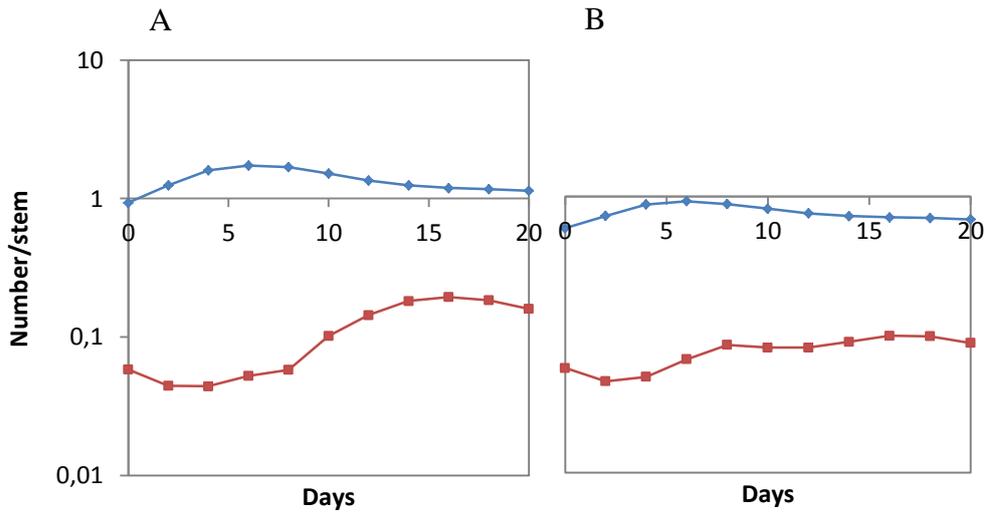


Figure 10. Initial phase of aphid population dynamics (A) in the absence and (B) presence of parasitoid migration between local populations showing the number of live (diamonds) and mummified (squares) aphids per stem.

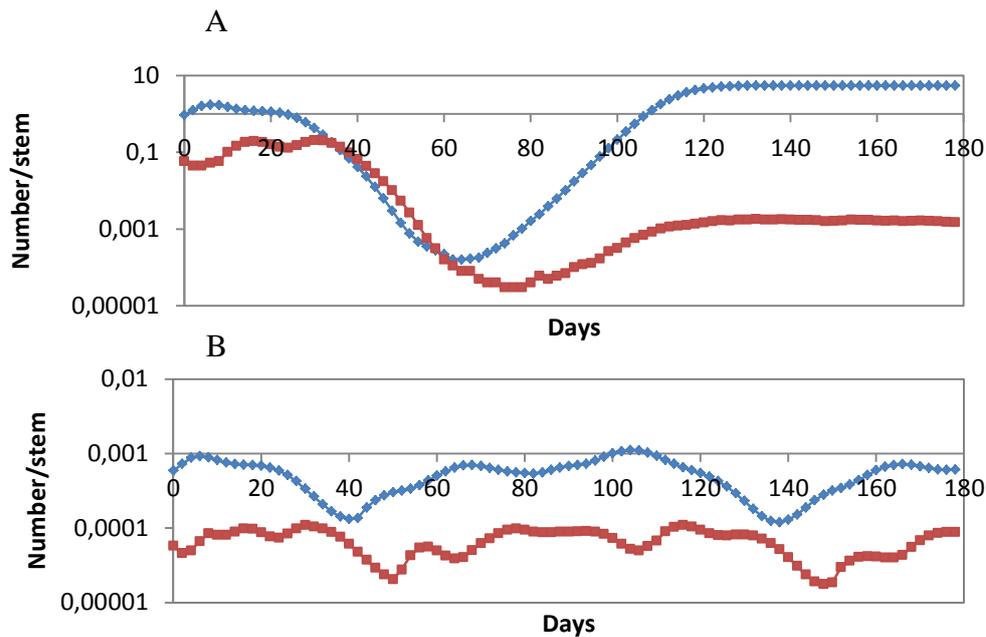


Figure 11. Aphid population dynamics (A) in the absence and (B) presence of parasitoid migration between local populations showing the number of live (diamonds) and mummified (squares) aphids per stem extended over full cropping season.

4 Conclusion

The objective of this study was to develop a model capable of simulating the dynamic interactions between pest populations and the farming landscapes. In achieving this it was desirable to pursue a modelling approach that was capable of representing a wide range of landscapes, crop production systems, and plant and animals species, including multi-trophic combinations. The result of this process was the development of the AgriBioScape modelling system, a generic modelling approach and framework that couples a discrete time approach to modelling population dynamics with a landscape simulation model that simulates both landscape structure and composition, including the dynamics of land use change and crop sequences. The application of AB-Scape to the development of models covering a range of systems has demonstrated that it provides a useful basis for the development of a wide range of models. Furthermore, on the basis of two applications described in this report, the approach has been satisfactorily verified. Therefore, we conclude that AB-Scape provides a suitable platform for the further development and analysis of models towards the objective of designing pest-suppressive landscapes.

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