Exploring trade-offs and synergies between biological pest control and species conservation

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For further information on this report please contact:

Cécile Smith
Scottish Natural Heritage
Caspian House
2 Mariner Court, 8 South Avenue
Clydebank Business Park
CLYDEBANK
G81 2NR
Telephone: 07769642191
E-mail: cecile.smith@snh.gov.uk

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Summary

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Keywords

Arable landscape; population model; biological pest control; agri-environment; pest regulation; species conservation.

Background

The management of uncropped land and in particular its reintroduction into the arable landscape has been a common approach to increasing biodiversity in arable systems. This is the principle that underlies the majority of agri-environment schemes (AES). In a parallel development, the introduction of conservation biological control (CBC) seeks to promote the regulation of crop pest populations by conserving their natural enemies typically through habitat management. Given the common approach to AES and CBC, the potential for AES to achieve added value by promoting pest regulation in addition to enhancing biodiversity more generally is clear. However, neither CBC nor AES are universally effective in promoting biodiversity or in achieving pest regulation and their effectiveness is complicated because management prescription can lead to multiple outcomes; these may be complementary but may also conflict with each other and so limit the success of such an approach. Therefore, we are not yet able to derive full benefit from CBC or AES and there is a clear need to develop strategies aimed at the effective delivery of multiple ecosystem services. In response to this need, SNH has commissioned a preliminary study of the potential trade-offs and synergies between the delivery of regulating ecosystem services, beneficial to arable production, and the support of key conservation species.

Main findings

- A multi-trophic, spatially explicit population model has been developed using the AgBioscape modelling framework built at the James Hutton Institute. Its use in exploring the trade-offs between the regulation of a crop pest and the conservation of a farmland bird population was demonstrated.
- Simulation results demonstrate the value of the modelling approach in exploring the behaviour of an ecosystem where the complexity and the spatial and temporal scale prevent empirical studies from being effective.
- Simulations revealed a strong positive response by grey partridge populations at the regional scale ($25km^2$) to the introduction of an agri-environment management prescription.
- The response by grey partridge took several decades to establish.

- Simulations revealed a potential trade-off between the conservation of partridge populations and the control of aphid pests as a result of top-down regulation by partridges on the carabid natural enemies in a simple linear food-chain.
- This trade-off was of little consequence due to the relatively weak control exerted by the natural enemies.
- A trade-off between conservation and pest regulation was not evident in the presence of more complex trophic interactions such as omnivory arising from grey partridge feeding on natural enemy and pest insect populations, or omnivory plus intra-guild predation, resulting from the introduction of a second species of natural enemy feeding on both the primary natural enemy and pests insect species.

On the basis of the technical and scientific progress made, it is recommended that future research should be focussed as follows:

1. *An extended analysis of the existing model to provide strategic insight into multi-trophic responses to land management.*

Further analysis of the model will capitalise on the existing research, providing a cost effective approach to understanding the competing demands within arable food webs and the impact of these on achieving sustainability objectives of future farmland management strategies.

2. *An assessment of the model's capacity to simulate food-webs of increasing size and complexity.*

Natural systems are substantially more diverse, with greater trophic complexity than considered here. To address the impact of characteristics associated with large food webs such as redundancy and connectance, it is necessary to simulate food webs of greater size and complexity.

3. *Application of the modelling approach to the development of a decision support tool for use in the design and assessment of land management options, including AES.*

The general nature of the model developed in the present study limits its capacity to predict outcomes for specific farmland systems. The potential to build decision support tools capable of assisting land managers and policy makers in identifying effective management options should be explored. The development of a system-specific model capable of capturing key features of an example farmland system will be an important test of the potential to develop these tools.

4. *A review and synthesis of community composition, food-web structure and the ecosystem functions of the Scottish arable system.*

A better understanding of the nature of farmland communities and food webs is necessary to support the application of the model-based findings to the practical management of real farmland systems and also to ensure the development of appropriate models, capable of capturing the important characteristics of farmland systems.

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1. INTRODUCTION

1.1 Background

Agricultural intensification, land abandonment and degradation of the landscape infrastructure is causing a 'biodiversity-crisis' in European farmland. A reduction in biodiversity and declines in regulatory ecosystem services are leading to losses in production. In response, it has been proposed that the reintroduction of habitat diversity and complexity might return agro-ecosystems to a position of ecological balance and reverse the adverse effects of intensive agriculture (Benton *et al.*, 2003; Nicholls & Altieri, 2004). The management of uncropped land and in particular its reintroduction into the arable landscape has been a common approach to increasing biodiversity in arable systems. This is the principle that underlies the majority of agri-environment schemes (AES) which are a common theme of agricultural policies throughout Europe (Berendse et *al.,* 2004; Uthes & Matzdorf, 2013).

Conservation biological control (CBC) seeks to promote the regulation of crop pest populations by conserving their natural enemies (Ehler, 1998). CBC strategies typically focus on habitat diversification strategies to encourage the abundance and diversity of natural enemies (Gurr *et al.,* 2004) and often adopt measures common to AES. Though CBC is a potentially important contributor to integrated pest management, the deployment of CBC specific measures is limited. In contrast, AES are widely adopted and account for a substantial proportion of rural development budgets in the EU (Uthes & Matzdorf, 2013). However, the similarities between AES and CBC measures could lead to synergies that enhance opportunities to deploy CBC measures and at the same time add value to AES by promoting pest regulation in addition to enhancing biodiversity more generally. This is an opportunity that may be used to positive effect in developing sustainable arable production systems (e.g. Holland *et al.*, 2012).

However, neither CBC nor AES are universally effective in promoting biodiversity (Kleijn *et al.*, 2006; Whittingham, 2007) or in achieving pest regulation (Letourneau *et al.*, 2011). Habitat diversification is a non-target approach that has the potential to influence populations from a wide range of taxa (Kleijn *et al.*, 2006). Consequently, any one management prescription can lead to a range of outcomes; these may be complementary insomuch as they are all considered beneficial, but there may also be conflicts that limit the success of such an approach. Predicting the outcome under such circumstances is likely to be problematic but will be particularly so where interactions between taxa create non-linear responses. As an example, the complexity of the interactions between pest and natural enemy assemblages including, for example, niche complementarity, intraguild predation, and functional redundancy place restrictions on the ability of CBC to enhance natural enemies in a way that achieves optimal levels of predation or pest suppression (Straub *et al.*, 2008).

Moreover, habitat diversification needs to be viewed in a spatial context. The typical approach to CBC and AES has been to introduce small patches of habitat within and between areas of cropped land (Whittingham, 2007). However, populations typically range across scales well beyond that of such habitat patches so that implementation of AES on a larger scale, in the form of protected area schemes (Whittingham, 2007) or the development of landscape scale strategies (Tscharntke *et al.*, 2007) should be considered (Birch *et al.*, 2011).

Policy initiatives such as the Scotland Rural Development Programme and those embodied in the 'greening' of the Common Agricultural Policy (CAP), continue to support the delivery of agri-environmental options for enhancing critical services provided by agricultural biodiversity. In pursuing this policy however, it should be recognised that we are not yet able to derive full benefit from these strategies and there is a need to develop approaches aimed

at the effective delivery of multiple ecosystem services. In response to this need, SNH has commissioned a preliminary study of the potential trade-offs and synergies between the responses of regulating ecosystem services, beneficial to arable production, and the support of key conservation species. This is a demanding but essential area of research to underpin a more integrated view on enhancing farmland biodiversity in which multiple objectives might be achieved from a single landscape prescription.

1.2 Objectives

Our aim is to assess the performance of a modelling approach to exploring the management of the arable landscape in a way that will enhance functional biodiversity and deliver wider conservation objectives. Ultimately the goal is to explore strategies that will help to promote a more integrated view on enhancing farmland biodiversity by taking into consideration the synergies/trade-offs between different ecosystem services.

The study has contributed to these aims by pursuing the following specific objectives:

1. To explore the impact of land use patterns on the population dynamics of a multi-trophic system consisting of an arthropod pest and natural enemies and a fourth trophic level predator of conservation importance.
2. To explore the trade-offs and synergies between conservation and the regulatory ecosystem service, biological control, associated with different land use/ management strategies.
3. To provide recommendations on the next steps required to take this work forward, including any technical and strategic improvements to the approach proposed.

The study represents an initial, exploratory phase of research to establish the viability of a modelling approach and its potential to gain insight into the multi-functionality of land use management and the trade-offs/synergies that may follow. This is recognised in the objective 3 above, which identifies the requirement to assess the performance of the approach with respect to objectives 1 and 2.

2. MODEL DESCRIPTION

2.1 Approach

Empirical studies have demonstrated the sensitivity of naturally occurring populations to the agricultural landscape, its composition and configuration (Petit *et al.*, 2011, Kovacs-Hostyanszki *et al.*, 2011, Gaba *et al.*, 2010, Chaplin-Kramer *et al.*, 2011, Veres *et al.*, 2013), showing responses of a range of taxa in both diversity and abundance to a variety of landscape characteristics. 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).

A modelling approach has been taken to address the objectives of this study. Specifically a multi-trophic spatially explicit population model has been developed to (i) test the population dynamics response of four species, a 'conservation' species, an agricultural pest, and two, functionally-distinct natural enemies, under different landscape scenarios; and (ii) explore whether trade-offs and synergies between enhancing a regulating service and wider conservation objectives can be established.

2.2 Model framework

The multi-trophic SEPM (Spatially Explicit Population Model) was built using an existing generic model platform AgBioscape, developed by the report's authors (GS Begg and R Dye) to implement a class of SEPMs capable of representing a range of landscapes, cropping systems and species. The development of the modelling framework was initiated in order to study the response of crop pests and their natural enemies to heterogeneity in crop management and habitat type at a landscape scale with the ultimate objective of designing pest suppressive landscapes. This work is funded by the EU FP7 Project PURE (Pesticide Use-and-risk Reduction in European farming systems with Integrated Pest Management). The scope was subsequently extended to assess the potential impact of land use change on biodiversity in the Scottish arable system as part of the Strategic Research Programmes funded by The Scottish Government's Rural and Environment Science and Analytical Services Division (RESAS).

The AgBioscape modelling system is described in detail in Annex 3 but in brief, is made up of two primary software modules: the landscape mosaic generator and population process module; data input, output and dispersal are handled by sub-modules within these.

The land use mosaic generator works by continually subdividing a 2 dimensional space to produce a network of rectangular land parcels or "fields". By specifying how the parcels of land are divided, the size, shape and clustering of fields 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 and other land use changes.

The population process module uses a matrix population model approach to simulate the population dynamics of many 'local' populations of a species across the simulated landscape. Local populations are arranged spatially on regular grids, one grid for each species being modelled. The population grids are overlaid on the land use mosaic and each local population responds uniformly within a grid-cell, even where several land uses (habitats) are present, in a way determined by a species and stage-specific model of habitat response. Each grid-cell holds a numerical vector to represent the stage structure of a local population at any particular time, 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.

Dispersal between local populations is modelled empirically using dispersal kernels, i.e. probability density functions that represent the probability of an individual dispersing a given distance and direction. 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.

2.3 Multi-trophic model

The model framework allows considerable flexibility in the representation of all aspects of the system, including the landscapes, habitat management, species type, spatial and temporal scale, etc. In this initial, exploratory phase, we have considered a generic system sufficient to capture the principle features of a multi-trophic arable system.

2.4 Landscape

The simulated landscape comprised arable fields and woodland. All arable fields were subject to a cereal-based rotation that, in addition to wheat, included a broad-leaf break-crop and grass ley (Fig. 1). Additional components were introduced into the landscape to represent hedgerows, areas of wild bird seed mix, uncropped grass or flowering margins, and conservation headlands. These are supported by the Land Managers Options of the

Scottish Rural Development Programme (2007-2013) under Axis 2 of the European Commission Regulation (EC 1698/2005) and are measures common to many agri-environment schemes.

Of these land uses, only woodland and hedgerows remain fixed for the duration of the simulation. Of the other land uses the cereal, broad-leaf crops, grass leys and conservation headlands vary on an annual basis with crop rotations modelled as a first-order Markov chain (Castellazzi *et al.*, 2008), while margins and wild bird seed areas persist for 5 years as dictated by the Land Managers Options of the Scottish Rural Development Programme.

As linear features, the hedgerows, margins and conservation headlands are considered in combination with the land use of adjoining land parcels giving rise to a composite habitat (Table 1). Grass margins and conservation headlands are only applied to cereal and broad-leaf crops while hedgerows are only considered in combination with cereal and broad-leaf crops, grass leys and areas of wild bird seed mix. This gives rise to a total of 17 possible habitat combinations present during the growing season, i.e. spring and summer. In order to distinguish between winter and spring crops and the winter or spring tillage in the absence of a winter crop, a number of additional habitat combinations are considered during autumn and winter (Table 2). The allocation of the possible habitat combinations can vary from simulation to simulation and is determined by the choice of parameter values (e.g. see Fig. A2.1, Table A2.1). A full description of the landscape simulation algorithm is given in Annex 3 including the rules used to simulate landscape composition, crop rotation and the allocation of agri-environment habitats.

Figure 1. Example of simulated arable landscape of 4 km^2 with wheat crops (yellow), grass ley (light green), woodland (red), agri-environment prescription habitats: grass margins (orange), and hedgerow (dark green).

Table 1. Possible habitat combinations present during crop growing season (spring and summer).

Code	Description
1	Cereal crop
2	Broad-leaf crop
3	Grass ley
4	Wild bird seed mix
5	Wood
6	Cereal crop + Grass margin
7	Broad-leaf crop + Grass margin
8	Cereal crop + Conservation headland
9	Broad-leaf crop + Conservation headland
10	Cereal crop + hedge
11	Broad-leaf crop + hedge
12	Grass ley + hedge
13	Wild bird seed mix + hedge
14	Cereal crop + hedge + grass margin
15	Broad-leaf crop + hedge + grass margin
16	Cereal crop + hedge + conservation headland
17	Broad-leaf crop + hedge + conservation headland

Table 2. Additional habitat combinations present during autumn and winter seasons.

Code	Description
18	Cereal crop stubble
19	Cereal crop stubble + hedge
20	Cereal crop stubble + grass margin
21	Cereal crop stubble + hedge + grass margin
22	Broad-leaf crop stubble
23	Broad-leaf crop stubble + hedge
24	Broad-leaf crop stubble + grass margin
25	Broad-leaf crop stubble + hedge + grass margin
26	Bare soil
27	Bare soil + hedge
28	Bare soil + grass margin
29	Bare soil + hedge + grass margin

2.5 Food-web

The food-web consisted of an archetypal arthropod herbivore (crop pest – 2nd trophic level, primary consumer), arthropod predator (natural enemy – 3rd trophic level, secondary consumer), arthropod parasitoid (natural enemy – 3rd trophic level, secondary consumer), and vertebrate predator (conservation species – 4th trophic level, tertiary consumer), their trophic interactions, and their interaction with the abiotic environment. The resulting model is strategic in nature, enabling the behaviour of the system to be analysed in terms of the multi-trophic population dynamics and the trade-offs and synergies in pest control and conservation that exist under alternative land use scenarios. Strategic models of this type are not suitable for predicting the abundance of specific species due to the generic structuring and parameterisation. However, for illustrative purposes and to provide a realistic basis for the structure and parameterisation of the model, we identify the herbivores, predators, parasitoids and conservation species as aphids, carabids, hymenoptera, and grey partridge in that order (Fig. 2).
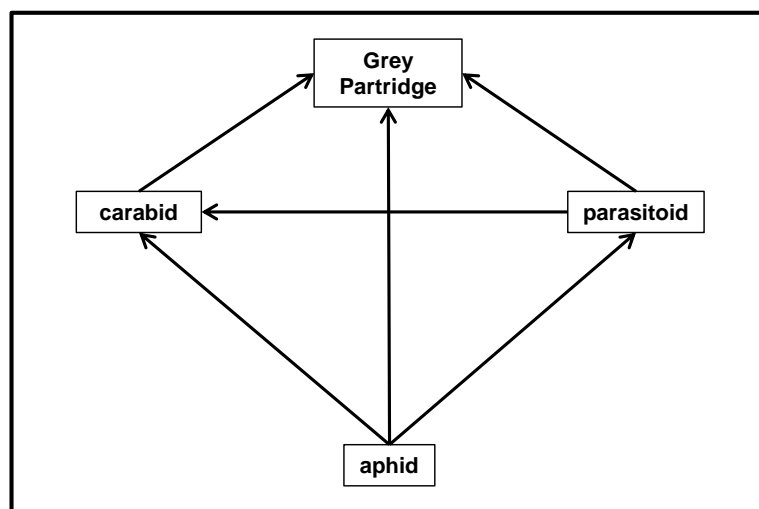

Figure 2. Food web diagram showing the interactions between the components of the four trophic levels represented in the model.

Grey partridge (*Perdix perdix*) populations have declined considerably in recent decades (Aebischer & Ewald, 2012); in response research efforts have identified the causes of this decline and driven the adoption by policy makers of AES that at least in part are hoped to act as conservation measures for this species (Aebischer & Ewald, 2012). Aphids provide an appropriate focus for pest control in this study as they are important pests of cereal crops, causing damage directly and also through the transmission of viruses such as potato virus Y and barley yellow dwarf virus. Carabids are introduced into the system as generalist predators with several species known to feed on cereal aphids while parasitoid wasps are a common biocontrol agent and another focus of conservation biocontrol strategies in Integrated Pest Management. Carabids consume parasitoid wasps when feeding on infected aphids, and both carabids and aphids are a significant component of the grey partridge diet.

2.6 Population dynamics

Stage-structure matrix population models were constructed to represent the local population dynamics of each species (Caswell, 2001). In this case, the demographic processes on which population size depends (i.e. survival, reproduction, and the transition between stages, plus the immigration and emigration of individuals that results from dispersal) are

represented by transitions between discrete life-cycle stages that take place in a series of discrete time-steps. Dispersal is an important element of the model as it links the, otherwise independent, local populations. Dispersal is assumed to take place on one or more occasion during the species' life-cycle. For each dispersal event, a stage and phase specific proportion of each local population disperses. These individuals leave a local population to be redistributed across the landscape according to species specific dispersal models (see Annex 1, section 7.5). The total number of individuals entering a local population at any given dispersal event is determined by summing the numbers that have dispersed to that population location from all possible source populations.

Trophic interactions are a key element of the model as they provide the mechanism by which trade-offs or synergies in the conservation of grey partridge and the regulation of aphids can occur. 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 influence of habitat on the dynamics of local populations is captured in a similar way by making one or more of the demographic transitions a function of habitat type.

In the absence of specific information on which to base the representation of habitat quality with respect to the four species, a simple dichotomous approach was adopted. In this, each habitat type (see Tables 1 and 2) was classified as either beneficial or not and the density independent survival rates adjusted to reflect this (see Annex 2). In addition, the habitat classification was used to drive active dispersal choices (see Annex 2) with habitat preferences being consistent with habitat quality. In addition, the AgBioscape system allows the use of pesticide to be simulated via the modification of survival rates (see Annex 3, section 9.2.5). However, pesticide use has not been incorporated here.

A full description of the models associated with the population processes is given in Annex 1.

2.7   Life-cycles

To build population projection matrices as outlined above requires the life-cycle of a population to be described and specified in terms of the stages present and the nature of the demographic transitions between them. Aphids have complex and varying life-cycles; they exhibit polymorphism and show interspecific variation in the type and timing of their development. Aphids may also have either one or two hosts, include sexual and asexual or just asexual generations in their life-cycles, and in the stage in which they overwinter. For the purpose of this study, we base the aphid life-cycle on the Grain aphid (*Sitobion avenae*), a species common to Scotland. The Grain aphid is monoecious, completing its life-cycle on cereals and grasses. The populations show a mix of holocyclic and anholocyclic forms, overwintering as eggs and viviparous females in proportions determined by climate. In spring, eggs hatch giving rise to fundatrix and then viviparous females. Several generations of wingless morphs then follow with winged forms being produced in late May and June when they disperse. Winged aphids continue to be produced and disperse amongst the crops and natural vegetation throughout the summer as a result of increasing population density and a reduction in food quality. In autumn, the life-cycle is completed with the migration of winged forms back to newly sown winter cereals or wild grasses present in the natural vegetation, where in the holocyclic case sexual reproduction follow the production of males and oviparous females.

The life-cycle of the parasitoid is based on a generalized braconid (Hymenoptera) life-cycle which 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.

Carabids are a diverse taxon with considerable variation in functional traits including diet, activity patterns, and life-cycles. An analysis of the functional traits of carabids inhabiting Scottish farmland identified seven functional groups (Cole *et al.*, 2002). For the purposes of this study we assumed the carabid species to be of group 6 (*sensu* Cole *et al.*, 2002), which is characterised by a generalist predatory diet and an annual life-cycle in which individuals overwinter as adults with subsequent breeding in spring followed by a single larval stage. The larvae pupate towards the end of the summer with adults emerging in autumn. *Bembidium tetracolum* and *Agonum muelleri* are both examples of this functional group which are commonly found in both crop and margin habitats of the Scottish arable ecosystem.

Grey partridge populations can be found in most arable systems where the open habitat provides suitable nesting habitat for these ground nesting birds, insects on which chicks feed, and seed and shoots for adult birds. During winter, the adult birds form territorial breeding pairs leading to the dispersal of young cocks in spring. This is followed by the main breeding season from April through to August during which time nesting takes place with nest sites ideally located in grassy areas. On average clutches of about 15 eggs are laid and hatch following and incubation period of 3 or 4 weeks. The chicks are nidifugous and feed on insects during which time they are brooded by both parent birds. During the summer and autumn the chicks develop but the family groups remain together as coveys only disperse in spring with the formation of breeding pairs.

The stage structures and transition matrices based on the generalised life-cycles as described are presented in Annex 1.

3. MODEL SIMULATIONS

3.1 Simulation conditions

3.1.1 *Preliminary simulations*

Preliminary simulations were performed under a wide range of conditions and the spatial and temporal patterns of population density examined to provide a qualitative assessment of the behaviour of the model. This included descriptions of the seasonal variation in the population densities and the patterns of spatial heterogeneity to illustrate the biological plausibility of the model.

3.1.2 *Simulation experiments*

A subsequent series of simulation experiments were conducted to explore the impact of land use patterns on the population dynamics of the system, including potential trade-offs or synergies between conservation and pest biocontrol. The model represents four habitat management measures that are supported as agri-environment schemes under the Land Managers Options of the Scottish Rural Development Programme (2007-2013). The effect of deploying grass margins was tested while other habitat management measures remained unchanged.

Examination of the preliminary simulations indicated that, for grey partridge, transient dynamics dominated over several decades following the introduction of a change to the land management. This implies that the effectiveness of a newly introduced land management option cannot be judged in terms of an equilibrium state. To accommodate this in the

simulation experiment, each simulation tested a fixed sequence of three land management options or AES treatments in which grass margins were deployed in either 5%, 10%, or 15% of fields. The order in which these treatments were deployed was fixed, i.e. 10%, 5%, 15%, 10%, 15%, 5%, 10%, and was selected to simulate a range of transitions between treatments. Each AES treatment was run over intervals of 50 years giving a total duration of 350 years for each simulation.

To examine the influence of food-web structure on the potential trade-offs or synergies in the response of populations these scenarios were repeated but assuming three simplified food-web structures that resulted from: 1) the exclusion of grey partridge, 2) exclusion of carabids, and 3) exclusion of parasitoids.

All simulations were based on a fixed set of parameter values for landscape, population dynamic and dispersal models (Annex 2) considered generally representative of the system under consideration. The landscape in this baseline scenario was predominantly arable subject to a cereal rotation with broad-leaf break crop, with the addition of both pasture and woodland (Table 3). Hedgerows, areas of bird seed mix, uncropped grass or flowering margins, and conservation headlands were included in the landscape in quantities based on an analysis of national adoption figures of the Land Managers Options of the Scottish Rural Development Programme provided by SNH.

Table 3. Land use conditions used as a baseline scenario for all simulations. The figures for agri-environment habitat use were based on an analysis of national adoption figures of the Land Managers Options of the Scottish Rural Development Programme provided by SNH. (*Arable = cereal crops + broad-leaf crops)

Land use	Quantity
Landscape structure	
Landscape extent	2km x 2km
Average land parcel size	12.5 ha
Landscape composition	
Cereal crop (% area)	55%
Broad-leaf crop (% area)	10%
Grass ley (% area)	30%
Wood (% area)	5%
Conservation headland (% of arable* fields)	5%
Grass margin (% of arable fields)	10%
Wildbird seed mix plot (% of arable fields)	1.5%
Hedgerow (length)	4km

3.2   Simulation results

3.2.1   Seasonal dynamics

An example of the seasonal dynamics for aphids, parasitoids, carabids and grey partridge are presented in Figure 3. These patterns were found to be highly consistent between replicate simulations and were also qualitatively similar even when simulations were run under a wide range of scenarios and parameterisations as was the case of the preliminary simulation exercise.

The aphid populations showed a simple unimodal pattern in seasonal density with peak density occurring during the growing season for the arable crops. This pattern is consistent with the dynamics of *Sitobion avenea* as described from diverse geographic regions (e.g. Schotzko & Bosque-Pérez, 2000; Chapin *et al.*, 2001; Buriro *et al.*, 2006). The parasitoid dynamics show a similar pattern, though the peak falls later in the growing season. This is consistent with observed seasonal patterns in aphid and parasitoid dynamics including those of grain aphid and the parasitoid *Aphidius rhopalosiphi* (Legrand *et al.*, 2004) which often exhibit a sequential peak in aphid and then parasitoid populations. Further simulations were conducted, excluding carabid and grey partridge populations, to explore the behaviour of the model with respect to the synchronisation of parasitoid and aphid populations. These established that the seasonal variation in regional populations was driven by predator (parasitoid) – prey dynamics taking place within local populations and were highly consistent with both experimental and modelling results reported by Snyder & Ives (2003).

Carabid and grey partridge populations showed distinctive seasonal patterns that are consistent with the general phenology of a spring breeding univoltine species. The patterns are consistent with observations on the activity patterns of adult carabids in arable systems (e.g. Thomas *et al.*, 2001) and with previous models of grey partridge phenology (e.g. Topping *et al.*, 2010).

3.2.2 Spatial patterns

Figure 4 shows a sequence of outputs that the model produces to screen throughout a simulation. Each panel shows the simulated landscape, i.e. the spatial distribution of habitat types, and the spatial variation in population density at various time points, in this case in November (A), June (B) and September (C). The changes over time are consistent with the seasonal patterns described above, winter populations are dominated by carabids and adult grey partridge, with aphid and grey partridge chick density peaking in summer and declines thereafter as parasitoid density increases and adult grey partridge and carabid populations rise again in autumn.

The results also demonstrate the effect of trophic interactions between the species. Clearest amongst these are the inverse relationships in the density of parasitoids and aphids in June and September, and the inverse relationship between the density of grey partridge chicks and carabids in June (Fig. 4). Though these are the clearest associations, a reduction in parasitoid density in areas of high chick density was also observed on occasion. The inverse nature of these relationships indicates that top-down regulation may be an important feature of this system. However, a strong bottom-up response of parasitoids to aphid density is also evident, albeit out of phase (compare pest – aphid panel in Fig. 4B with natural enemy – parasitoid panel in Fig. 4C).

A comparison of the spatial variation in population density with the patterns of land use is also indicative of the importance of habitat quality in driving this system. For example, the aggregation by grey partridges in hedgerow habitats (dark green) and grass margins (orange), is evident during the summer, consistent with the behaviour of grey partridge in nature (Fig. 4). At the same time, the response of aphid numbers to cereal crops (yellow) can also be seen (Fig. 4).

3.2.3 Land use pattern

The response of populations to the land use patterns is considered further in the simulation experiment designed to test the effect of grass margins. Simulations complete under constant conditions showed a high degree of consistency in terms of the response by populations to changing habitat treatment (e.g. Fig. 5).

Grey partridge populations were highly sensitive to changing margin treatments, responding positively to the introduction of grass margins. The response was not immediate but took several decades to stabilise. In the case of 5% margin treatments, grey partridge populations consistently fell to below 50 birds km^{-2} in comparison to densities that reached well in excess of 100 birds km^{-2} when margins were increased to 15% (Fig. 5). A preliminary analysis estimated the density in June to be an average of 63.8, 127.9, and 176.4 individuals km^{-2} at 5%, 10% and 15% grass margins respectively, all with a 95% confidence interval of ± 6.8. The preliminary analysis found these differences to be highly significantly different. Both the September densities and full year average densities exhibited patterns that were entirely consistent with these (Fig. 7, 9).

Carabid populations also show a significant response to the proportion of fields in the landscape supporting grass margins (Fig. 5) However, the response was negative with the June densities decreasing on average from 0.63, to 0.620 and 0.61 (±0.0018 95% C.I.) individuals m^{-2} as grass margins increased from 5 to 10, and 15%. Again these results were supported by figures for the September and yearly average densities (Fig 7, 9). Closer examination of the long-term population trends suggest that the carabid population density is negatively correlated with the density of grey partridge populations (Fig. 5, 7, 9). This was confirmed by a preliminary analysis of data from Landscape 1 (Fig. 5) which showed a significant linear response of carabid to grey partridge in a manner consistent of top-down regulation. The influence of this was demonstrated in a subsequent simulation in which grey partridge were excluded and the significant effect of grass margin on carabid density was no longer observed.

The long-term trends in aphid and parasitoid density exhibit similar patterns to one another with large inter-annual variation masking any grass margin effect (Fig. 6, 8, 9). However, in June the regional aphid population showed a significant increase in response to the introduction of grass margins with density increasing from 396.4 to 404.1 and 409.1 (±1.1 95% C.I.) individuals m^{-2} as the margin percentage increased from 5% to 15%. There was no significant effect of margins on aphid populations in September while the parasitoid population showed no response in June or September, although the yearly average density showed a significant increase in response to the introduction of grass margins (16.1 individuals m^{-2} at 5%, 16.3 at 10%, and 16.5 at 15 % with 95% confidence interval of ±0.2).

The extent to which the carabid or parasitoid populations are acting as effective biocontrol agents in this system is not clear. There is a significant negative relationship between aphid density and carabid density and although the direction of the relationship between aphid and parasitoid density varies with season, it is negative when yearly averages are considered. These results suggest that aphid populations are being regulated top-down by both carabids and parasitoids, the effect of which can be seen at the local scale in the eradication of local aphid populations (Fig. 4). Despite this, the introduction of grass margins appears to have little benefit in promoting pest regulation and so is of little value as a conservation biocontrol strategy in this model system. In fact the only significant effect of grass margins was to increase aphid population densities. This counterproductive effect may explained simply by the fact that the grass margins are also considered beneficial to the cereal aphids, however, it is unclear to what extent the failure of natural enemies to over-ride this effect is due to weak, bottom-up conservation of the carabids or parasitoids or top-down constraints on them by intra-guild predation (carabids eating parasitoids) or 4th trophic level predators (grey partridge).

Insight into the effect of food-web structure was gained by excluding one or other species from the food-web and re-running the simulations. For example, on the removal of parasitoids, a trophic cascade is observed in which top-down regulation by partridges suppresses carabid populations allowing the aphid populations to benefit (Fig. 10). From this

it is evident that simple linear food-chain exemplified by the aphid-carabid-partridge system has the potential to generate trade-offs between conservation and pest regulation. However, despite the potential for a damaging trade-off, it was of little consequence in the current system, having only a slight impact on aphid density. This highlights the importance of understanding the relative strength of the competing effects when considering the influence of potential trade-offs. In contrast, no trade-off was observed in the absence of carabids as parasitoids continued to show top-down regulation of aphids regardless of partridge density. Comparing the behaviour of these apparently similar systems highlights the importance of a detailed understanding of the trophic interactions in predicting the outcome of trade-offs.
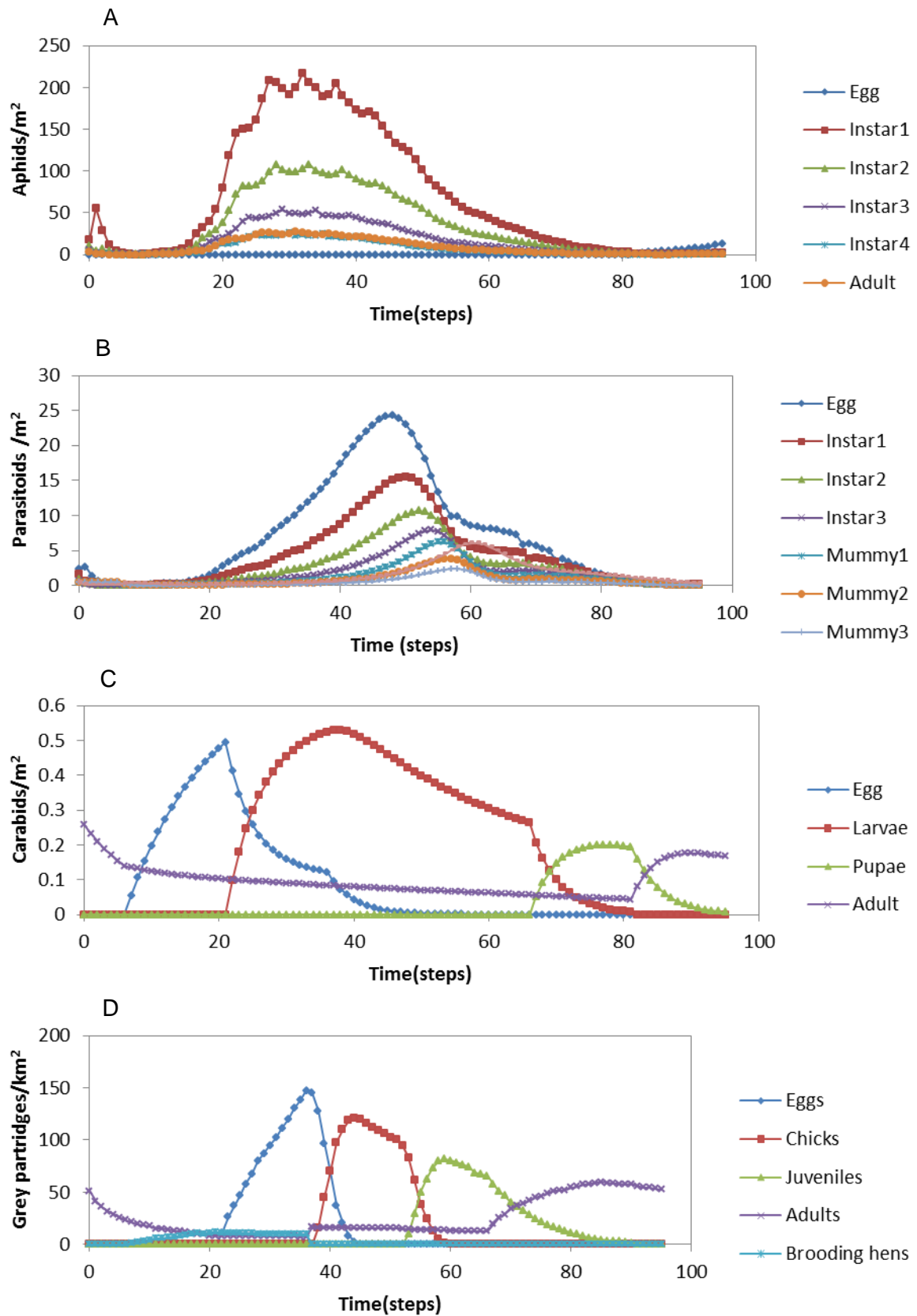
Figure 3. Seasonal variation in the regional population densities for (A) aphids, (B) parasitoids, (C) carabids, and (D) grey partridge.

A

B
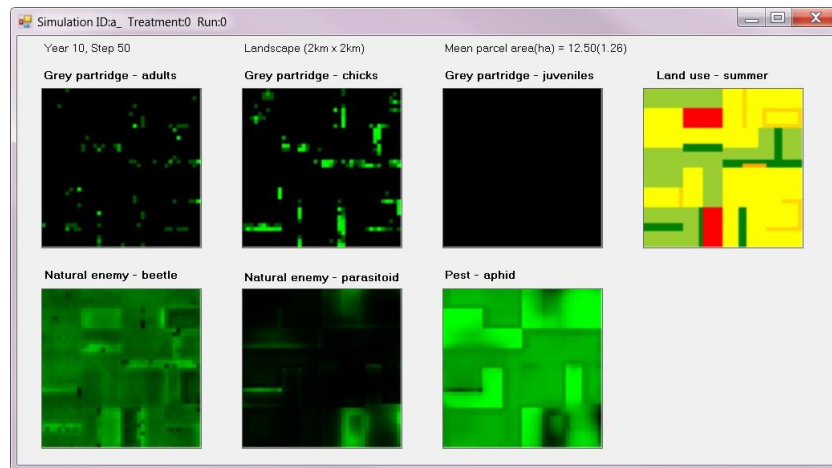
C
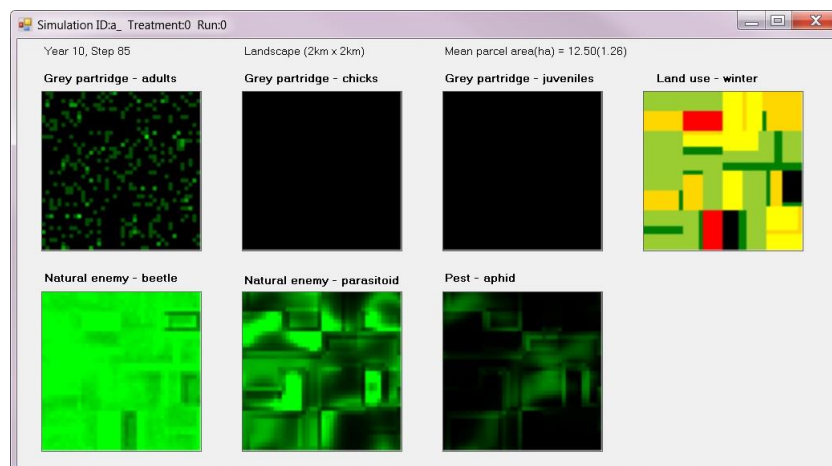
Figure 4. Outputs from an example simulation showing the spatial patterns in land use and population density in (A) November, (B) June and (C) September. Land use panels include wheat crops (yellow), grass ley (light green), fallow (black), woodland (red), agri-environment prescription habitats: grass margins (orange), and hedgerow (dark green).
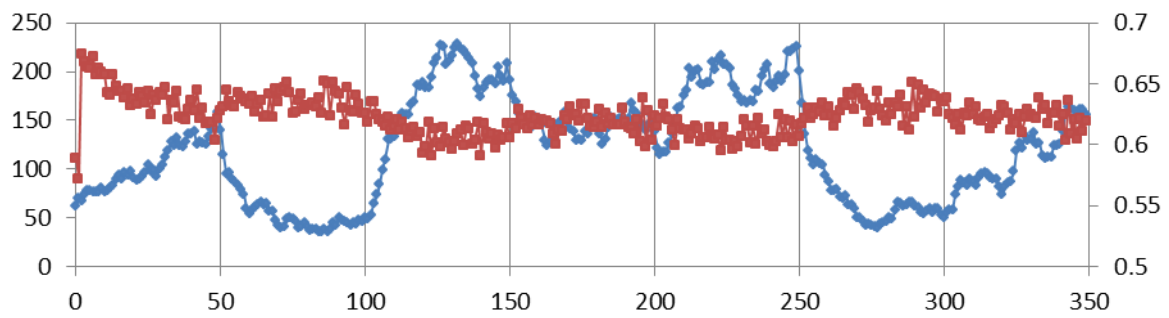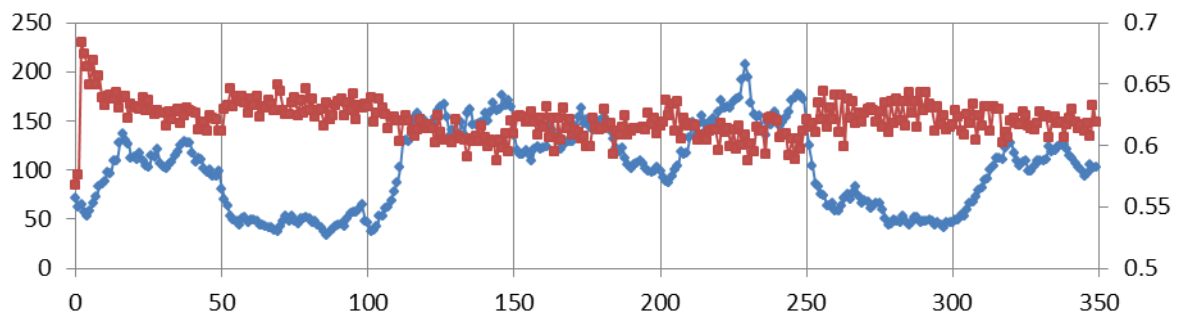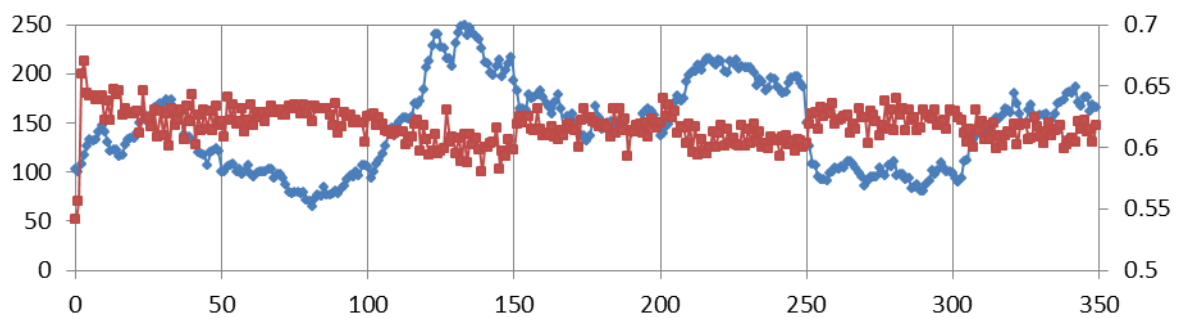
Figure 5. Variation in the June population density of carabids (red line, square symbol; y-axis right, carabids m^{-2}) and grey partridge (blue line, diamond symbol; y-axis left, grey partridge km^{-2}) over a 350 year duration in 4 replicate landscapes undergoing a sequence of margin treatments in which the proportion of arable fields with margins varies between 5%, 10% and 15% and were deployed for periods of 50 years duration.

15

Landscape 1

Lansdscape 2

Landscape 3

Landscape 4

10%   5%   15%   10%   15%   5%   10%
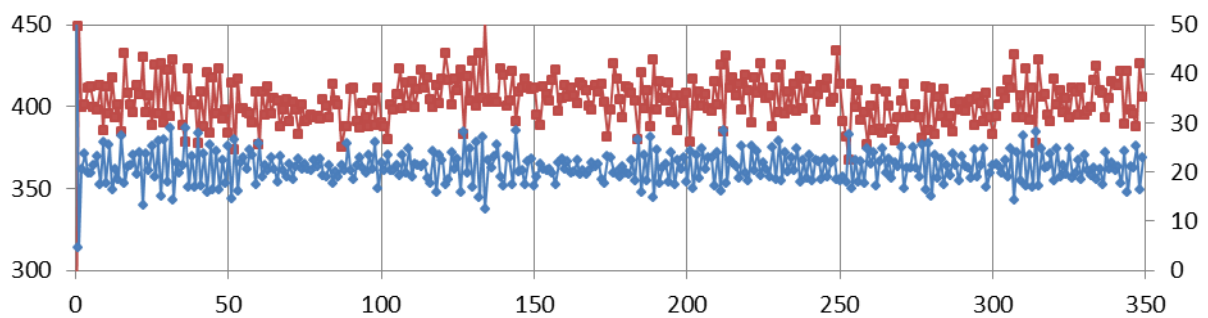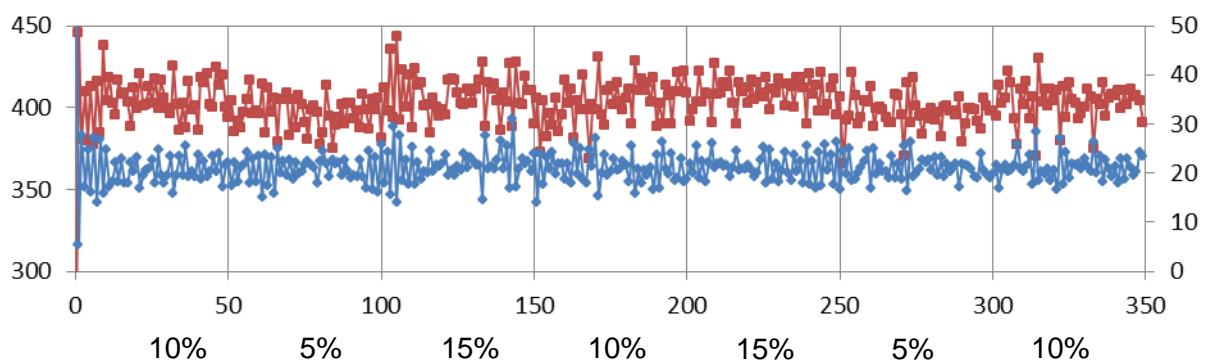
Figure 6. Variation in the June population density of aphid (red line, square symbol; y-axis left, aphids m^{-2}) and parasitoid (blue line, diamond symbol; y-axis right, parasitoids m^{-2}) over a 350 year duration in 4 replicate landscapes undergoing a sequence of margin treatments in which the proportion of arable fields with margins varies between 5%, 10% and 15% and were deployed for periods of 50 years duration.

Landscape 1

Landscape 2

Landscape 3

Landscape 4

10%   5%   15%   10%   15%   5%   10%
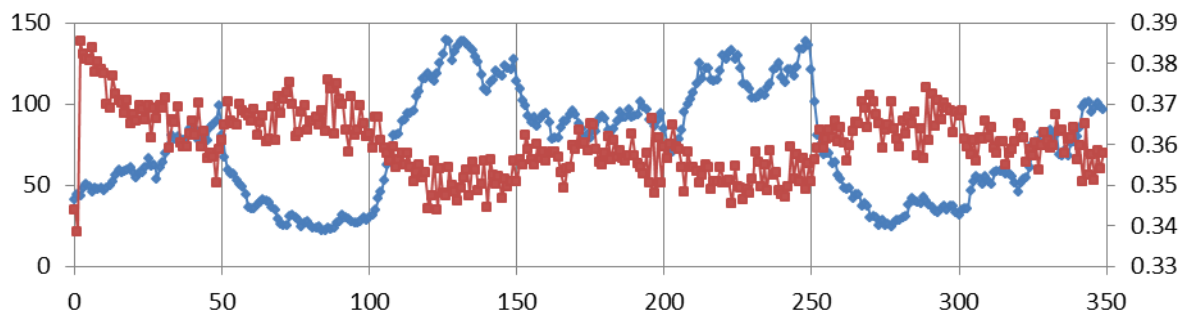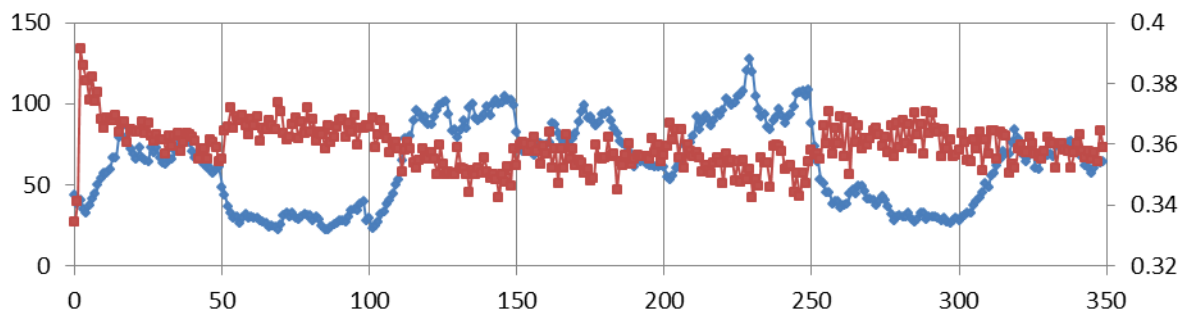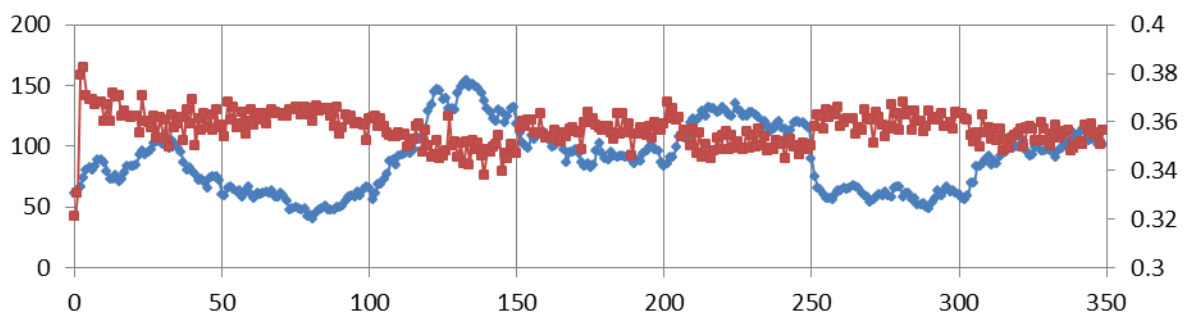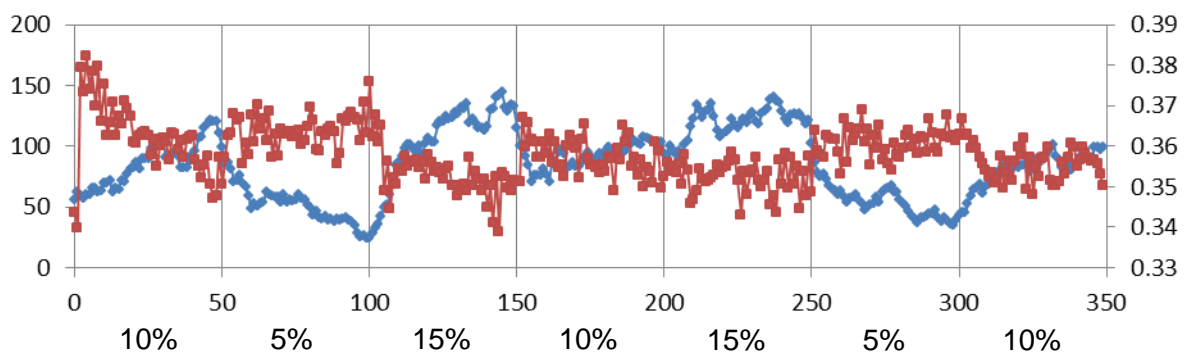
Figure 7. Variation in the September regional population density of carabids (red line, square symbol; y-axis right, m^{-2}) and grey partridge (blue line, diamond symbol, y-axis left, grey partridge km^{-2}) over a 350 year duration (x-axis) in 4 replicate landscapes undergoing a sequence of margin treatments in which the proportion of arable fields with margins varies between 5%, 10% and 15% and were deployed for periods of 50 years duration.

Landscape 1

Landscape 2

Landscape 3

Landscape 4

10%   5%   15%   10%   15%   5%   10%
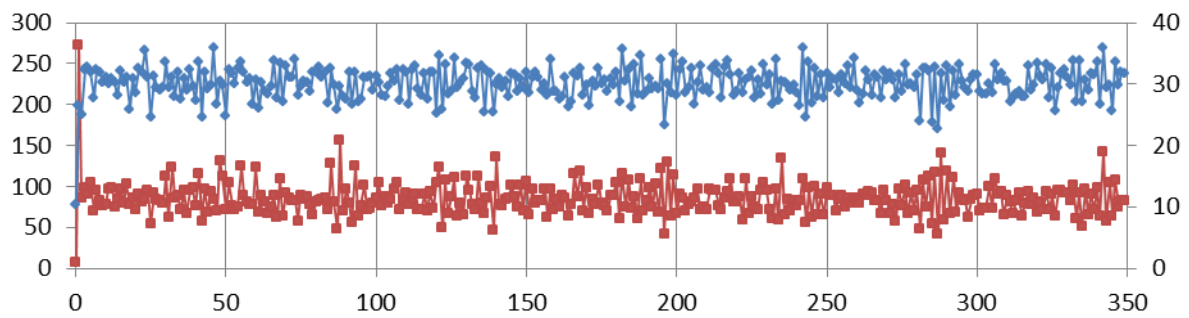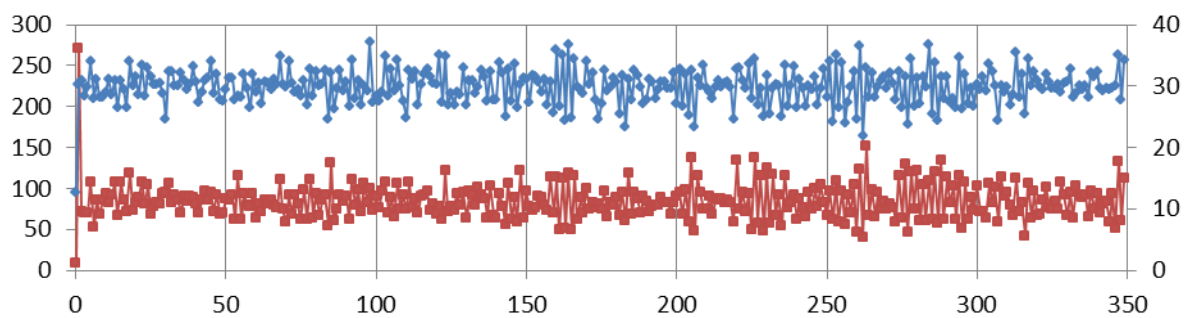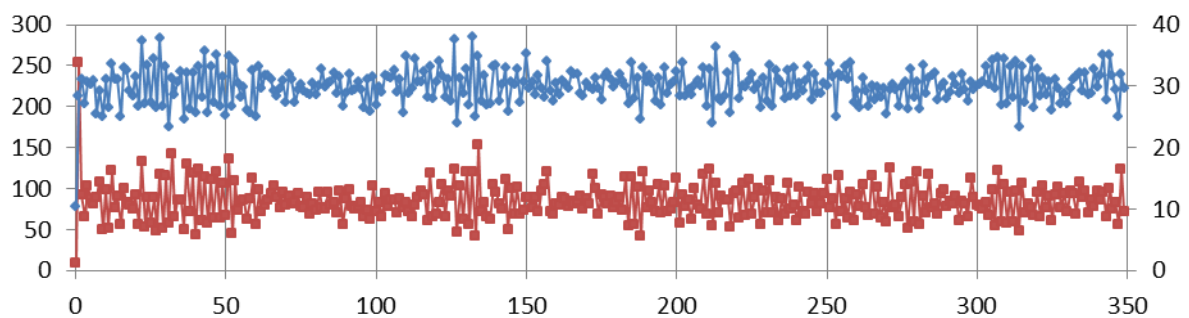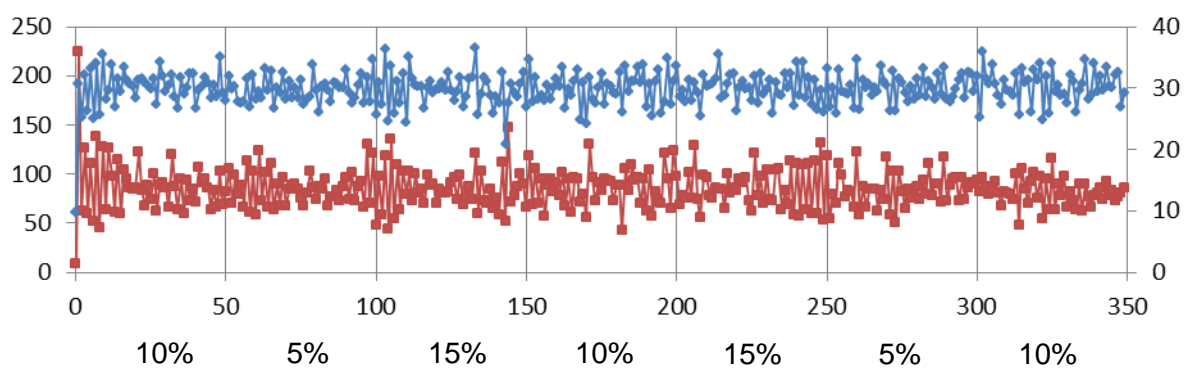
Figure 8. Variation in the June regional population density of aphid (red line, square symbol; y-axis left, aphids m^{-2}) and parasitoid (blue line, diamond symbol; y-axis right, parasitoid m^{-2}) over a 350 year duration (x-axis) in 4 replicate landscapes undergoing a sequence of margin treatments in which the proportion of arable fields with margins varies between 5%, 10% and 15% and were deployed for periods of 50 years duration.
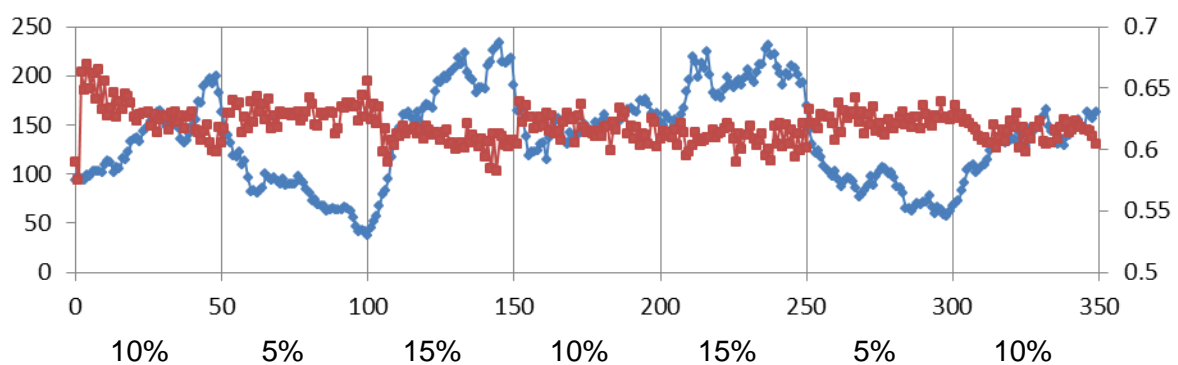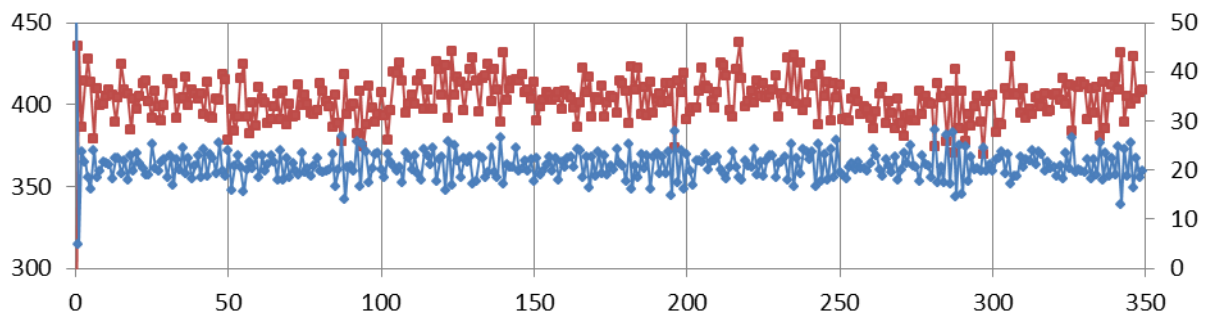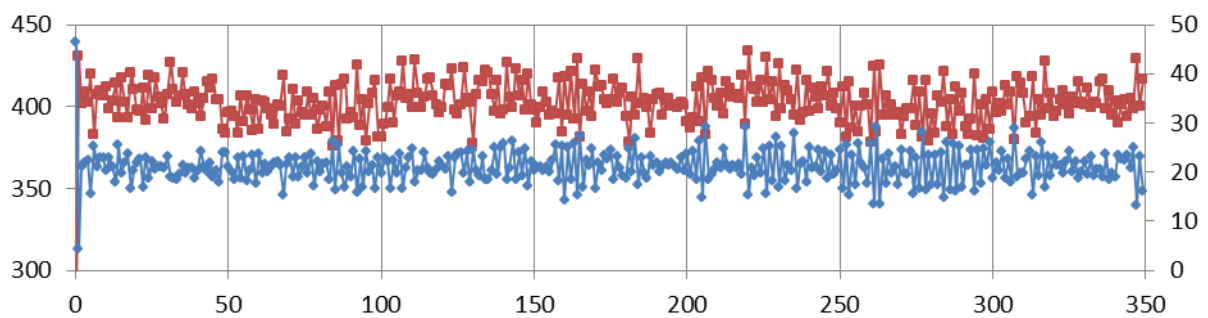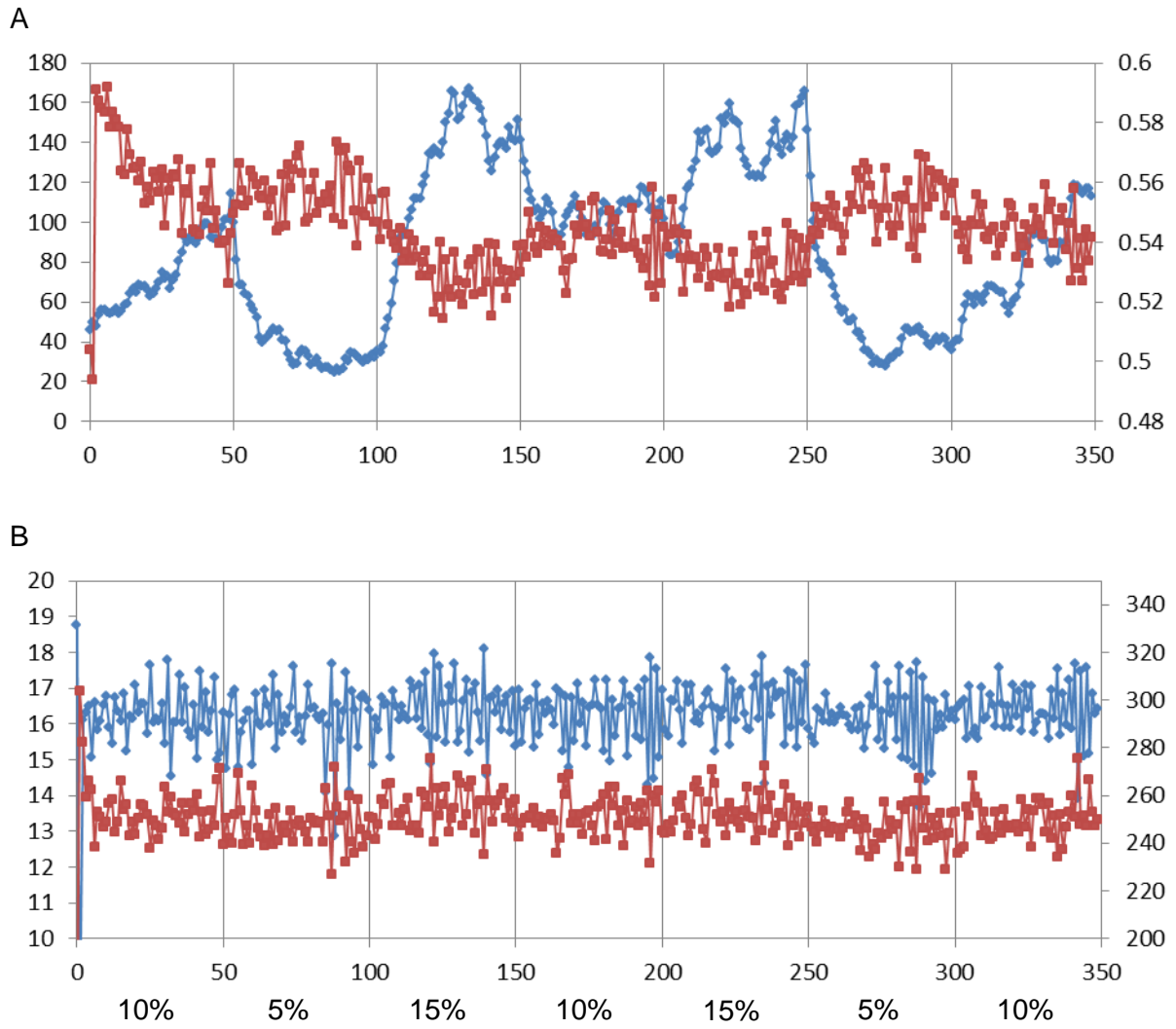
Figure 9. Variation in the average annual population density of (A) carabids (red line, square symbol; y-axis right, carabids m⁻²) and grey partridge (blue line, diamond symbol; y-axis left, grey partridge km⁻²) and (B) aphids (red line, square symbol; y-axis right, aphids m⁻²) and parasitoids (blue line, diamond symbol; y-axis left, parasitoids m⁻²) over a 350 year duration (x-axis) in Landscape 1 undergoing a sequence of margin treatments in which the proportion of arable fields with margins varies between 5%, 10% and 15%.

A

B
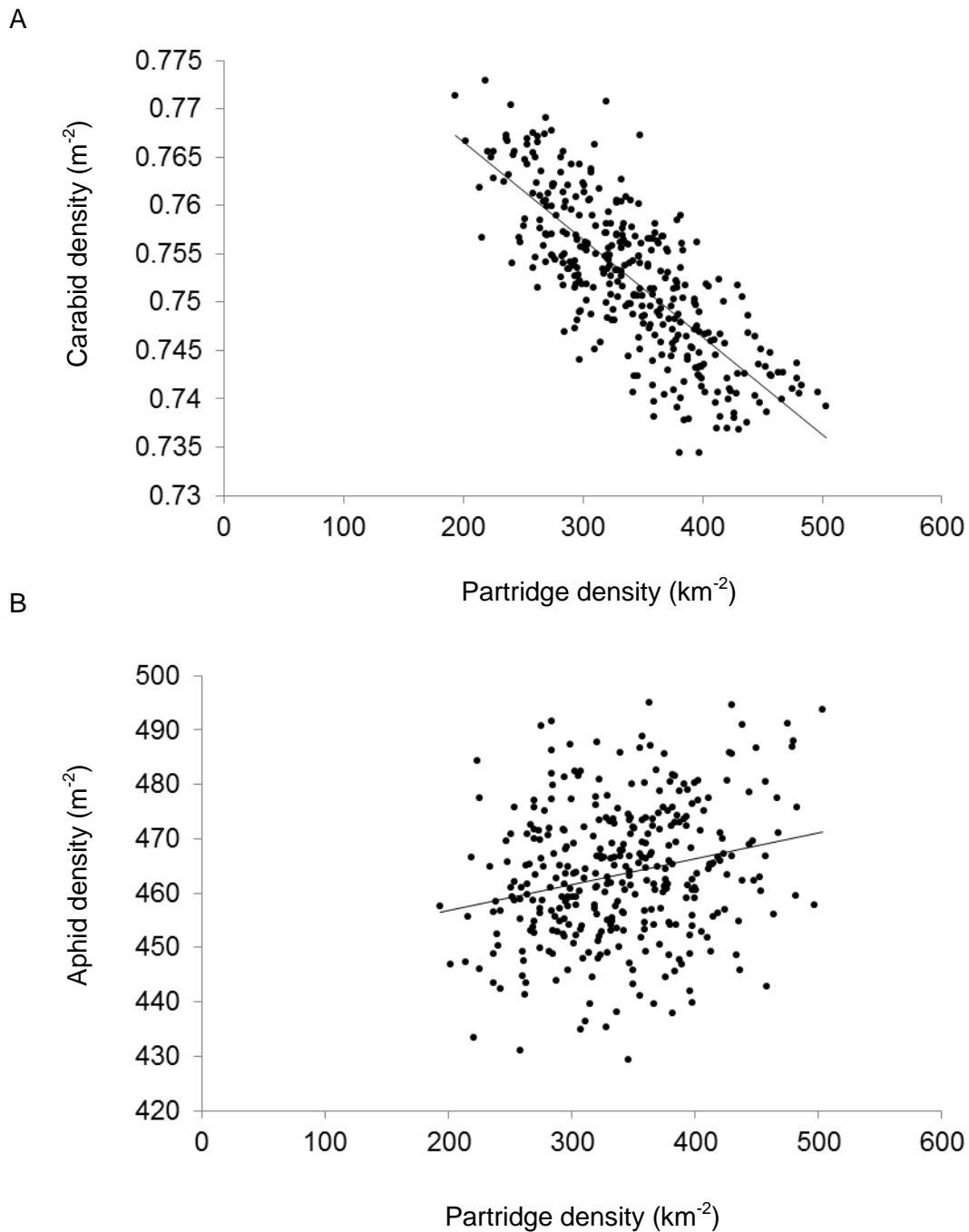
Figure 10. Example from one simulation of the response of the average annual density of carabids (A) and aphids (B) to the average annual population density of grey partridge following removal of parasitoids from the food-web. Both relationships are statistically significant: (A) $F_{(1, 343)} = 504.64$, $P < 2.2 \times 10^{-16}$; (B) $F_{(1, 343)} = 19.99$, $P = 1.06 \times 10^{-5}$. Data exclude first five years of simulation.

4. CONCLUSIONS

The model and associated simulation results described in this report constitute the findings from an exploratory research exercise conducted over 3 months. In this time, substantial progress was made in developing a working multi-trophic, spatially explicit population model and demonstrating its effective use. The model effectively simulated the dynamics of a multi-trophic system on landscapes with complex, spatio-temporal habitat patterns and was used to explore the behaviour of the system at a scale that would be impossible by empirical study. On this basis it can be concluded that the approach adopted has substantial potential for exploring trade-offs and synergies arising from the design and management of sustainable landscapes.

The rapid development of the model was facilitated by the use of the AgBioscape modelling framework recently developed at the James Hutton Institute. The model simulations produced results that compare favourably with components of the system where these were known, indicating that the behaviour of the model is biologically credible. In particular it establishes the capacity of the modelling approach to accommodate multi-scalar systems. This is an important result in the context of multi-trophic modelling.

The simulation results illustrate the value of the modelling approach in exploring the behaviour of an ecosystem where the complexity and the spatial and temporal scale prevent empirical studies from being effective. For example, the simulations revealed a strong response of regional populations of a farmland bird modelled on the grey partridge, to the introduction of an agri-environment scheme but also that the full extent of this takes several decades to establish. Furthermore, the simulations revealed a potential trade-off between the conservation of the farmland bird populations and the control of crop pests as a result of top-down regulation by birds on a generalist predator and natural enemy of the crop pest.

However, this proved to be of little consequence in the model system due to the relatively weak control exerted by the natural enemy. Furthermore, trade-offs between conservation and pest regulation were not evident in the presence of the more complex trophic interactions that result from the introduction of an omnivorous tertiary consumer and a second natural enemy and intra-guild predator. By incorporating complex food-web behaviour, the model goes some way to accommodating the reality of food-webs and influence of features like omnivory and intra-guild predation that are suspected of generating unexpected outcomes in habitat management strategies. However, consideration of potentially important food-web characteristics such as size and complexity, i.e. connectance, was outside the scope of this preliminary study as the ability of the model to handle species rich systems has not been fully tested, though it is expected that large food-webs of up to 200 species could be simulated where the number of species interactions is limited.

In the model, survival rates are modified to represent the differences in habitat quality experienced by organisms. These can be manipulated to create habitat profiles which represent differential responses between species, life-cycle stage and over time. In this study, a set of plausible habitat quality profiles were assumed, including that for grass margins which provided the basis for the simulated AES. However, habitat quality profiles are not well established and many equally plausible alternative patterns were not tested here. Therefore, there is both scope and need to explore the sensitivity of our findings to assumptions about habitat quality.

The simulations described in this report give rise to nearly 8 billion data points per simulation. This level of detail, combined with the richness in model behaviour that arises from its multi-trophic and multi-scalar properties, provides substantial opportunities to further investigate the behaviour of the model system and so better understand the response of populations to land use and its management. On this basis, it is clear that further testing of

the model behaviour is required before we can fully understand and interpret the observed patterns. This should extend beyond the exploration of habitat quality profiles and food-web structures identified above to include, for example, consideration of spatial processes and the interactions between landscape configuration and dispersal behaviour.

In addition to the pursuit of a strategic understanding of the type described above, we believe consideration should be given to targeted investigations of a specific system or systems that would benefit management or policy advice. The development of an example application will be an important test of the potential to develop a model-based impact assessment tool capable of predicting the effectiveness and impact of actual or proposed land management strategies on specific, i.e. real rather than archetypal, food webs and the ES they provide.

Finally, to guide the model-based approach described in this report requires a more comprehensive understanding of the nature of arable communities and food-webs, particularly those supported by non-crop habitats; only by assessing the common features of these, will we be able to develop models designed to address questions appropriate to these systems.

5. RECOMMENDATIONS

As a proof of concept this study has established the viability of the modelling approach and highlighted its potential to gain substantial insight into the multi-functionality of land use management and the trade-offs that may follow. Drawing on the conclusions of this study, we recommend that 4 research activities are adopted as steps in achieving this potential:

1. An extended analysis of the existing model to provide strategic insight into multi-trophic responses to land management.

Further analysis of the model will capitalise on the existing research. It will provide a cost effective approach to understanding the competing demands within arable food webs and the impact of these on achieving sustainability objectives of future farmland management strategies.

2. An assessment of the model's capacity to simulate food-webs of increasing size and complexity, if necessary developing AgBioscape to include a computationally efficient solution.

The results of this study demonstrate clearly the importance of food web structure in determining the outcome of land management options. However, natural systems are substantially more diverse, with greater trophic complexity than that considered here. To address the impact of characteristics associated with large food webs such as redundancy and connectance, it will be necessary to simulate food webs with increasing size and complexity.

3. Application of the modelling approach to the development of a decision support tool for use in the design and assessment of land management options, including AES.

The general nature of the model developed in the present study limits its capacity to predict outcomes for specific farmland systems. The potential to build decision support tools capable of assisting land managers and policy makers in identifying effective management options should be explored. The development of a system-specific model capable of capturing key features of an example farmland system will be an important test of the potential to develop these tools.

4. A review and synthesis of community composition, food-web structure and the ecosystem functions of the Scottish arable system with a focus on non-crop habitats.

A better understanding of the nature of farmland communities and food webs is necessary to support the application of the model-based findings to the practical management of real farmland systems and also to ensure the development of appropriate models, capable of capturing the important characteristics of farmland systems.

Of these, activity 1 should be pursued as a priority as it provides a cost-effective way to significantly extend our understanding of the impact of land management on ecosystem services in arable systems. Activity 2 would make a useful contribution if incorporated into such a strategic study but is unlikely to yield much value if pursued in isolation. The development of a system specific model in activity 3 would be a challenging exercise, most notably in terms of models parameterisation. However, this activity is an essential step if the approach described in this report is to be extended with the objective of contributing to the policy and management decisions for specific, key systems. Finally, activity 4 will be of considerable value in directing the overall research effort, informing model development and application, while also providing an overview of this important component of Scotland's biodiversity.

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ANNEX 1: LOCAL POPULATION DYNAMIC MODELS

A matrix projection approach is taken to modelling the local population dynamics, representing the stage-specific demographics of the species to be modelled. The matrix projection models are constructed as per Caswell (2001), using the general framework for the model as follows,

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

Here the state vector $\mathbf{n}(t)$ is the density of individuals in each of the stage 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 θ. The effect of immigration as a result of dispersal from other local populations is captured in the model by the addition of the vector $\mathbf{m}(t)$ which gives the sum of the individuals of each stage or age entering the population from other local populations.

A1.1 Stage structures

From the descriptions of the life-cycles given in section 2.7 appropriate life-cycle stages were identified (Table A1.1).

Table A1.1. The stage structure for each of the model species, describing the relationship between the populations density vectors, the life-cycle stages, and the stage numbers as used in indexing of stage-specific model terms.

Stage number	Aphid		Carabid		Parasitoid		Grey partridge	
1	n_{a1}	Egg	n_{c1}	Egg	n_{p1}	Egg	n_{b1}	Egg
2	n_{a2}	Instar 1	n_{c2}	Larvae	n_{p2}	Instar 1	n_{b2}	Chick
3	n_{a3}	Instar 2	n_{c3}	Pupae	n_{p3}	Instar 2	n_{b3}	Juvenile
4	n_{a4}	Instar 3	n_{c6}	Adult	n_{p4}	Instar 3	n_{b4}	Adult
5	n_{a5}	Instar 4			n_{p5}	Mummy 1	n_{b5}	Brooding hen
6	n_{a6}	Adult			n_{p6}	Mummy 2		
7					n_{p7}	Mummy 3		
8					n_{p8}	Adult		

A1.2 Projection matrices

As stated above the transitions between stages over time are represented by the projection matrix $\mathbf{A}$. The form of the projection matrix is dependent on the length of time over which the population is being projected relative to the generation time, i.e. the length of the life-cycle. It is possible to capture a complete life-cycle with a single matrix, in which case the transition interval is equal to one generation. However, it is often beneficial to decompose the life-cycle into a series of phases with transitions between these represented by its own projection matrix, in which case the full life-cycle is represented by multiplying the matrices in correct order (see Annex 3, section 9.2.3).

In this model, the year has been broken down into a number of time periods and the life-cycles of each species represented by a series of 7 phases. However, the phases have been further subdivided so that the projection interval matches the aphid stage duration and consequently each projection corresponds to the transition of individuals from one stage to the next. Seasonal differences in the rate of aphid development are approximated by setting the projection interval to 2 days from April to September and to 1 month from October to March. This gives rise to a sequence of 96 transitions (Table A1.2) so that the annual

projection matrix is decomposed as follows: $\mathbf{A} = \mathbf{B_{96}} \ldots \mathbf{B_2} \mathbf{B_1}$. The same duration and timing of transitions is applied to parasitoid, carabid and grey partridge in order to ensure the populations are synchronized.

Table A1.2. The duration and timing of stage transitions applied to the matrix projection models for aphid, parasitoid, carabid and grey partridge populations.

Phase	Duration (months)	Month	Number of transitions	Step number	Projection interval (days)
1	6	October - March	6	0-6	31
2	1	April	15	7-21	2
3	1	May	15	22-36	2
4	1	June	15	37-51	2
5	1	July	15	52-66	2
6	1	August	15	67-81	2
7	1	September	15	82-96	2

Within each phase the projection matrix is fixed so that the same matrix is applied for each transition of a phase. This gives rise to a total seven, potentially unique, phase specific projection matrices.

In the case of aphids, a summer (April - September), $\mathbf{B_{a,summer}}$, and winter projection matrix, $\mathbf{B_{a,winter}}$, is specified, i.e.

$$\mathbf{B}_{a,summer} = \begin{bmatrix} 0 & 0 & 0 & 0 & 0 & 0 \\ s_{s,1} & 0 & 0 & 0 & 0 & f_s \\ 0 & s_{s,2} & 0 & 0 & 0 & 0 \\ 0 & 0 & s_{s,3} & 0 & 0 & 0 \\ 0 & 0 & 0 & s_{s,4} & 0 & 0 \\ 0 & 0 & 0 & 0 & s_{s,5} & (1-d_s)s_{s,6} \end{bmatrix}$$

$$\mathbf{B}_{a,winter} = \begin{bmatrix} (1-p)s_{s,1} & 0 & 0 & 0 & 0 & f_w \\ ps_{s,1} & (1-p)s_{w,2} & 0 & 0 & 0 & 0 \\ 0 & ps_{w,2} & (1-p)s_{w,3} & 0 & 0 & 0 \\ 0 & 0 & ps_{w,3} & (1-p)s_{w,4} & 0 & 0 \\ 0 & 0 & 0 & ps_{w,4} & (1-p)s_{w,5} & 0 \\ 0 & 0 & 0 & 0 & ps_{w,5} & (1-d_w)s_{w,6} \end{bmatrix}$$

Here the vital rates considered are stage specific survival, $s_{s,1-6}$ and $s_{w,1-6}$, fecundity, development, and dispersal. Though structurally similar, the two transition matrices differ with respect to the treatment of fecundity where f_s specifically refers to parthenogenetic reproduction which gives rise directly to instar 1 individuals during the summer phases, and f_w which refers to sexual reproduction giving rise to eggs during winter phases. The indexing of the survival and dispersal terms by s and w, also represents seasonal

differences. Furthermore, in summer, all surviving individuals within a stage develop into the subsequent stage compared to a fraction, p, that develop during each winter transition.

Aphid survival depends on season, and habitat as well as being stage-specific. It includes density-independent and density-dependent components, and also the effect of parasitism and predation, i.e.

$$s_i = z_i \times \frac{1}{\left(1 + k\left(\sum_{j=1}^{6} n_{aj}(t) + \sum_{j=1}^{4} n_{pj}(t)\right)\right)} \times 1 - c_{parasit} \times 1 - c_{carabid} \times 1 - c_{partridge}$$

Here the survival of the ith stage is given by the product of density-independent survival (z_i), density-dependent survival which is a function of parasitized ($\sum_{j=1}^{4} n_{pj}(t)$) and non-parasitized larvae ($\sum_{j=1}^{6} n_{aj}(t)$), and the parasitism, $c_{parasit}$, and predation rates, $c_{carabid}$ and $c_{partridge}$. The seasonal subscript has been suppressed for ease. The parameters are presented in Table A2.2 and aphid habitat preferences in Table A2.6.

The form of the parasitoid transition matrix follows that of the aphids. Again we distinguish between transitions taking place during the summer, $\mathbf{B}_{p,s}$ and winter, $\mathbf{B}_{p,w}$, i.e.

$$\mathbf{B}_{p,s}\begin{bmatrix} 0 & 0 & 0 & 0 & 0 & 0 & 0 & f_s \\ s_{s,1} & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & s_{s,2} & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & s_{s,3} & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & s_{s,4} & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & s_{s,5} & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & s_{s,6} & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & s_{s,7} & (1-d_s)s_{s,8} \end{bmatrix}$$

$$\mathbf{B}_{p,w}\begin{bmatrix} (1-p)s_{w,1} & 0 & 0 & 0 & 0 & 0 & 0 & f_w \\ ps_{w,1} & (1-p)s_{w,2} & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & ps_{w,2} & (1-p)s_{w,3} & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & ps_{w,3} & (1-p)s_{w,4} & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & ps_{w,4} & (1-p)s_{w,5} & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & ps_{w,5} & (1-p)s_{w,6} & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & ps_{w,6} & (1-p)s_{w,7} & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & ps_{w,7} & (1-d_w)s_{w,8} \end{bmatrix}$$

In this case the matrices are structurally similar, though seasonal differences in survival, dispersal, and rates of reproduction are assumed. As for aphids, all surviving individuals within a stage develop into the subsequent stage during the summer transition intervals, while in winter only a fraction p develop. The trophic interaction between parasitoid and aphid is captured in the the reproductive rates, f_s and f_w, which are determined by the parasitism rates (see later). The survival of the parasitoids is assumed to be stage, season and habitat-dependent. For the egg and larval stages, it is assumed 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), i.e.

$$s_i = z_i \times \frac{1}{\left(1 + k\left(\sum_{j=1}^{6} n_{aj}(t) + \sum_{j=1}^{4} n_{pj}(t)\right)\right)} \times 1 - c_{carabid} \times 1 - c_{partridge}.$$

For subsequent stages, the survival rates are assumed to be constant and density independent, though subject to habitat-specific differences. Again seasonal subscripts have been suppressed for ease. Parameters for the parasitoid population model are described in Table A2.3 and parasitoid habitat preferences in Table A2.7.

The annual carabid life-cycle is represented by seven distinct phases (Table A1.3). Individuals overwinter as adults during which time they experience a monthly survival rate of $s_{w,4}$. In April and May, the surviving adults reproduce at a rate, f_s, while the remaining adults and newly produced eggs have a survival rate of $s_{s,4}$ and $s_{s,1}$ respectively. In May and June, the eggs hatch at a rate p_1. By July, any unhatched eggs die leaving only adults and larvae in the population which survive through the remaining summer months at the rate of $s_{s,4}$ and $s_{s,2}$ per 2 days. A fraction p_2 of larvae pupate every 2 days during August and subsequently emerge in September at a rate of p_3. During these months, the pupae survive at a rate of $s_{s,3}$. Adults are mobile during the spring and summer months, moving out of local populations at a rate d_s. In addition a more substantial migration, d_w, is assumed to take place in September in response to harvest time disturbances.

Table A1.3. Transition matrices representing the demographic transitions that take place during an annual life-cycle of the carabid population.

Phase	Month	Transition matrix ($\mathbf{B}_c$)
0	October - March	$\begin{bmatrix} 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & s_{w,4} \end{bmatrix}$
1	April	$\begin{bmatrix} s_{s,1} & 0 & 0 & f_s \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & (1-d_s)s_{s,4} \end{bmatrix}$
2	May	$\begin{bmatrix} (1-p_1)s_{s,1} & 0 & 0 & f_s \\ p_1 s_{s,2} & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & (1-d_s)s_{s,4} \end{bmatrix}$
3	June	$\begin{bmatrix} (1-p_1)s_{s,1} & 0 & 0 & 0 \\ p_1 s_{s,2} & s_{s,2} & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & (1-d_s)s_{s,4} \end{bmatrix}$
4	July	$\begin{bmatrix} 0 & 0 & 0 & 0 \\ 0 & s_{s,2} & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & (1-d_s)s_{s,4} \end{bmatrix}$

5	August	$\begin{bmatrix} 0 & 0 & 0 & 0 \\ 0 & (1-p_2)s_{s,2} & 0 & 0 \\ 0 & p_2 & s_{s,3} & 0 \\ 0 & 0 & 0 & (1-d_s)s_{s,4} \end{bmatrix}$

6	September	$\begin{bmatrix} 0 & 0 & 0 & 0 \\ 0 & s_{s,2} & 0 & 0 \\ 0 & 0 & (1-p_3)s_{s,3} & 0 \\ 0 & 0 & p_3(1-d_w)s_{s,4} & (1-d_w)s_{s,4} \end{bmatrix}$

Similar to the parasitoid group, the survival of the carabids is assumed to be stage dependent. For the egg and pupal stages, survival is entirely density independent; larval stages are exposed to an additional density dependent survival so that

$$s_2 = z_2 \times \frac{1}{(1+kn_{c2}(t))},$$

recalling that z_2, the density independent survival term is season and habitat specific, though the indexing to this effect has been suppressed here.

The survival of adult carabids comprises both density independent and density dependent terms but it is assumed that the density dependence acts via predator:prey ratios and their effect on rate of predation both on and by carabids,

$$s_4 = z_4 \times 1 - c_{carabid} \times 1 - c_{partridge}$$

Parameters for the carabid population model are described in table A2.4 and carabid habitat preferences in Table A2.8.

Though the generation time of the grey partridge is greater than a year, its development is completed as an annual cycle and, like the carabid, the life-cycle is composed of intra-generational phases that are seasonally well defined. Each phase represents a different life-history process that has to be captured by the transition matrices (Table A1.4). This is achieved by reference to just three demographic processes, survival (e.g. s_4) development and growth leading to transitions between stages (e.g. p_1) including hatching, and reproduction (f). All birds reach maturity by the onset of winter so that the overwintering population is comprised solely of adults which survive at a monthly rate of s_4. In spring mating takes place at a bi-daily rate, p_1, principally determined by sex ratio. Eggs are laid in the following month at a rate f determined by the required brood size. In June, egg laying is complete and eggs hatch at a rate, p_1. In the remaining months, the chicks develop becoming first juveniles at a rate, p_2, and maturing into adults in August and September (p_3). Throughout their life-cycle, with the exception of the nesting and egg rearing periods, a proportion of the birds may disperse, leaving the local population at rates reflecting differences in summer foraging, d_s, nesting, d_n, and dispersal with the onset of winter, d_w.

Table A1.4. Transition matrices representing the demographic transitions that take place during an annual component of the grey partridge life-cycle.

Phase	Month	Transition matrix ($\mathbf{B}_g$)
0 Overwinter	October-March	$\begin{bmatrix} 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & (1-d_w)1 & (1-d_w)s_4 & 0 \\ 0 & 0 & 0 & 0 & 0 \end{bmatrix}$
1 Nesting	April	$\begin{bmatrix} 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & (1-d_n)(1-p_4)s_4 & 0 \\ 0 & 0 & 0 & (1-d_n)p_4 s_5 & 0 \end{bmatrix}$
2 Egg laying	May	$\begin{bmatrix} s_1 & 0 & 0 & 0 & f \\ 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & s_4 & 0 \\ 0 & 0 & 0 & 0 & s_5 \end{bmatrix}$
3 Chick hatching and rearing	June	$\begin{bmatrix} (1-p_1)s_1 & 0 & 0 & 0 & 0 \\ (1-d_s)p_1 s_2 & (1-d_s)s_2 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & (1-d_s)s_4 & s_5 \\ 0 & 0 & 0 & 0 & 0 \end{bmatrix}$
4 Chick hatching and rearing	July	$\begin{bmatrix} 0 & 0 & 0 & 0 & 0 \\ 0 & (1-d_s)(1-p_2)s_2 & 0 & 0 & 0 \\ 0 & (1-d_s)p_2 s_3 & (1-d_s)s_3 & 0 & 0 \\ 0 & 0 & 0 & (1-d_s)s_4 & 0 \\ 0 & 0 & 0 & 0 & 0 \end{bmatrix}$
5 Juvenile development	August	$\begin{bmatrix} 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 \\ 0 & (1-d_s) & (1-d_s)(1-p_3)s_3 & 0 & 0 \\ 0 & 0 & (1-d_s)p_3 s_4 & (1-d_s)s_4 & 0 \\ 0 & 0 & 0 & 0 & 0 \end{bmatrix}$
6 Juvenile development	September	$\begin{bmatrix} 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 \\ 0 & (1-d_s) & (1-d_s)(1-p_3)s_3 & 0 & 0 \\ 0 & 0 & (1-d_s)p_3 s_4 & (1-d_s)s_4 & 0 \\ 0 & 0 & 0 & 0 & 0 \end{bmatrix}$

Finally, grey partridge are subject to stage and phase specific survival rates throughout the life-cycle. The survival of eggs, juveniles, adults and brooding hens experienced a constant, density independent survival rate. This varies in response to habitat and between stages, for example to reflect the higher predation rates experienced by nesting females. In the case of chicks, survival is sensitive to the ratio of predator:prey densities thereby accounting for the influence of predation success on survival, i.e.

$$s_2 = z_2 \times s_{consumption}$$

Parameters for the grey partridge population model are described in Table A2.5 and their habitat preferences in Table A2.9.

A1.3 Predation and parasitism

The trophic interactions are a key element of the model, providing the mechanism by which trade-offs or synergies in the conservation of grey partridge and the regulation of aphids can occur. 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.

In general terms the effect of predation on survival can be written as $s_{predation} = 1 - c_{predator}$ and a specific form of this has been used in the preceding text. Here $c_{predator}$ is the mortality rate due to predation and for all prey, i.e. aphids, parasitic stages of the parasitoid wasp, and adult carabids. This is based on the predator's instantaneous per capita predation rate which is calculated on the basis of a type 2 functional response, so that

$$c_{predator} = \frac{\left(\frac{r_{predator} \cdot n_{prey}}{1 + h_{predator} \cdot n_{prey}}\right) \cdot n_{predator}}{n_{prey}}$$

Here n_{prey} is the prey density, $r_{predator}$ is the attack rate and $h_{predator}$ the handling time of the predator. Where there is more than one predator species or stage, the mortality rate is calculated independently.

Predation is also assumed to affect the survival of the predators. In this case, the beneficial effect of consuming prey on predator survival is considered to be ratio dependent with the general form,

$$s_{consumption} = \frac{\sum w_{prey} \cdot n_{prey}}{\sum w_{prey} \cdot n_{prey} + \sum k_{predator} \cdot n_{predator}}$$

Here the combined effect of consuming multiple prey types is accounted for by inclusion of the weighted sum of prey density, $\sum w_{prey} \cdot n_{prey}$; the weighting is used to reflect the relative nutritional value of the prey, and the competitive effect of alternative predators is accounted for by the weighted sum of predator density. In this case, predator density is weighted by the competition coefficient, $k_{predator}$.

It is assumed that a parasitic wasp lays a single egg within an aphid, or at least only one survives, and that it results inevitably in the death of the infected aphid. Therefore both the aphid mortality rate due to parasitism and parasitoid fecundity are determined by the stage specific parasitism rate, i.e.

$$C_{parasit} = e^{-ar_i n_{p8}/1 + ga\left(\sum_{j=1}^{6} n_{aj} + \sum_{j=1}^{4} n_{pj}\right)}$$ and

$$f = e^{-ar_i n_{p8}/1 + ga\left(\sum_{j=1}^{6} n_{aj} + \sum_{j=1}^{4} n_{pj}\right)},$$

Where a is the overall attack rate, r_i the relative attack rate for the ith stage and g determines the degree to which a type 1 or type 2 functional response is followed.

A1.4 Habitat quality and preferences

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 absence of specific information on which to base the representation of habitat quality with respect to the four species, a simple dichotomous approach was adopted. In this, each habitat type (see Tables 1 and 2) was classified as either beneficial or not and the density independent survival rates adjusted to reflect this (see Annex 2). In addition, the habitat classification was used to drive active dispersal choices (see below) with habitat preferences being consistent with habitat quality.

A1.5 Dispersal

Dispersal is assumed to take place on one or more occasions during a specie's life-cycle. For each dispersal event, a stage and phase specific proportion of each local population disperses, i.e. d in the transition matrices **B**. These individuals are redistributed across the landscape according to a number of alternative dispersal models described below.

For each species, dispersal may be entirely passive or combination of passive and active. Passive dispersal is modelled using a 2-dimensional dispersal kernel. 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:

Exponential dispersal kernel for short range foraging:

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

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

Uniform dispersal kernel for long-range migration:

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

Again, $p(r|\theta)$ is the probability of a dispersal event to radial distance r along a bearing θ, and r_{max2} is the maximum dispersal distance.

These may be used either individually or in combination, in which case the proportion of the migrating individuals undertaking either dispersal type is specified.

To represent habitat selection associated with active dispersal, the passive dispersal processes is supplemented, for a proportion of the migrating individuals, by a second process in which 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.

During the spring and summer phases, the growing season, both aphids and carabids are assumed to be relatively immobile. However, in the case of aphids winged adults are present (see above) and both aphids and carabids are assumed to make relatively small movements represented by the passive, exponential dispersal kernel model described above. In response to disturbance associated with the end of the growing season (autumn and September), the adults of both species are assumed to undergo a more significant migration. These, are relatively long-range movements and are modelled by a uniform dispersal kernel in combination with active dispersal.

Adult parasitoids undergo a relatively short-range dispersal event every 10 days throughout the spring and summer months to mimic foraging. This is modelled using an exponential dispersal kernel in combination with an active dispersal element. This continues through winter but with the frequency reduced to once in every three months.

The dispersal behaviour of the grey partridge involves three annual migration episodes. In April, a single dispersal event takes place in which adults undergo a relatively long-range dispersal in search of suitable nesting habitat. This is modelled by a uniform dispersal kernel in combination with active dispersal. During the summer, all birds are assumed to forage across the landscape in search for food, this is represented by a uniform dispersal but with small r_{max2} in combination with active dispersal. Finally, the birds undergo a winter dispersal in response to end of the growing season for which a uniform dispersal kernel is assumed.
For all dispersal parameters including habitat preferences see Annex 2, tables A2.2 – A2.5.

ANNEX 2: PARAMETER VALUES

A2.1 Parameterisation

The objective of modelling a generic system in which the food-web was constructed from archetypes provided a degree of flexibility in setting the parameter values for the model which would not have been possible had the objective been to predict the behaviour of a specific system. However, the choice of parameter values was facilitated by having a specific species or group of similar species in mind. For the aphid, carabid, and parasitoid populations, identification of parameter values was made with reference to a wide range of published studies but with particular reference to cereal aphids, predatory carabids of arable systems and to braconid wasps parasitic on aphids. By identifying grey partridge as the example of the 4th trophic level predator we were able to derive parameter values based on the extensive literature base for this species including those modelling studies for which parameter values had already been calculated (e.g. Topping *et al.*, 2010). The parameter values used in the simulation experiments conducted in this study are presented below.

A2.2 Landscape model parameters
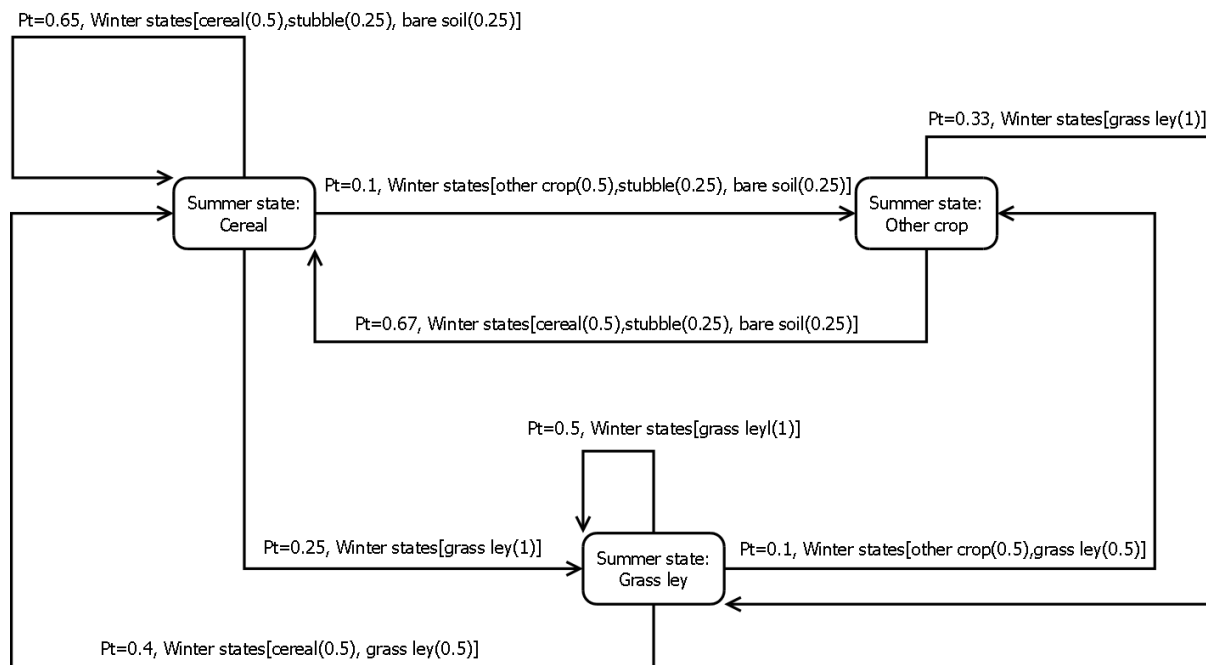
Figure A2.1. State diagram representing the Markov chain for the cereal based crop rotation. Summer crops states are indicated at the nodes with the probability of transitions (Pt) between states given as annotations on transitions (arrows) linking nodes. Winter crop states and associated probabilities are given in parentheses following summers state transition probabilities.

Table A2.1. Land use conditions used as a baseline scenario for all simulations. The figures for agri-environment habitat use were based on an analysis of national adoption figures of the Land Managers Options of the Scottish Rural Development Programme provided by SNH. (Arable = cereal crops + broad-leaf crops)*

Land use	Quantity
Landscape structure	
Landscape extent	5km x 5km
Number of land parcels	200
Landscape composition	
Crop rotation (% area)	95%
Wood (% area)	5%
Conservation headland (% of arable* fields)	5%
Grass margin (% of arable* fields)	10%
Wildbird seed mix plot (% of arable* fields)	1.5%
Hedgerow (length)	4km

A2.3 Local population dynamic model parameters

Table A2.2. Parameters and parameter values for the aphid population dynamic and dispersal models.

Parameter description	Parameter	Parameter values
Survival		
Density-independent in poor habitat, summer (stage specific)	$[z_1, z_2, z_3, z_4, z_5, z_6]$	[0.99, 0.80, 0.80, 0.80, 0.80, 0.80]
Density-independent in poor habitat, winter (stage specific)	$[z_1, z_2, z_3, z_4, z_5, z_6]$	[0.95, 0.32, 0.32, 0.32, 0.32, 0.22]
Density-independent in beneficial habitat, summer (stage specific)	$[z_1, z_2, z_3, z_4, z_5, z_6]$	[0.99, 0.94, 0.94, 0.94, 0.94, 0.94]
Density-independent in beneficial habitat, winter (stage specific)	$[z_1, z_2, z_3, z_4, z_5, z_6]$	[0.95, 0.35, 0.35, 0.35, 0.35, 0.25]
Density-dependent survival coefficient	k	0.0016
Parasitism		
Attack rate	a	1.46
Relative attack rate (stage specific)	$[r_2, r_3, r_4, r_5, r_6]$	[0.12, 0.27, 0.39, 0.16, 0.06]
Functional response type	g	0.0011
Predation		
Carabid search efficiency	$r_{carabid}$	0.5
Carabid handling time	$h_{carabid}$	0.1
Partridge search efficiency	$r_{partridge}$	10
Partridge handling time	$h_{partridge}$	0.001
Reproduction		
Summer fecundity	f_w	8
Winter fecundity	f_s	8
Development		
Egg and larvae development rate	p	0.2
Dispersal		
Emigration rate	d	0.18
Maximum dispersal distance, uniform dispersal kernel (m)	r_{max}	500
Median dispersal distance, exponential dispersal kernel (m)	λ	25
Maximum dispersal distance, exponential dispersal kernel (m)	r_{max}	100

Table A2.3. Parameters and parameter values for the parasitoid population dynamic and dispersal models.

Parameter description	Parameter	Parameter values
Survival		
Density-independent in poor habitat, summer (stage specific)	$[z_1, z_2, z_3, z_4, z_5, z_6, z_7, z_8]$	[0.80, 0.80, 0.80, 0.80, 0.62, 0.62, 0.62, 0.80]
Density-independent in poor habitat, winter (stage specific)	$[z_1, z_2, z_3, z_4, z_5, z_6, z_7, z_8]$	[0.32, 0.32, 0.32, 0.32, 0.95, 0.95, 0.95, 0.22]
Density-independent in beneficial habitat, summer (stage specific)	$[z_1, z_2, z_3, z_4, z_5, z_6, z_7, z_8]$	[0.94, 0.94, 0.94, 0.94, 0.62, 0.62, 0.62, 0.82]
Density-independent in beneficial habitat, winter (stage specific)	$[z_1, z_2, z_3, z_4, z_5, z_6, z_7, z_8]$	[0.35, 0.35, 0.35, 0.35, 0.95, 0.95, 0.95, 0.25]
Density-dependent survival coefficient	k	0.0016
Predation		
Carabid search efficiency	$r_{carabid}$	0.5
Carabid handling time	$h_{carabid}$	0.1
Partridge search efficiency	$r_{partridge}$	10
Partridge handling time	$h_{partridge}$	0.001
Reproduction		
Attack rate	a	1.46
Relative attack rate (stage specific)	$[r_2, r_3, r_4, r_5, r_6]$	[0.12, 0.27, 0.39, 0.16, 0.06]
Functional response type	g	0.0011
Development		
Egg and larvae development rate	p	0.1
Dispersal		
Emigration rate	d	0.36
Median dispersal distance, exponential dispersal kernel (m)	λ	50
Maximum dispersal distance, exponential dispersal kernel (m)	r_{max}	150
Active sensory range (m)		100

Table A2.4.Parameters and parameter values for the carabid population dynamic and dispersal models.

Parameter description	Parameter	Parameter values
Survival – density independent		
Density-independent in poor habitat (stage specific)	$[z_1, z_2, z_3, z_4]$	[0.98, 0.992, 0.992, 0.992, 0.90]
Density-independent in beneficial habitat (stage specific)	$[z_1, z_2, z_3, z_4]$	[0.98, 0.992, 0.992, 0.992, 0.94]
Survival – density dependent		
Density-dependent survival coefficient	k	0.04
Survival – predation		
Partridge search efficiency	$r_{partridge}$	10
Partridge handling time	$h_{partridge}$	0.1
Survival – consumption		
Prey weighting, aphid	w_{aphid}	1
Prey weighting, parasitoid	$w_{parasitoid}$	1
Predator competition coefficient	$k_{carabid}$	2
Reproduction		
Fecundity	f	0.7
Development		
Egg hatching rate	p_1	0.2
Pupation rate	p_2	0.2
Adult emergence rate	p_3	0.2
Dispersal – September		
Emigration rate	d_w	0.83
Maximum dispersal distance, uniform dispersal kernel (m)	r_{max}	250
Active sensory range (m)		100
Dispersal – Summer		
Emigration rate	d_s	0.83
Median dispersal distance, exponential dispersal kernel (m)	λ	25
Maximum dispersal distance, exponential dispersal kernel (m)	r_{max}	100

Table A2.5. Parameters and parameter values for the grey partridge population dynamic and dispersal models.

Parameter description	Parameter	Parameter values
Survival – density independent		
Density-independent in poor habitat (stage specific)	$[z_1, z_2, z_3, z_4, z_5]$	[0.98, 0.98, 0.98, 0.98, 0.88, 0.98]
Density-independent in beneficial habitat (stage specific)	$[z_1, z_2, z_3, z_4, z_5]$	[0.99, 0.992, 0.993, 0.994, 0.993, 0.993]
Survival – consumption		
Prey weighting, aphid	w_{aphid}	1
Prey weighting, parasitoid	$w_{parasitoid}$	1
Prey weighting, carabid	$w_{carabid}$	10
Predator competition coefficient	$k_{partridge}$	7000
Reproduction		
Fecundity	f	1
Development		
Egg hatching rate	p_1	0.1 x nth transition in June
Chick to juvenile development	p_2	0.1 x nth transition in July
Juvenile to adult development	p_3	0.15
Mating	p_4	0.046
Dispersal – Nesting		
Emigration rate	d_n	0.98
Maximum dispersal distance, uniform dispersal kernel (m)	r_{max}	[0.67, 0.67, 2000, 0.67]
Active sensory range, adults only (m)		400
Dispersal – Summer		
Emigration rate	d_s	0.67
Maximum dispersal distance, uniform dispersal kernel (m)	r_{max}	100
Active sensory range (m)		100
Dispersal – Winter		
Emigration rate	d_w	0.95
Maximum dispersal distance, uniform dispersal kernel (m)	r_{max}	1000
Active sensory range (m)		400

A2.4 Habitat quality and associated parameters

Table A2.6. Aphid habitat quality classifications, good quality habitats indicated by + symbol and poor quality habitat by – symbol.

Code	Description	Autumn – Winter survival	Spring – Summer survival
0	Matrix		
1	Cereal crop	+	+
2	Broad-leaf crop	-	-
3	Grass ley	-	-
4	Wild bird seed mix	+	-
5	Wood	+	-
6	Cereal crop + Grass margin	+	+
7	Broad-leaf crop + Grass margin	+	-
8	Cereal crop + Conservation headland	na	+
9	Broad-leaf crop + Conservation headland	na	-
10	Cereal crop + hedge	+	+
11	Broad-leaf crop + hedge	+	-
12	Grass ley + hedge	+	-
13	Wild bird seed mix + hedge	+	-
14	Cereal crop + hedge + grass margin	+	+
15	Broad-leaf crop + hedge + grass margin	+	-
16	Cereal crop + hedge + conservation headland	na	+
17	Broad-leaf crop + hedge + conservation headland	na	--
18	Cereal crop stubble	-	na
19	Cereal crop stubble + hedge	+	na
20	Cereal crop stubble + grass margin	+	na
21	Cereal crop stubble + hedge + grass margin	+	na
22	Broad-leaf crop stubble	-	na
23	Broad-leaf crop stubble + hedge	+	na
24	Broad-leaf crop stubble + grass margin	+	na
25	Broad-leaf crop stubble + hedge + grass margin	+	na
26	Bare soil	-	na
27	Bare soil + hedge	+	na
28	Bare soil + grass margin	+	na
29	Bare soil + hedge + grass margin	+	na

Table A2.7. Parasitoid habitat quality classifications, good quality habitats indicated by + symbol and poor quality habitat by – symbol.

Code	Description	Autumn – Winter survival	Spring – Summer survival
0	Matrix		
1	Cereal crop	+	+ (- for adults)
2	Broad-leaf crop	-	-
3	Grass ley	-	-
4	Wild bird seed mix	+	- (+ for adults)
5	Wood	+	-
6	Cereal crop + Grass margin	+	+
7	Broad-leaf crop + Grass margin	+	-
8	Cereal crop + Conservation headland	na	+
9	Broad-leaf crop + Conservation headland	na	-
10	Cereal crop + hedge	+	+
11	Broad-leaf crop + hedge	+	-
12	Grass ley + hedge	+	-
13	Wild bird seed mix + hedge	+	-
14	Cereal crop + hedge + grass margin	+	+
15	Broad-leaf crop + hedge + grass margin	+	-
16	Cereal crop + hedge + conservation headland	na	+
17	Broad-leaf crop + hedge + conservation headland	na	-
18	Cereal crop stubble	-	na
19	Cereal crop stubble + hedge	+	na
20	Cereal crop stubble + grass margin	+	na
21	Cereal crop stubble + hedge + grass margin	+	na
22	Broad-leaf crop stubble	-	na
23	Broad-leaf crop stubble + hedge	+	na
24	Broad-leaf crop stubble + grass margin	+	na
25	Broad-leaf crop stubble + hedge + grass margin	+	na
26	Bare soil	-	na
27	Bare soil + hedge	+	na
28	Bare soil + grass margin	+	na
29	Bare soil + hedge + grass margin	+	na

Table A2.8. Carabid habitat quality classifications, good quality habitats indicated by + symbol and poor quality habitat by – symbol.

Code	Description	Autumn – Winter survival
0	Matrix	
1	Cereal crop	-
2	Broad-leaf crop	-
3	Grass ley	-
4	Wild bird seed mix	+
5	Wood	+
6	Cereal crop + Grass margin	+
7	Broad-leaf crop + Grass margin	+
8	Cereal crop + Conservation headland	+
9	Broad-leaf crop + Conservation headland	+
10	Cereal crop + hedge	+
11	Broad-leaf crop + hedge	+
12	Grass ley + hedge	+
13	Wild bird seed mix + hedge	+
14	Cereal crop + hedge + grass margin	+
15	Broad-leaf crop + hedge + grass margin	+
16	Cereal crop + hedge + conservation headland	+
17	Broad-leaf crop + hedge + conservation headland	+
18	Cereal crop stubble	-
19	Cereal crop stubble + hedge	+
20	Cereal crop stubble + grass margin	+
21	Cereal crop stubble + hedge + grass margin	+
22	Broad-leaf crop stubble	-
23	Broad-leaf crop stubble + hedge	+
24	Broad-leaf crop stubble + grass margin	+
25	Broad-leaf crop stubble + hedge + grass margin	+
26	Bare soil	-
27	Bare soil + hedge	+
28	Bare soil + grass margin	+
29	Bare soil + hedge + grass margin	+

*Table A2.9. Grey partridge habitat quality classifications, good quality habitats indicated by +
symbol and poor quality habitat by – symbol.*

Code	Description	Autumn – Winter survival	Nesting survival	Spring – Summer survival
0	Matrix			
1	Cereal crop	+	-	-
2	Broad-leaf crop	-	-	-
3	Grass ley	-	-	-
4	Wild bird seed mix	+	-	+
5	Wood	-	-	-
6	Cereal crop + Grass margin	+	+	+
7	Broad-leaf crop + Grass margin	-	+	+
8	Cereal crop + Conservation headland	na	-	+
9	Broad-leaf crop + Conservation headland	na	-	+
10	Cereal crop + hedge	+	+	+
11	Broad-leaf crop + hedge	-	+	+
12	Grass ley + hedge	-	+	+
13	Wild bird seed mix + hedge	+	+	+
14	Cereal crop + hedge + grass margin	+	+	+
15	Broad-leaf crop + hedge + grass margin	-	+	+
16	Cereal crop + hedge + conservation headland	na	+	+
17	Broad-leaf crop + hedge + conservation headland	na	+	+
18	Cereal crop stubble	+	na	na
19	Cereal crop stubble + hedge	+	na	na
20	Cereal crop stubble + grass margin	+	na	na
21	Cereal crop stubble + hedge + grass margin	+	na	na
22	Broad-leaf crop stubble	+	na	na
23	Broad-leaf crop stubble + hedge	+	na	na
24	Broad-leaf crop stubble + grass margin	+	na	na
25	Broad-leaf crop stubble + hedge + grass margin	+	na	na
26	Bare soil	-	na	na
27	Bare soil + hedge	-	na	na
28	Bare soil + grass margin	-	na	na
29	Bare soil + hedge + grass margin	-	na	na

ANNEX 3: DESCRIPTION AND BACKGROUND OF THE AGBIOSCAPE MODELLING SYSTEM

A3.1 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.*, 2013; Kovács-Hostyánszki *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 Integrated Pest Management (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, AgBioscape, capable of achieving these goals.

A3.2 Theoretical model development

A3.2.1 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 three 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 of which 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 described 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 & 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 sufficiently small to permit the population to fully mix 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 such as mortality and fecundity 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.*, 2012). 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.

A3.2.2 Description of modelling approach

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. A3.1). 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.

A3.2.3 Landscape model

In simulating the landscape, two 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.
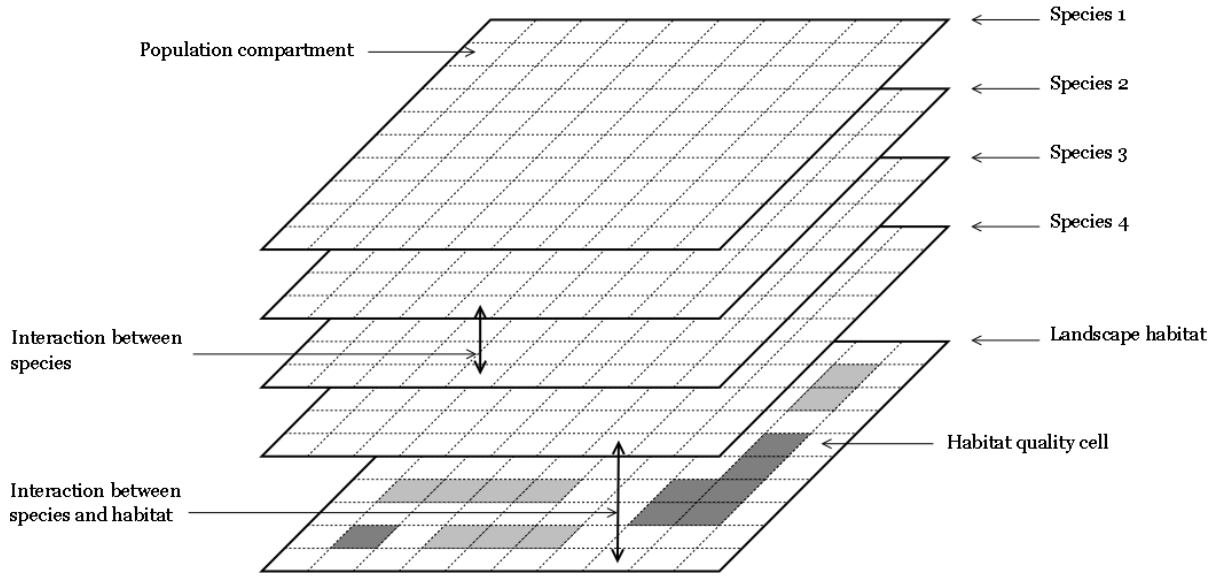
Figure A3.1. Diagram showing the multiple lattice structures used in AgBioscape that are used to resolve the spatial variation in habitat, and population states and examples of the links between each lattice

To simulate the landscape structure, a rectangle representing the landscape is specified including its height, width, and the total number of land parcels contained, $N_{lptotal}$. The initial landscape rectangle is then split recursively until the desired number of land parcels is produced (Fig. A3.2). 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 $N_{lpdaughter1} = \|L_{split}N_{lpparent}\|$ and $N_{lpdaughter2} = \|(1 - L_{split})N_{lpparent}\|$. The splitting process is repeated for each rectangle until $N_{lp} = 1$ (Fig A3.2).

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. A3.3),

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

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.

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.
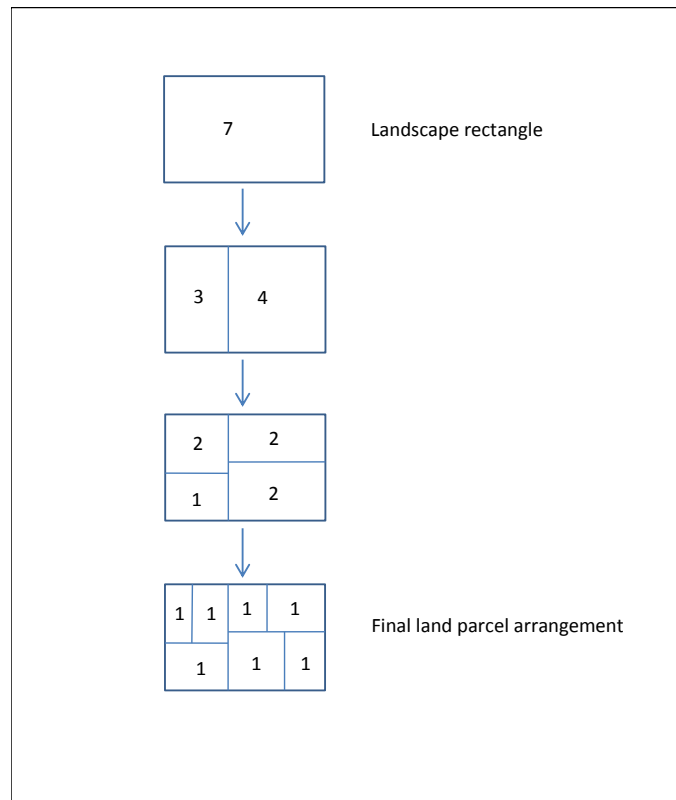

Figure A3.2. Diagram showing the recursive partitioning of the landscape into a target number of land parcels, $N_{lptotal}$. In this example $N_{lptotal} = 7$. The integer values indicate the number of land parcels, N_{lp}, to be generated from each rectangle. See text for explanation of the algorithm used to determine N_{lp} for each rectangle.

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 a 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".
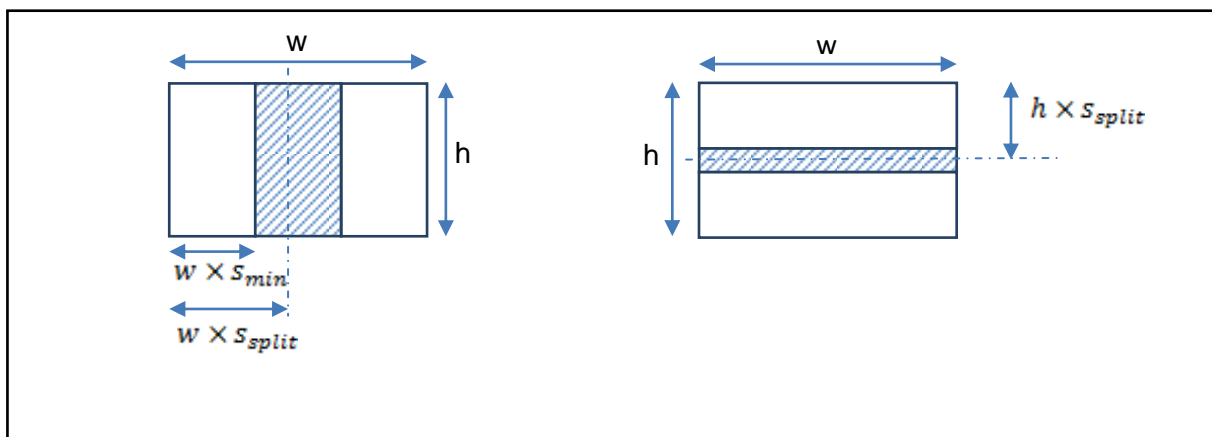

Figure A3.3. The position at which a vertical or horizontal split is made in a parent land parcel to produce two daughter parcels falls on the intervals $[w \times s_{min}, w \times (1 - s_{min})]$ or $[h \times s_{min}, h \times (1 - s_{min})]$ thereby setting the minimum parcel area of $(w \times s_{min})$ or $(h \times s_{min})$ for any given split.

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 (2007-2013) 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. A3.1). 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.

A3.2.4 Population model

To simulate 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,

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

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 A is the population projection matrix which depends on p parameters represented by the $p \times 1$ vector θ. The effect of immigration as a result of dispersal from other local populations is captured in the model by the addition of the vector $\mathbf{m}(t)$ which gives the sum of individuals of each stage or age 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.

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

A3.2.5 Trophic interactions

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.

A3.2.6 Habitats and management

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.

A3.2.7 Dispersal

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 process 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.

A3.2.8 Stochasticity

The approach used to simulate 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 in section 9.2.5, 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).

A3.3 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. A3.4). The sub-modules interact with each other through the "species population lattices" data structure (Fig. A3.1).

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.
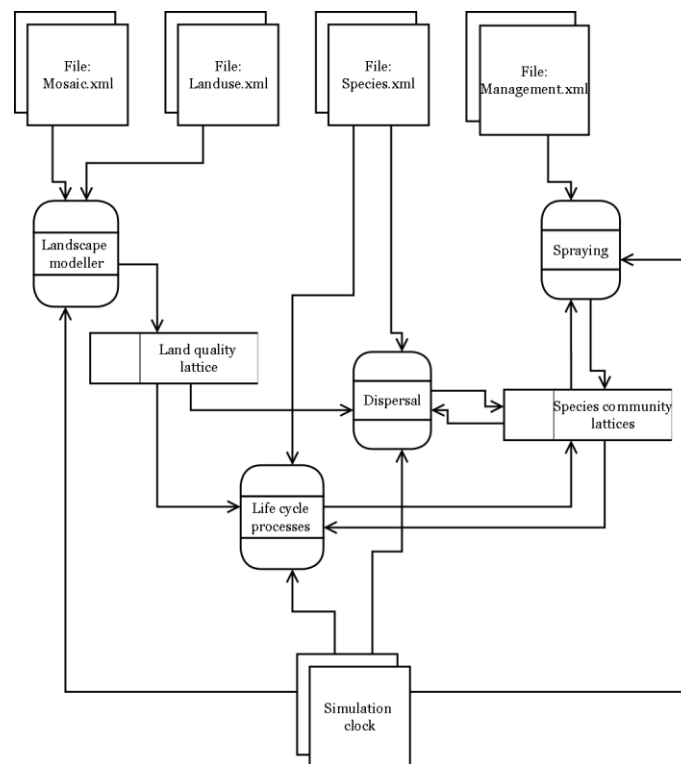

Figure A3.4. Software design: Data flow diagram showing the flow of data between sub-modules of the programme and the interface with the XML input files that are used to configure the programme.

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