The role of landscape context in biological control of cereal aphids

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The candidate confirms that the work submitted is his own and that appropriate credit has been given where reference has been made to the work of others.

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Abstract

Producing enough food to sustainably meet the demands of a growing global population is one of the greatest challenges we face. In wheat, 8% of yield is lost to insect herbivores before harvest, so improving pest control would contribute significantly to food security. Given the negative effects of chemical insecticides, managing habitat to boost numbers of pest natural enemies offers a promising alternative. Recent studies highlight the importance of wider landscape context for natural enemy management, but there is uncertainty over which landscape characteristics are most important for different natural enemies, how this varies temporally, and which management strategies are worthwhile.

In this thesis novel analytical approaches using random forests were used to explore temporal and inter-specific variation in the influence of landscape context on species of aphid and hymenopterous parasitoid in winter wheat fields in the UK, and to produce models predicting the abundance of aphids, parasitoids and syrphid larvae as functional groups.

Aphid and parasitoid numbers responded strongly to the spatial configuration of vegetation parcels, both being more common in more fine-grained landscapes. Syrphid larvae were more abundant when arable land was rare within 1500 metres. Seasonal variation in landscape influence was more important than annual or inter-species differences for both aphids and parasitoids.

Map-based simulations were then performed to predict the outcome of hypothetical land-use scenarios, using a novel method based on statistical models. Displacement of non-crop vegetation by arable land, alongside increased aggregation, produced consistently undesirable results.

Estimates of the economic value of natural enemies to farmers were made, showing the potential to reduce yield loss and insecticide cost by at least £55 per hectare through beneficial habitat management. At high aphid densities, natural enemies were more valuable under insecticide free management.

Future work and implications of these results are discussed in chapter 6.

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1. General Introduction

1.1 The need for agricultural intensification

The global human population more than doubled between 1960 and 2011 (UNDESA, 2011). Over the same period, an unprecedented growth in global agricultural production occurred - a “green revolution” - matching the demands of population growth.

The UN predicts a continued population increase, exceeding 9 billion by 2050 and 10 billion by 2100 (UNDESA, 2011). Furthermore, demand for meat and dairy products is also likely to grow (Tilman et al., 2002), which require more land and energy to produce per calorie than does vegetable food. With more mouths to feed and higher per-capita consumption, the global demand for agricultural production in 2050 could be 70 – 110% higher than today (Tilman et al., 2011, Bruinsma, 2009).

To meet this demand, either the area of agricultural land, yield per unit area or a combination of both must increase. During the green revolution, yield per unit area rose by 106%, but a 10% and 12% increase in the land area under permanent pasture and cropland respectively also occurred, mostly in tropical developing regions (Lambin and Meyfroidt, 2011, Green et al., 2005).

There would however be limited scope for, and serious negative impacts of, further conversion of land to agriculture. In developed regions, most suitable land is already farmed, precluding expansion here. Habitat loss and fragmentation from land conversion has a much higher biodiversity cost in tropical than in temperate regions (Fischer, 2000, Ney-Nifle, 2000), and is having major repercussions for global carbon storage and hydrology there (Tilman et al., 2011, Tilman et al., 2002). Moreover, net increases in area might be hampered by the conspiring effects of climate change, soil degradation and competition for irrigation, rendering large areas unsuitable or uneconomic for arable farming (Battisti and Naylor, 2009, Döös, 2002). For similar reasons, productivity under current farming practices is also predicted to decrease, particularly in regions where increases in food supply will be most urgently needed (Schlenker and Lobell, 2010).

The most strongly advocated path to food security therefore, is to prioritise finding ways to further increase the productivity of existing farmland – i.e. intensification. This applies to both the developing and developed world, accompanied by different challenges. In the UK for instance, recent trends have been towards incentives for reduced production through payment schemes, to reverse declines of farmland wildlife. However, as part of the global food system, it is arguably unethical and unstable to protect our wildlife through a “virtual land (and water) grab” from the developing world; we must produce our fair share of crops, such as wheat, which grow well here. In contrast, intensification has historically been limited in developing regions by poor access to machinery and agrochemicals, and to the knowledge on how to use them effectively (Tilman et al., 2011). An important caveat to consider however, is the relationship between increased yields and area of land in production; further conversion can be stimulated by the promise of high yields (Matson and Vitousek, 2006).

1.2 Intensification and ecosystem services

Intensification has been a multifaceted phenomenon, encompassing changes in fertilisation, mechanisation, irrigation, pest control, crop choice, crop breeding, rotation patterns, and spatial arrangement of landscapes. The goal common to all of these processes is to increase the productivity, or profitability, of farmland. However, some aspects of intensification can damage the future ability of the land to produce food, and cause wider environmental problems; the total external cost of UK agriculture was estimated at £1514 million in 2005 (Pretty et al., 2005). Several authors have suggested that the value of a particular land use regime should incorporate potential future yields, and take external costs and benefits arising from that land use into account (e.g. Balmford et al., 2002, Sutherland, 2004).

It is useful to compare the costs and benefits of different routes to intensification in the framework of the goods and services – “ecosystem services” (ES henceforth) – that an agricultural landscape provides, accruing at all scales (Power, 2010). Agricultural yield can be thought of as a “provisioning service”; processes supporting yield such as decomposition or pollination are “supporting services”; natural pest control, carbon storage and flood management are “regulating services”, and the maintenance of charismatic wildlife and aesthetic value are “cultural services”. The term “productivity” is used here to refer to the net value of all of these services.

1.2.1 Knowledge intensification

Several authors have argued (e.g. Foley et al., 2011, Tilman et al., 2011) that the best way forward is intensification through increased precision of inputs, and application of knowledge to avoid waste and maintain or enhance supporting and regulating services to increase yields. This is referred to here as “knowledge intensity” (KI). Examples of this would be improving crop varieties, including GM crops with traits such as drought resistance or natural pest resistance which reduce the need for irrigation and insecticide application (Edwards and Poppy, 2009), ensuring the adoption of best practice soil management, or using past yield maps of fields to target fertiliser application. Recent success stories include the adoption of the “system of rice intensification” (SRI), which resulted in a record rice yield of 22.4 tonnes per hectare in Bihar, India in 2011 (Uphoff, 2012), and reduced insecticide spraying on Bt producing cotton has decreased aphid outbreaks on neighbouring crops by increasing natural enemy abundance (Lu et al., 2012).

A major challenge to increasing KI however is making sure farmers have access to the knowledge and technology necessary to implement new management practices, and that the practices do not damage other important functions of agricultural land. For example, zero-tillage management has been widely advocated to reduce soil erosion, and help retain organic carbon, moisture and plant nutrients in the soil (e.g.Triplett and Dick, 2008). However, successful implementation of zero-tillage crop rotations generally requires the retention of crop residues in the field, specialised seed drills and extensive herbicide use for weed control; conditions which cannot always be met. In smallholder and subsistence systems in Africa, where the environmental benefits of zero-tillage could be high, crop residue retention for zero-tillage competes with its use as animal feed or conversion to biofuel (Giller et al., 2009), and access to safe herbicides is limited (Johansen et al., 2012). Therefore, zero-tillage management has up to now been mainly adopted in large-scale mechanised systems.

As a counter-example, the outstanding rice yields obtained from SRI management in India are largely due to labour intensive transplantation and weeding by hand, throwing doubt on the scalability of these practices to large-scale mechanised systems.

1.2.2 Input intensification

Increasing the volume of inputs - input intensity (II) – offers little scope for sustainable intensification. Cereal yield responses to Nitrogen application have shown signs of saturating over the last 40 years (Tilman et al., 2002), indicating diminishing returns of further increases. External disservices of II are of even greater concern. Heavy use of irrigation can lead to salinisation of soils and depletes river flows or competes with demand for drinking water (Ghassemi et al., 1995); increased tillage and profligate use of artificial fertilisers has reduced soil carbon content, eroded soil (Pimentel et al., 1995), and led to widespread eutrophication in both aquatic and terrestrial systems, with far reaching biodiversity impacts (Tilman et al., 2002); excessive non-selective insecticide use drives the evolution of resistance and decreases populations of insect natural enemies, in some cases resulting in secondary outbreaks (Pimentel et al., 1992). As such, the optimal sustainable productivity is likely to be a unimodal function of II, where beyond the optimum the erosion of supporting and regulating services will decrease current and especially future crop yield, and cause external disservices (Matson et al., 1997). Moreover, maximum productivity per unit input – profitability – will peak at an even lower II than productivity *per se*, barring subsidies.

1.2.3 Spatial intensification

A similar situation is likely to apply to a third aspect of intensity, here termed “spatial intensity” (SI). This can include the trend towards spatial aggregation of cultivated land, the removal of non-crop vegetation, increasing field sizes, reduced area of fallow land, and the specialisation to fewer crop types (Tscharntke et al., 2005). On the one hand, specialisation allows crops to be grown in the most suitable locations; farmers can invest in specialist knowledge and machinery; removal of field boundaries makes machinery easier to use, and restricting non-crop vegetation to infertile soils should maximise yield on fertile land. Equally however, high SI has been linked to low levels and potentially poor robustness of natural pollination and pest control (Kremen et al., 2007, Tscharntke et al., 2005) and a decline in charismatic farmland wildlife (Benton et al., 2003). Specialisation can also make farm businesses more vulnerable to environmental and economic stochasticity (Ikerd, 1990). Therefore the relationship between SI and long-term productivity is also likely to be unimodal.

1.2.4 Sustainability

Drawing these separate discussions together is one common theme. Sustainable intensification can only occur if the effects of individual management practices are valued across all of the services a landscape provides, accruing at all scales from local to global. Many of these services or disservices are difficult to value economically, but this does not mean that they do not have an economic value. The varying ease with which different costs and benefits associated with production practices can be transmitted to the producer creates mismatches between the economic returns of intensification for landowners, and those for society at large (Balmford et al., 2002). Additionally, buffering of farmers from even direct input costs through “perverse” production subsidies has historically distorted their decisions (Myers, 1998). By removing production subsidies and improving the accuracy of valuation, farmers can be made aware of the monetary benefit they receive directly from supporting services, and payments can be made to landowners for services of benefit to wider society. This framework can provide the economic incentives for sustainable intensification (van der Horst, 2011).

In the remainder of the chapter, the focus of discussion will be one aspect of intensification and its effect on ES, which will be the broad topic of this thesis; the relationship between insect crop pest regulation and the composition and spatial configuration of vegetation in agricultural regions.

1.3 Insect crop pests and biological control

1.3.1 Chemical control

Worldwide, an estimated 8% of wheat, 10% of maize, and 15% of rice production is lost due to feeding and pathogen transmission by arthropod pests (Oerke, 2006). Insecticidal chemicals have been the primary weapons for controlling pest outbreaks in arable crops over recent decades, and on average reduce yield losses to insects by 39% (Oerke, 2006).

However there are drawbacks which make reliance upon insecticides alone untenable. Resistance to compounds has evolved in some cases, for example in the peach-potato aphid *Myzus persicae* to organophosphates, carbamates and pyrethroids, limiting their efficacy (Devonshire and Moores, 1982). The cost of obtaining and applying insecticides can also be high; current costs range from £13 to £20 per hectare in the UK (NAAC, 2011) and are likely to rise in real terms due to fuel price increases. Furthermore, public health concerns over exposure to drift and residues in food and water continue to restrict the range of products available (Pimentel et al., 1992). However, the disadvantage of insecticides most relevant to this thesis, and to sustainable intensification, is that of non-target insect mortality. Poor timing or over-dosage of application of broad-spectrum insecticides causes significant mortality of non-target insects including pollinators, and predators and parasitoids of the target herbivore itself. Often the herbivore population can recover more rapidly than that of the natural enemies, resulting in an increased likelihood of further outbreaks (Pimentel et al., 1992).

In effect, increasing the intensity of non-selective insecticide use creates a positive feedback, whereby further application becomes increasingly necessary due to the low abundance of natural enemies, and the yield per unit of input decreases.

1.3.2 Integrated pest management

The recognition that insecticide use has important feedbacks on natural pest regulation has led to the concept of integrated pest management (IPM), where insecticides form just one part of a more reliable control strategy. Farmers are advised to use economic thresholds for spraying decisions, and to restrict spraying to suitable weather conditions, times of year, and particular products which will minimise adverse sideeffects. Cultural control (using crop rotation, sowing dates, or push–pull intercropping) and biological control are other strategies involved in IPM.

Biological control falls into two categories: “classical” biological control where (often non-native) predators or pathogens are bred and released *en masse*, and “conservation” biological control which seeks to increase populations of wild natural enemies or to attract them into crop fields. Classical biological control is most often successful in greenhouses, where artificially high natural enemy densities can be introduced and maintained in the enclosed space, and has also been useful in the control of non-native herbivores through introduction of enemies from their native range. However, in open cropping systems most recent research has been directed towards improving conservation biological control (CBC) strategies.

1.4 Management for conservation biological control, and the influence of landscape context

Biological control by the natural enemies of herbivores is estimated to be worth about $4.5 billion annually in the US alone (Losey and Vaughan, 2006).

CBC has the potential to enhance this value, by boosting both the abundance of natural enemies for short term impact on herbivore populations, and also the long-term robustness of control by maintaining functional redundancy and response diversity of the natural enemy assemblage (Laliberté et al., 2010). In addition to reducing the need for spraying, natural enemies can reduce crop yield loss to pests at below economic threshold densities. In effect, increasing biological control potential would constitute a form of intensification, provided it results in higher overall crop yields.

In the UK and EU, the main focus of recent CBC research has been the efficacy of field-scale provision of food resources such as nectar-rich margin strips or artificial food sprays, and shelter from disturbance through beetle banks and intercropping. However, an increasing number of studies have observed that the efficacy of field-scale management in promoting natural enemy diversity and enhanced pest control is dependent upon the composition and configuration of vegetation in the wider landscape surrounding the field – the “landscape context”. In addition, much recent research has been directed towards looking at landscape context in the absence of any field-scale management.

1.4.1 The nature of agricultural landscapes

Several features of agricultural environments make interactions of large-scale habitat structure and biological control likely. Insect pests and their natural enemies are usually part of both crop-based and non-crop based food webs. Annual crops are an ephemeral but exceptionally rich food resource for herbivores, and therefore also for their predators, parasites and pathogens. The process of harvesting and tillage limits which insects can permanently remain in a field; most will only persist in non-crop vegetation, before re-colonising crops when they are planted once more. Wissinger (1997) called annual cropping systems (ACS) “predictably ephemeral” environments, with many crop pests sharing features with herbivores from other regularly disturbed systems. Thus, repeated dispersal of insects between spatially and temporally separated resources such as overwintering sites, prey on crops and non-crop vegetation (Langer and Hance, 2004, Muller and Godfray, 1997), and non-prey resources such as nectar (Wäckers et al., 2008) is necessary for persistence of natural enemies. Landscape composition and configuration mediates the quantity and spatial arrangement of these resources and thus the degree to which natural enemy population size is “subsidised” by other asynchronous resources when a key prey resource is scarce. This “subsidy” has been identified as an important feature in most cases of effective top-down herbivore control (Polis, 1999). Resource separation also influences the speed of crop colonisation (Banks et al., 2008). Colonisation speed is critical to effective biological control, as natural enemies are always “one step behind” their prey (Ehler and Miller, 1978). Spill-over effects can occur between crops acting as temporally separated resources (Stary and Havelka, 2008, Vorley and Wratten, 1987, Rusch et al., 2011) and in both directions between crop and non-crop habitat (Haenke et al., 2009, Gladbach et al., 2011).

1.4.2 Scale-specific responses

The scale at which the spatial arrangement and composition of landscapes affect arthropod abundance and distribution varies from species to species, depending (among other things) on passive and active dispersal ability, resource needs, and foraging behaviour (Gabriel et al., 2010, Holland et al., 2004, Steffan-Dewenter et al., 2002). For example, Steffan-Dewenter et al. (2002) found that solitary bees, bumble bees and honey bees responded to increasingly large spatial scales respectively, due to difference in body size and degree of sociality, and Schmidt et al. (2008) found that the best fitting scale in explaining spider abundance varied between 95 and 3000 metres depending on the species.

Furthermore, a single species may respond to landscape context at more than one spatial scale sequentially or simultaneously, because there are usually several different processes contributing to field-scale abundance, both intrinsic to a species or involving interactions with others (Rusch et al., 2011, Gabriel et al., 2010). Landscape may affect the overall population density of an insect in the region through inter-annual concentration or dilution effects (Thies et al., 2008), or metapopulation-like dynamics (Ives and Settle, 1997), at a scale depending on that of dispersal. For example, Vialatte et al. (2007) showed that over two years, due to weather differences, the main provenance of cereal aphids shifted from high altitude dispersers, whose abundance is dependent on the vegetation composition over hundreds of kilometres, to overwintering sources in the local area. Loxdale et al. (1993) distinguish long-range migration as having an initial vertical flight then a subsequent attraction to green targets, whereas short-range dispersal lacks the initial behavioural phase. Thus, the scale at which “landscape context” is most important can vary over time, depending on what process is dominating the colonisation of crop fields. Relative attractiveness of habitat types affects small-scale distribution through directed movement (Hamback et al., 2009, Bommarco and Banks, 2003), adding another layer of interaction with landscape structure onto larger scale abundance patterns. This potentially could lead to very low numbers of an insect in an unattractive patch despite the large scale abundance being high, because many higher quality patches are in close proximity.

Consequently, landscape context should ideally be measured at an appropriate scale for the organisms and processes in question in observational studies, and is thus frequently quantified at multiple nested spatial scales when the appropriate scale is unknown *a priori,* to ensure a relevant scale is included*.*

1.4.3 Evidence for landscape effects

The results of recent studies have generally been clear. A review by Bianchi et al. (2006) found that 74% of studies of the effect of the proportion of non-crop land or landscape “complexity” *per se* on natural enemy abundance and diversity showed a positive effect. These findings pertained to diverse systems, including both specialist natural enemies such as parasitic hymenopterans (Cronin and Reeve, 2005, Marino and Landis, 1996, Rusch et al., 2011, Thies et al., 2005), and generalists including coccinellids, carabids and spiders (e.g. Ostman et al., 2001, Perovic et al., 2010, Winqvist et al., 2011), suggesting a degree of generality. The spatial scale at which landscape context is important has often been different for herbivores and their natural enemies, with aphids for example, responding to larger scale patterns than their parasitoids (Thies et al., 2005). Landscape context effects are most frequently attributed to the increased availability of alternative resources in close proximity to crop fields, increasing the tendency for apparent competition to impact crop-pest populations (Alhmedi et al., 2011, Bonsall and Hassell, 1999, Hamback and Bjorkman, 2002, Langer and Hance, 2004, Van Veen et al., 2008, von Berg et al., 2009).

Interactions between field-scale management and landscape context have also shown fairly consistent patterns. Haenke et al. (2009) showed that the effect of floral resource margins on syrphid abundance was greatest in less complex landscapes, due to the higher relative attractiveness of the margins there. Similar patterns have also been observed extensively in biodiversity responses to agri-environment schemes (Batáry et al., 2011), though Tscharntke et al. (2012) have hypothesised that the efficacy of field-scale management will be highest in landscapes of intermediate complexity. This pattern would result from the lack of source populations for colonisation in extremely simple landscapes, whereas in highly complex landscapes constant immigration of insects from large local sources means abundance and diversity of insects is high even in the absence of beneficial field management, and other nearby patches would compete in attractiveness with a floral margin, for example. Somewhere between these extremes lies the region of highest efficacy.

Large effects of field-scale management in intermediate landscapes were hypothesised to be mainly driven by redistribution of natural enemies, rather than population responses, and therefore field-scale management might be of lesser importance for CBC than landscape-scale manipulation. However, several authors (Bianchi et al., 2006, Gabriel et al., 2010, Sutherland et al., 2012) have pointed out that that if field-scale management is implemented on a large enough scale – perhaps on several contiguous farms - it will make an appreciable difference to landscape complexity, influencing population sizes of natural enemies as well as spatial distribution.

Meta-analyses by Chaplin-Kramer et al. (2011) and Griffiths et al. (2008) have qualified the enthusiasm over studies claiming success of CBC, by noting that although increases in parasitoid and generalist predator abundances had been shown in most cases, translation into reduced pest populations had not often been demonstrated, with some exceptions (e.g. Ostman et al., 2003, Thies et al., 2011). This may in part relate to the unpredictable relationship between the species diversity of a guild of natural enemies, and the degree of pest suppression (Straub et al., 2008, Straub and Snyder, 2006, Tscharntke et al., 2008), and can result in the optimal management for conservation of diversity and the provision of an ecosystem not necessarily being aligned (Macfadyen et al., 2012). Given spatial and temporal variation in the identity of the natural enemy species having the largest impact on pest populations (Chambers et al., 1986, Ostman et al., 2003, Thies et al., 2011, Tscharntke et al., 2008), landscape-scale management for CBC would ideally represent a balance between the needs of most effective natural enemies, promoting functional diversity rather than species richness *per se*.

In summary, on the basis of the accumulated research, many authors now advocate a shift towards landscape-scale management to promote CBC, and ecosystem service provision generally (e.g. Kremen et al., 2007, Tscharntke et al., 2005, Concepción et al., 2012). Landscape management has also been highlighted as potentially important for the success of natural enemy attraction methods using synthetic herbivore induced plant volatiles (HIPVs) (Kaplan, 2012), and is likely to enhance the successful use of crop varieties genetically modified to produce herbivore repellent or predator attractant compounds (Yu et al., 2012). Two clear caveats emerging from the literature are that for landscape management for natural enemies to improve herbivore suppression, it must be targeted at the scales important for the most effective natural enemy species; and that valuation of the effects of management must be a priority to ensure adoption by farmers (Cullen et al., 2008, van der Horst, 2011).

1.5 Research gaps

As discussed above, landscape management for CBC and other ecosystem services has great potential for application to sustainable intensification of crop production.

However, before this can become a reality, there are several under-studied aspects need further attention. These are outlined below (see the introductions of chapters 2 – 5 for more detail).

1.5.1 The complexity of complexity

A large proportion of the studies of landscape context on natural enemy numbers and biocontrol have characterised landscape "complexity" very simply; as the percent cover of either arable land, or non-arable (or "semi-natural") land. Percentage arable land has often been shown to correlate with other measures of landscape complexity, such as perimeter-area ratio, habitat diversity and field boundary density (Roschewitz et al., 2005, Steffan-Dewenter et al., 2002, Thies et al., 2005), and so used as a representative measure. However terms such as complexity or "heterogeneity" incorporate several independent (logically, if not statistically) aspects of landscape structure (Abson, 2011), which may affect organisms in different ways. For example, linear boundaries such as hedgerows can provide nesting habitat and movement corridors for pollinators (Cranmer et al., 2011, Osborne et al., 2008), or overwintering refuges for pests and natural enemies (Hand, 1989). Boundaries constitute both a resource in their own right, and a means of dividing up farmland into more accessible chunks, but dense field boundary networks can be found in otherwise homogeneous landscapes. Likewise, crop diversity, and the degree of aggregation of single crop types may vary independently of the proportion of arable land in an area, with implications for between-crop movement processes of pest insects and their natural enemies.

If the influence of different aspects of landscape complexity and input intensity in studies of pest and natural enemy populations could be disentangled, this would better inform how landscape management should be carried out for maximum CBC benefit, at the minimum cost to agricultural yield. This is especially important if the correlations between different aspects of complexity break down in certain areas or under future land use change; then a single measure will be a poor indicator of other aspects of complexity.

However, doing this poses challenges for study design, and for the analysis and interpretation of results, which is no doubt why such attempts have been rare (but see Rusch et al., 2011). Finding sets of study sites where different aspects of landscape complexity are uncorrelated requires a larger sample size than has previously been normal, and a greater degree of planning. For post-hoc analyses, use of a large number of land use classes, measures of landscape structure, and interactions between them renders traditional statistical model selection either unfeasibly complex (in the case of all-subsets approaches) or liable to give spurious results (for stepwise approaches) (Graham, 2003). Moreover, landscape characteristics are often described at multiple scales around focal fields to account for uncertainty over the correct scale of measurement, further multiplying the number of candidate explanatory variables and the colinearity among them.

There is thus clearly a need to use alternative approaches to statistical analysis when attempting to study the influence of different aspects of complexity and their interactions, without confident prior knowledge of what these might be.

1.5.2 Temporal variation in landscape context effects

From farm-scale studies, temporal changes in the status of crops and non-crop vegetation as net sources and sinks of pests and natural enemies have been apparent (Macfadyen, 2009, Stary and Havelka, 2008, Vorley and Wratten, 1987, Vorley, 1986), and are implied in many discussions of natural enemy dynamics.

This is especially relevant for biological control, because there is often temporal turnover in the species composition of the pest and natural enemy assemblages, and each species may respond in a different way to landscape context. Additionally, parasitism or predation pressure at one point in the season may be more crucial for pest dynamics than at other times; a small delay in predator immigration into fields can result in the failure of pest control (Tenhumberg and Poehling, 1995).

Individual pest or natural enemy species must switch between alternative hosts or host-plant complexes at different times of the year which influences the suitability of different vegetation types as sources of colonists through the season. Some plants species have relatively short windows of high palatability to herbivores (e.g. Feeny, 1970), thus a peak of net emigration of multi-voltine herbivores and their natural enemies occurs at the end of this window. Equally, some parasitoid species display strong fidelity to natal host-plant complexes, acquired through learning of olfactory cues (Powell et al., 2003, van Emden et al., 1996). This fidelity may inhibit the migration of a single adult generation between a given pair of host-plant complexes at one point in the season, but this preference can be overridden if the non-natal host-plant complex is dominant enough (Chow and Mackauer, 1991), which might be the case in another part of the season.

In more replicated studies exploring landscape-natural enemy interactions, enemy abundance or parasitism rates only tend to be measured once or twice during the season (Chaplin-Kramer et al., 2011), limiting the information obtainable about temporal variation in landscape effects from such studies. Integrating this temporal dimension into analyses would avoid conclusions being contingent on study timing.

1.5.3 Combining responses of pests and multiple natural enemies for informing landscape-scale management

Landscape context can act on herbivore populations through effects on different natural enemies, which may have differing responses. Though some disagree (Chaplin-Kramer et al., 2011), herbivore densities are also likely to respond directly to landscape structure through movements between temporally separated resources (Vialatte et al., 2007, Hamback et al., 2007). Evaluating the outcome of landscape-scale changes on CBC may therefore become complex, if several agents act in contrasting ways.

Patterns modelled with spatially explicit predictor variables present additional challenges for making recommendations. Spatial dependencies between different landscape alterations mean that regression coefficients cannot be used as a guide for appropriate management changes. If for instance the proportional area of grassland increases, that of another vegetation type must decrease in turn. The effect of a change also depends on the initial conditions, so even if the proportion of non-crop land is positively linked to natural enemy abundance, increasing the proportion from 5 to 10% will likely have a vastly different effect to a change from 85 to 90%.

Due to the great difficulty and expense involved in landscape scale manipulations and rarity of long term datasets covering periods of change, spatial simulation of land-use change using digital maps is an increasingly popular means to evaluate the likely effects of alternative landscape-scale management scenarios on multiple objectives. Land-use or land cover change simulations deal automatically with varying initial conditions and non-independence of predictors in spatial planning problems, and in theory any process or outcome that can be modelled as a function of land cover patterns can be evaluated. This adaptability has led to their being used to explore trade-offs and synergies between different ecosystem services (e.g. Nelson et al., 2009). Assessing alternative land-use scenarios for multiple natural enemies is a conceptually similar problem, but to my knowledge has not yet been studied using land-use simulation. Doing so should provide a good way of assessing the potential benefits of planned landscape management, or the effects of unplanned change.

Existing spatial planning software is available to facilitate the analysis of land-use scenarios. Some, such as “marine spatially explicit annealing” (MARXAN) (Ball et al., 2009) and “the soil and water assessment tool” (SWAT) (Gassman et al., 2007) are designed for sophisticated modelling of single objectives - spatial conservation planning and hydrological monitoring respectively. Others however feature built-in models to evaluate the production of a variety of different goods and services from a landscape, which is what is needed to evaluate synergies and trade-offs between multiple objectives. The Natural Capital Project’s “integrated valuation of environmental services and trade-offs” tool (InVEST), and the “artificial intelligence for ecosystem services” (ARIES) platform (Villa et al., 2009) are two well-developed examples of this. Supplied with user-defined land-use maps, mechanistic models are created describing how ecosystem services are produced and used by different land-use types. These are then be used to generate output maps to compare the provision, use and value of multiple ecosystem services. ARIES incorporates sophisticated agent-based models for how services flow from sources to recipients, allowing barriers to flow or rival users of a service to be identified, and mitigatory actions to be assessed.

A key decision is how to create maps of alternative land-use to input into InVEST or ARIES. In many studies, the objective is to evaluate the likely impact of a small set of plausible future economic and political conditions on ecosystem service outcomes, such as the ALARM project storylines (EU project code: GOCE-CT-2003-506675). The storylines are then translated into predictions of spatially explicit land-use change using a variety of coupled social-ecological models, often including agent-based simulations to mimic the land-use decision making of landowners (Parker et al., 2003).

An alternative approach is to use a spatial optimisation algorithm, that iteratively evaluates an objective as a function of land-use, whilst making small changes in each iteration. MARXAN performs optimisation for nature reserve planning, but a more flexible tool is the “land-use pattern optimisation library” (LUPOlib) (Holzkämper and Seppelt, 2007b), which can be programmed to optimise any set of objectives depending on landscape context. Optimisation has the advantage of finding the set of best-case scenarios for multiple objectives, varying with the weighting given to each outcome along an “efficiency frontier”. Lautenbach et al. (2010) favour this approach to ecosystem service trade-off analysis for its objectivity, as compared with supplying a limited number of user defined land-use maps. The obvious drawback with optimisation is that it does not enable you to evaluate the performance of realistic scenarios, such as the ALARM storylines, which do not lie on the optimum efficiency frontier.

There is potential therefore to use existing software tools and methods to predict trade-offs and synergies in managing for multiple natural enemies. Unfortunately, both ARIES and InVEST are however constrained to model a finite set of ecosystem services built-in to the software, and neither framework contains models for agricultural pest control, or indeed other tri-trophic interactions which could be adapted for this purpose. LUPOlib is also unsuitable, as it relies on a fixed land parcel structure, when as discussed above, field boundary alterations are an important part of land-use change in agricultural contexts both due to the habitat they provide directly, and their influence on the spatial grain of a landscape by changing field size. Moreover, as will be explained more fully in chapter 4, optimisation of landscape structure for a limited set of objectives is unlikely to yield useful results, as in practice there are likely to be many other important processes dependent on landscape structure not accounted for in the optimisation.

Thus, there is a need to develop a new land-use simulation and evaluation procedure that can both simulate alterations to the land parcel structure of maps, and predict the consequences of land-use changes on pest and natural enemy populations.

1.6 Thesis aims

This thesis will address the above issues using observational and simulation studies of a model pest-natural enemy system. The system chosen is the interaction between aphids (Homoptera: aphididae), their hymenopterous parasitoids, and their syrphid predators, in winter wheat fields in the UK. The thesis will aim to do the following:

1. Present new insights into the interactions of multiple taxa with landscape context, disentangling the several aspects of “complexity” not previously investigated simultaneously, in order to better inform the nature and scale of management for conservation biocontrol.

2. Explore the variation in the role of landscape and local factors depending on species and time of year, and its implications for the possibility of optimising landscapes.

3. Address these challenges using novel analytical methods to deal with a multifaceted characterisation of landscape context, which are intended to be generalisable to questions sharing the same challenges.

4. Create a framework using statistical models, coupled to simulations of land-use change, in order to predict trade-offs and synergies between the responses of multiple natural enemies to landscape scale changes. This framework should be flexible, in order to consider the trade-offs and synergies between management for any set of goals. Given the number of different ecosystem services being demanded of farmed landscapes, this is the challenge at the very heart of sustainable intensification of agriculture.

5. Place an estimate of the economic value to farmers of aphid control by natural enemies in the study system. By doing this, a link between the character of farmed landscapes and the crop yields attainable from them can be made, moving towards a cost-benefit framework for evaluating potential multiple-farm scale conservation biocontrol management.

1.7 Overview of the study system

1.7.1 UK wheat production

Around 2 million hectares of winter wheat is grown annually in the UK, occupying 43% of all arable land. The climate of the arable lowlands in the UK is extremely favourable for wheat production, supporting average yields of 7.7 tonnes per ha in 2011 (DEFRA, 2011a), compared to only 2.92 tonnes per ha worldwide (USDA, 2011). The growing season in many areas is over 300 days in length, annual rainfall is neither too much or too little (usually!) at 600 – 1000 mm (MetOffice, 2012), and winter minima and summer maxima of temperature are rarely extreme enough to cause severe stress (Acevedo et al., 2002). Consequently, the UK has in recent years been a net exporter of wheat by weight, and the total value of the UK crop is about £1.2 billion per year (agriStats, 2012). Winter wheat is therefore a crop which is both ubiquitous enough to enable suitable study sites to be found easily, and a valuable enough to be a worthwhile crop to study.

1.7.2 Aphids as pests on wheat

Aphids were not thought of as a serious summer pest of wheat in the UK until 1968, when the first major outbreaks occurred (Vickerman and Wratten, 1979). These were attributed to changes in farming practice, such as increased application of Nitrogen, fungicides and growth regulators, which make wheat a more nutritious resource for aphids (e.g. Kolbe and Linke, 1974). Following these outbreaks, research into the effects of aphids on wheat yield and natural enemies of aphids began in earnest, resulting in a large body of literature to build upon.

Aphids cause damage and grain yield loss to wheat in three main ways. Firstly, aphid feeding causes direct loss of sugars and amino acids from the phloem, and so grain weight and protein content (and therefore quality for bread making) are reduced, particularly when aphid infestations are located in the ear, between flowering and the milky-ripe growth stages. Secondly, honeydew secreted by aphids impairs gas exchange through the leaves, and encourages fungal growth. Lastly, aphids can act as vectors of important cereal viruses, such as barley yellow dwarf virus (BYDV), to which plants are most susceptible as seedlings (Poehling et al., 2007).

In the UK and Northern Europe, there are three main species of wheat feeding aphid: the grain aphid *Sitobion avenae* (Fabricius); the rose-grain aphid *Metopolophium dirhodum* (Walker), and the bird cherry-oat aphid *Rhopalosiphum padi* (Linnaeus). *S.avenae* feeds on grasses all year round, migrating to cereals in May and June. Colonies form on upper leaves and ears during summers, so *S.avenae* has the largest effect per aphid through direct feeding. In autumn, migration to newly sown cereals makes it an important BYDV vector too. *M.dirhodum* alternates between *Rosa spp.* in winter and spring, and grasses in summer, migrating in late April or early May. *M.dirhodum* colonies are found mainly on leaves, so their primary negative effect is through honeydew secretion, but at high densities direct feeding is problematic. BYDV transmission is not an issue, as alatae migrate back to *Rosa spp.* in autumn. *R.padi* alternates feeding between *Prunus padus* in winter and spring, and grasses in summer and autumn. Spread of BYDV to early-sown cereals is the major cause of concern for this species, especially during mild winters where asexual forms can overwinter on cereals. Insecticides are applied most often in autumn prophyllactically against BYDV vectors, usually being non-selective synthetic pyrethroids such as cypermethrin or seed treatments (neo-nicotinoids) which limit aphid and natural enemy overwintering in autumn sown cereals. In summer, spraying is limited to when aphid densities exceed the economic threshold for direct feeding damage (Poehling et al., 2007).

Numbers of all three aphids tend to have a single summer peak in wheat, in June or July, followed by a rapid decline – the mid-season crash. The densities attained before the crash, and its timing, affect the economic injury to wheat yield. The reasons behind the dramatic nature of the population crash have been debated, but Karley et al. (2004) showed that it could result from relatively slow changes in mortality due to natural enemies, in combination with reduced birth rates and increased emigration due to declining plant quality.

In addition to the economic importance of aphids, they also represent a good choice of herbivore to study for practical reasons. Ubiquity of cereal aphids on winter wheat makes them excellent for studying interactions with the trophic levels above and below. Aphids are easily visible, and apterous forms remain stationary for long periods, facilitating field counts.

1.7.3 Aphid natural enemies

The natural enemy assemblage attacking cereal aphids consists of aphid specialist parasitic hymenoptera, polyphagous predators such as coccinellids, carabid and staphylinid beetles, predatory heteropterans, syrphid fly and neuropteran larvae, spiders, and entomopathic fungi. In this thesis, the role of hymenopterous aphid parasitoids and aphidophagous syrphid (hoverfly) larvae will be investigated. These two groups are in many years the most common aphid natural enemies (Chambers and Adams, 1986, Tenhumberg and Poehling, 1995), but have very different biology, making an excellent pair for comparison of the effects of landscape context on aphid control.

1.7.4 Parasitic Hymenoptera

The parasitoid fauna is dominated by braconid wasps of the genus *Aphidius*, but significant parasitism by the genera *Praon*, *Ephedrus* and *Aphelinus* can also occur. Female parasitoids lay eggs inside aphids, the larvae forming a papery cocoon (a “mummy”) and killing the aphid as it pupates, preventing that aphid reproducing.

Given that individual crop species are not available for the whole year in annual cropping systems, the ability to efficiently switch between aphid species or aphid-plant combinations is thought to be important for effective biological control by parasitoids via “indirect competition” between crop pests and alternative aphid hosts. Although single parasitoid species are observed to parasitise several aphid species on a number of different plants (Stary and Havelka, 2008), it is possible that separate races of parasitoid specialising on individual hosts are present. Laboratory studies have found that specialisation increases fitness of *Aphidius ervi*, with a genetic trade-off in the ability to parasitise one host over another (Henry et al., 2008). Powell and Wright (1988) also noted a genetic component to specialisation in laboratory reared *A.ervi*, but found no such pattern for wild-caught specimens, implying that inherited preferences in laboratory populations may be due to founder effects and genetic bottlenecks. Lozier et al. (2009) likewise found no host associated genetic differentiation in wild *Aphidius transcaspicus* populations.

Evidence of strong learned preference of parasitoids for specific aphid-plant complexes has also generated doubt concerning their ability to switch between aphids feeding on non-crop vegetation and different crop species. Adult female parasitoids locate suitable aphid hosts from a distance using olfactory cues, or “semiochemicals” emitted by both aphids and their host plants (Wickremasinghe and Emden, 1992). They have been to prefer olfactory cues specific to their natal environment. Females find their natal aphid species on a different plant species, or a different aphid species on her natal host plant, less attractive than their natal aphid-plant complex (Chow and Mackauer, 1991, van Emden et al., 1996). Powell et al. (2003) showed that for *Aphidius colemani* females, olfactory cues found on the outside of the mummy case are responsible for learned preferences, as when pupae were artificially excised, emerging adults could be trained to prefer non-natal aphid-plant combinations if given them to examine. However, Chow and Mackauer (1991) demonstrated in the laboratory that when the ratio of preferred to non-preferred aphid-plant complexes is very low, switching to the non-preferred complex can occur. In the field, as aphid populations peak asynchronously on different vegetation types, this situation may indeed often occur, and thereby facilitate switching.

In general then, there may be genetic and behavioural constraints which, while not absolutely preventing switching of parasitoids between aphid or plant species, are likely to influence the relative likelihood of this happening depending on the aphid-plant combinations involved.

Landscape context may also affect parasitoids in other ways. For instance, although adults can subsist on honeydew if necessary, the longevity and fecundity of adult female parasitoids is increased with access to floral nectar (Wäckers et al., 2008), so provision of this near to crop fields may enhance aphid parasitism. Secondly, the directed dispersal capacity of adult parasitoids is limited by their small size, so the spatial separation of resources may limit their fitness. *Aphidius spp*. can complete several generations using aphids on crops as hosts, and can overwinter in UK temperatures as diapausing larvae, so are likely to be favoured by asynchronously maturing crops in summer and potential overwintering sites (any vegetation where mummies are undisturbed) in relatively close proximity.

1.7.5 Aphidophagous syrphid larvae

Adult syrphids need to feed, mate and (for females) lay eggs to complete their life cycle. The most abundant species of syrphid in wheat, *Episyrphus balteatus* (de Geer) consume several hundred aphids during larval development, showing a functional as well as numerical response to aphid densities. Adult *E.balteatus* are active flyers, and this makes them more reliant on floral nectar for their energy needs than are parasitoids (Almohamad et al., 2009). Similarly to parasitoids, the fecundity, longevity and oviposition rate of females is significantly enhanced by access to preferred flower species (Laubertie et al., 2012). Female *E.balteatus* must continually switch between oviposition and feeding during their second week as adults (White et al., 1995), so one would expect an oviposition preference for aphid colonies close to floral resource patches in order to reserve as much energy as possible for egg production. At what spatial scale this reliance on flowers limits access to suitable oviposition sites is not clear however. Tinkeu et al. (1996) found no preference for aphid colonies near to floral margins within fields, but in another study species richness of syrphid larvae was greater adjacent to floral margins than to grassy ones (Haenke et al., 2009). In general, the high mobility of syrphid adults probably allows them to search over spatial scales larger than single fields.

In contrast to parasitoids, *E.balteatus* overwinters in Northern Europe in only low numbers due to poor cold tolerance (Hart and Bale, 1997), and observations suggest that migrations to and from Southern Europe occur every autumn and spring (Aubert et al., 1976). The role of local population persistence in determining the local abundance of this species is therefore likely to be small in comparison to redistribution according to foraging decisions made by the mobile adults, whereas the former may be significant for parasitoid populations. There is some evidence that female *E.balteatus* have preferences for particular aphid species and aphid-plant complexes (Almohamad et al., 2007), and preference tends to vary between individuals (Sadeghi and Gilbert, 1999). Given that many females laying eggs in wheat are likely to be long-distance migrants however (Tenhumberg and Poehling, 1995), the effect of these preferences on the ability of female *E.balteatus* to switch between different aphid-plant complexes in the local area, is unlikely to be as important a factor in their biological control potential as it may be for parasitoids.

This variation in traits between the two groups makes a very useful comparison, for studying the effects of different aspects of landscape context on different taxa with similar functional roles. Pragmatically too, they are the most common aphid natural enemies observed in the field, and as with the aphids themselves syrphid larvae and mummified aphids are very easily spotted on close inspection, so accurate counts can be made in the field.

1.7.6 Study location

The work described in this thesis was carried out in lowland England, primarily in the Vale of York due to the proximity to the University of Leeds (see figure 1.1). The areas shown in figure 1.1 roughly correspond to “Planned” countryside, where historically open-field cultivation was dominant due to high arable suitability (Rackham, 1986). While cropping patterns and farming system are environmentally determined to a large degree (Gabriel, 2009), cultural and historical idiosyncracies less closely linked to agricultural suitability provide useful variation. For example, disused aerodromes from the Second World War, equine studs, parkland estates, and re-vegetated coal mines and spoil heaps are common in the Yorkshire lowlands and provide heterogeneity of vegetation, yet their location does not seem to be confounded with environmental drivers. The degree of historic enclosure of open fields by hedges, which form a valuable resource and dispersal route for many arthropods (Cranmer et al., 2011), was also determined to some extent by the vagaries of local politics (Rackham, 1986). These features offer an excellent opportunity to disentangle the different aspects of landscape complexity, and control for the confounding effects of the abiotic environment in an observational study, through careful selection of study sites.

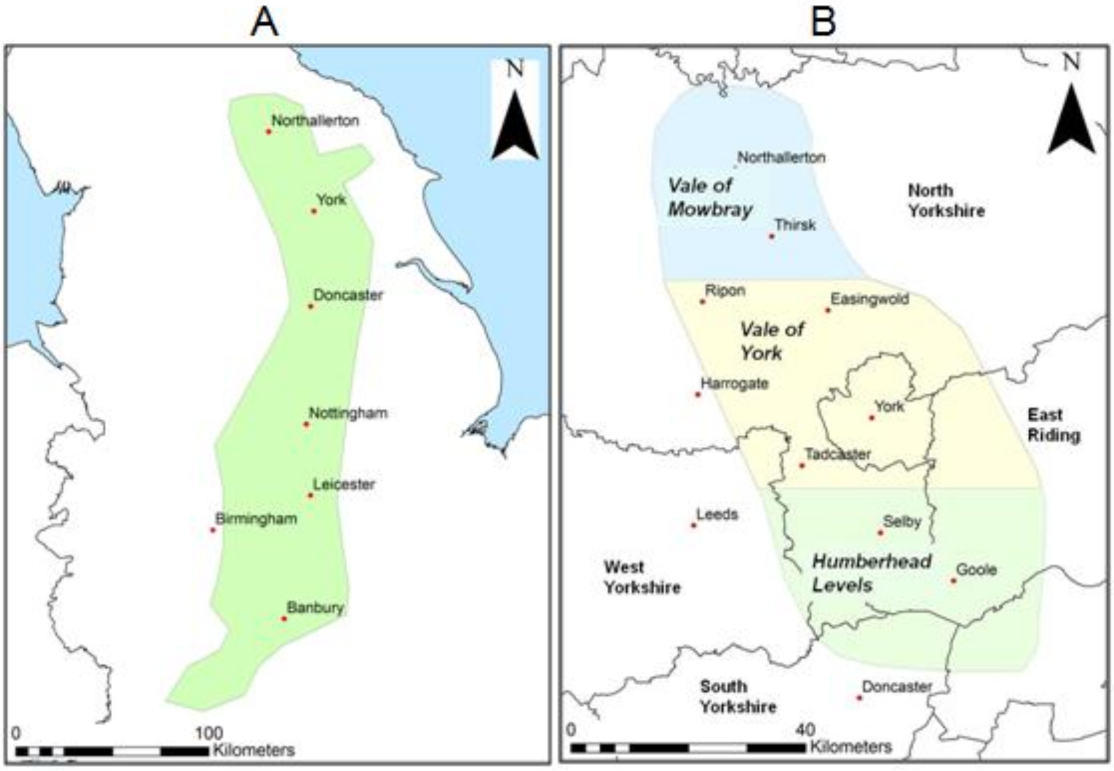

Figure 1.1: The location and extent of regions used for fieldwork in this thesis. Panel A: Green shading represents the convex polygon around study fields sampled in 2010, covering a swathe of lowland England with mixed farms. Panel B: Shaded areas are the convex polygon of sampled fields in 2011, focusing on the Vale of Mowbray, Vale of York, and the Humberhead levels. Maps created in ESRI ArcGIS 9.2 (ESRI (UK) Limited, 2006). National and county outline data obtained from EDINA UKBORDERS © Crown Copyright/database right 2012.

1.8 Thesis objectives and outline

This thesis will be presented in four main chapters, each of which will address a different part of the thesis aims outlined in section 1.6. These will be followed by a general discussion.

Chapter 2 explores temporal and taxonomic differences in the field-scale and landscape-scale correlates of aphid and parasitoid abundance. Specifically it asks: i) how does the importance of landscape context and field management changes over the season, for the aphid and parasitoid species making up the system?; ii) how does the role of different vegetation types in driving landscape effects differ between taxa and seasonally?; iii) are differences between species more important than the temporal change in the role of landscape for a single species? Several ways to quantify landscape context in terms of configuration and shape are introduced, with the aim of disentangling often correlated but theoretically separate axes of complexity. A new approach to analysis is taken, using multivariate techniques to compare variable importance measures from a machine-learning algorithm, for multiple species.

Chapter 3 aims to find parsimonious statistical models of the abundance of aphids, parasitoids and syrphid larvae at the functional group level, for interpreting the coarse-level effect of field and landscape-scale patterns on the aphid-natural enemy system. The resulting models demonstrate, more explicitly than in the previous chapter, the role that previously under-studied aspects of complexity play in influencing the abundance of the different functional groups. A novel variable selection procedure is used to deal with the large number of explanatory variables encountered when describing landscape complexity according to several different axes and at multiple spatial scales. The approach in this chapter allows interactions between different predictors to be modelled.

Chapter 4 investigates the trade-offs and synergies resulting from scenarios of potential changes in landscape composition and configuration, between desired outcomes for aphid, syrphid larvae and parasitoid abundance. A simulation method is used to create a number of altered maps, to which the models from the previous chapter are applied to produce predictions of likely outcomes. The simulation method acknowledges that modelling patterns is fundamentally different to predicting the outcome of future changes in landscape context, and provides a means to bridge the gap between heuristically simple habitat manipulations and the more abstract metrics of landscape structure introduced in the previous chapters. Land cover changes are discussed in relation to historic and potential future drivers. This aims to be an extensible methodology of forecasting for landscape optimisation problems.

Chapter 5 models the economic effect of parasitoids and syrphid larvae on aphid populations in the study system, using a correlative model of population dynamics. This chapter links the results of previous chapters, which studied the effect of landscape on natural enemy abundance, to the demonstrated economic returns necessary to make natural enemy management a key part of sustainable intensification. The analysis draws three comparisons: i) the difference in crop yield saved attributable to the action of syrphid larvae and parasitoids; ii) the difference in natural enemy value between fields in which they were scarce and those where they were abundant; and iii) the difference in value estimates for farmers who do not spray and for those who do.

Chapter 6 is a general discussion and synthesis of the findings of the preceding chapters, which then explores wider issues associated with sustainable intensification of agriculture and suggests future research directions.

2. Temporal variation in the effect of landscape context on cereal aphids and their primary parasitoids

Abstract

The character of agricultural landscapes affects populations of mobile insect pests and their natural enemies in crops, by influencing large scale abundance and movement patterns. However, there has been little study of how this influence might vary within a season, due to turnover in species composition of pests and natural enemies, or changing resource use by individual species.

In this chapter, a novel multivariate analysis based on the Random Forests algorithm was used to investigate how different aspects of landscape composition and configuration varied in their ability to predict the abundance of cereal aphids and parasitoids in wheat fields, between different species and between four sampling occasions. The analysis was based on field observations made in winter wheat fields in Eastern England, in the summers of 2010 and 2011.

For both aphids and parasitoids, the importance of different landscape variables varied more between the four sampling occasions than between species in both years, with the between-species differences becoming smaller over time. This may reflect a shift in the source of colonising aphids and parasitoids between sampling occasions, with different species showing increasingly similar movement pattern towards the end of the season. Landscape variables influencing parasitoid abundance appeared to shift from primarily measures related to semi-natural land in early visits to arable land related ones later on. Implications for control of aphid populations at different times of year are discussed.

Further research is required to evaluate the importance of inter-crop movements of pests and natural enemies, using landscape maps which distinguish different crop types over large areas.

2.1 Introduction

An increasing number of studies in recent years have highlighted the crucial influence of patterns of habitat composition and configuration – the “landscape context” - at a larger scale than the experimental plot or field, in determining the abundance and distribution of mobile organisms. Much of the research has concerned evaluating how farmland biodiversity benefits from subsidised agri-environment schemes, such as organic management (e.g. Gabriel et al., 2010), and interactions thereof with landscape context. Strong dependence on large scale vegetation patterns has been demonstrated for the abundance and diversity of groups as varied as birds (e.g. Haslem and Bennett, 2008), bees (e.g. Steffan-Dewenter et al., 2002), butterflies (e.g. Rundlof et al., 2008), beetles (e.g. Weibull et al., 2003), annual plants (e.g. Winqvist et al., 2011) and spiders (e.g. Schmidt et al., 2008). A particular emphasis has been placed on organisms providing supporting ecosystem services (or disservices) such as crop pollinators or crop pest natural enemies, because of their role in sustainable agriculture (Kremen et al., 2007, Tscharntke et al., 2008, Tscharntke et al., 2005).

Despite this proliferation of research, there are two aspects in particular which deserve more attention than they have previously received: the way in which landscape context is characterised in analyses, and temporal variation in the importance of landscape context.

2.1.1 The description of landscape context

The extent, diversity, shape and spatial arrangement of resource patches may all influence the abundance of pest insects and their natural enemies in crops, at scales appropriate for the species in question (Fahrig et al., 2011). Despite this, landscape context is described very simply in most cases, as the proportional area of one or a few vegetation types of relevance within a specified distance of the focal site (e.g. Roschewitz et al., 2005, Thies et al., 2005). Extracting proportional area information from thematic maps is relatively easy, and the meaning is intuitive. In contrast, measures of the shape, patch area distribution, diversity, cost-distance and the degree of aggregation of different vegetation classes are in general more abstract and ambiguous for interpretation, and often require more specialised software to calculate from habitat maps, which combine act as a deterrent. Nevertheless, deciding to omit these aspects of landscape context can lead to underestimates of the landscape dependence of species abundance (Perovic et al., 2010).

Often a single variable, such as the proportion of arable land, may be correlated with other features of agricultural landscapes like field size or habitat diversity, and on this basis used as an index of overall landscape "complexity" (e.g. Steffan-Dewenter et al., 2002, Thies and Tscharntke, 1999). This is legitimate, as long as the aim of the study is to describe responses of systems to the suite of correlated patterns which has characterised agricultural intensification until now, in the region of study only (e.g. Thies et al., 2011). However, drivers in the future, or in other regions may decouple these linked aspects of intensification and landscape complexity, reducing the strength of correlations. Using a single variable as a proxy for others when making generalisations to other regions, or into the future, is therefore less valid. Rather, when weaker correlations are present, this should present an opportunity for teasing apart the contributions of different aspects of complexity, to promote greater understanding.

Ideally then, metrics capturing all aspects of landscape complexity which could have plausible biological effects on the study system would be included in analyses, and studies designed to minimise the correlations between them, so their unique contribution can be inferred. The existence of any intrinsic set of fundamentally independent metrics of complexity is debatable, but for specific regions and species in question independent axes can be derived empirically through multivariate dimension reduction, as exemplified by Abson (2011). This is recognised, and some authors have achieved this, for example contrasting the effects of soil tillage (Rusch et al., 2011), length of field boundaries (Concepción et al., 2012), land use intensity (Jonsson et al., 2012) and dispersal costs between sources and sinks (Perovic et al., 2010) with proportion of semi-natural habitats.

Nonetheless, studies doing this are still surprisingly rare. In addition to differences in the research question being asked (see above), the difficulty of selecting study sites and the relatively recent recognition of the multiple meanings of "complexity" likely contributes to this rarity. However, an added deterrent is the computational and statistical difficulties associated with using large numbers of explanatory variables relative to the number of observations ("large p - small n") in traditional linear or additive models, often with high colinearity (Graham, 2003, Strobl et al., 2008). This leads to high type II error rates and uncertainty of parameter estimates (Carrascal et al., 2009). The problem is made more severe when landscapes are quantified over several spatial scales (commonly five or more), and for several different patch types. This is done, rightly, to account for uncertainty in the correct scale over which to measure the predictor, and to distinguish the effect of different vegetation types. In addition, including interactions between different scales or aspects of landscape context would be desirable, but in linear models these must be expressed explicitly, and would therefore further inflate the number of potential explanatory variables. Even if fitting a linear model is possible, there is high uncertainty over the choice of variables in the best model if simplification is carried out (Burnham and Anderson, 2002).

2.1.2 Temporal variation in landscape effects

The second area to which more attention should be drawn is that of temporal changes in landscape context effects.

For biological control of cereal aphids by parasitoids, temporal changes in the importance of different aspects of landscape context could arise from two sources.

Firstly, there are several species of both aphids and parasitoids interacting in this model system in the UK, each likely to respond to a slightly different aspect of landscape context, or at a different scale. For example, the aphid *Sitobion avenae* feeds only on grasses, whereas *Metopolophium dirhodum* inhabits roses when not on cereals, so the kinds of habitat acting as colonisation sources for these two won't be identical. Different parasitoid species have different host aphid preferences (Stary and Havelka, 2008), which will interact with the plant preferences of their preferred aphid species to determine which vegetation types constitute the best sources of parasitoid colonists of crop fields. If there is temporal turnover within or between years in the relative abundances of the species of aphid and parasitoid, analyses of overall parasitism or aphid abundance will be weighted towards the most abundant species at a given time, so studies conducted at different times would reveal different landscape drivers.

Secondly, for a single species, the status of different vegetation types as sources or sinks for colonisers will change during a season. In spring, early maturing crops receive net immigration from non-crop sources, but later these can be more important sources of colonisers for later maturing crops (Vorley and Wratten, 1987, Vorley, 1986, Stary and Havelka, 2008). For example, Pons and Stary (2003) showed a successive alfalfa-wheat-maize movement by several *Aphidius* species during one season in Catalonia. Although source-sink dynamics have been studied on a small scale, few studies have looked at the changing role of landscape complexity for species over the course of a season or between years (Kremen et al., 2007). In the light of studies showing strong learned preferences of aphid parasitoids for the olfactory cues associated with their natal aphid host and plant species (e.g. Powell et al., 2003, van Emden et al., 1996), it may be predicted that the odour of later maturing fields of the same crop species and cultivar would be the most attractive stimulus to parasitoids emerging from an earlier maturing field waning in suitability for aphid feeding. In the case of aphid movement, the provenance of migrants can shift substantially between years (Vialatte et al., 2007), so the landscape effects influencing early season colonisation may differ inter-annually, and more so perhaps than late-season effects.

So, both changes in how species respond to landscape and in species composition may alter the effect of landscape on pest-natural enemy systems over time.

This question is not of purely academic interest. The time period during which the interaction of landscape context with the species involved in pest-natural enemy system is most important economically may be restricted by the duration of crop susceptibility, the ability of pest populations to escape those of their enemies, and the times at which decisions about chemical pest management are made. For instance, winter wheat decreases in vulnerability to barley yellow dwarf virus (BYDV) infection from aphid vectors as it grows, whereas direct feeding by aphids causes most damage between flowering and milky-ripe growth stages in summer, and aphid abundances at these two times of year might be greatest in quite different sorts of landscape. Equally two valuable crops, such as winter wheat and winter barley, share pest and natural enemy associations but have differing phenology, so an optimum landscape context for biocontrol on wheat may differ from the optimum for barley.

2.1.3 An alternative analysis framework

Incorporating both of the issues discussed above, this chapter will investigate how the landscape context variables and field-scale factors most strongly affecting aphid and parasitoid abundance vary between different taxa, between sampling occasions in a season, and between the two years of sampling in this study. The landscape metrics will include measures of patch shape and configuration in addition to their proportional area, and be quantified at several spatial scales, to account for uncertainty of the correct scale, and differences between species.

The pre-requisites for incorporating these features into my analysis are: i) the method must be able to deal with large p – small n problems; and ii) it should allow comparison of the environmental correlates of several different response variables (different species and time points in this case). This second point has two implications. Firstly, the sets of predictor variables used to model the different response variables of interest should be identical to facilitate comparisons, meaning that the analysis method cannot involve model simplification. Secondly, it must be possible to estimate the relative importance of each variable in the model describing the response.

2.1.4 Random forests

These requirements will be addressed by using ensembles of classification and regression trees, using the “random forests” algorithm (Breiman, 2001). Single classification (regression) trees model a response variable by binary recursive partitioning, whereby at each split a threshold value is sought within all explanatory variables resulting in the largest decrease in the classification error (or increase in a goodness-of-fit criterion). The tree-like structure allows non-linear relationships and complex interactions among predictors to be modelled, without the need to express them explicitly. Random forests are ensembles of tree models, which, by introducing randomness into the tree-building process, often give better accuracy of predictions compared to single tree models (Strobl et al., 2008). For each tree, slightly different training data is obtained by sampling observations with replacement (a “bootstrap” sample). This helps prevent overfitting to idiosyncratic aspects of the data set. A second kind of randomness is added when at each split, a random subset of predictor variables is made available for splitting upon. This creates even more diverse trees, and allows explanatory variables with weak marginal influence to be included in interactions (where they may have strong explanatory power). The predicted value for each observation from the forest is the average of those from individual trees (Breiman, 2001).

It is not the accuracy of random forests however that is especially useful for this chapter, but the ability to calculate an importance score for each variable in the set used to construct the forest. The measure of importance used will be based on the permutational variable importance (PVI). Random forests have a measure of accuracy called the out-of-bag (OOB) error rate, which is the prediction accuracy for the observations left out of bootstrapped samples in the construction of each tree (the “out-of-bag” observations). The PVI is calculated by permuting the values of the variable in question, which should remove any relationship with the response variable, then recalculating the OOB error rate. The increase in the OOB error rate after scrambling is the PVI for that variable, and simulates the effect of removing the variable from the forest. Although it should be used with caution (see Strobl et al., 2008), this PVI should make a suitable measure for comparison between different responses.

If each response variable is then presented as a vector of numbers, representing the importance scores of all the predictor variables used to model the response, a “predictor importance by response” table is formed. Common multivariate techniques can then be applied to compare the similarity of different response variables, and the trends in importance of particular explanatory variables between responses. In essence, such a table is directly analogous to a “species by site” table, which is the most familiar setting for multivariate analysis in ecology.

Using exploratory machine-learning methods such as this sacrifices parsimony of the resulting models, and gives alone no insight into the direction or the magnitude of the effects of important variables. Instead, the emphasis is on comparison of the environmental correlates of different predictor variables, and for this purpose I think that these are worthwhile trade-offs.

2.1.5 Objectives

Using the variable importance based framework described above, this chapter will specifically focus on 3 questions, relating to taxonomic and temporal variability in the important variables influencing abundance:

1. What are the relative contributions of annual, seasonal and taxonomic variation in the importance of predictor variables, to overall differences? This will show whether turnover in taxonomic composition or temporal change in the variables influencing individual taxon abundance might be more important in creating temporal patterns for the groups as a whole.
2. Is landscape context dependence of aphid and parasitoid abundance greater earlier in the season, relative to other kinds of driver? If the main effect of landscape scale variables on aphid and parasitoid numbers is during initial colonisation, the importance of these is expected to decrease later in the season.
3. How do the identities of the most important predictor variables change within a season? It may be hypothesised that the importance of variables relating to non-crop vegetation availability will decrease in favour of variables describing the amount or aggregation of arable land.

2.2 Methods

2.2.1 Study site selection

Fields were selected to balance three competing goals:

- i) Maximising variation in aspects of landscape context relevant to aphids and their natural enemies.
- ii) Minimising the colinearity between these landscape variables of interest (VOI).
- iii) Minimise correlation of VOI with confounding spatial environmental variables (such as topography, climate and soil type), that would otherwise hamper statistical inference.

Choosing suitable wheat fields over a large study area, based on the surrounding land cover, posed challenges due to the lack of available data. Digital land-cover maps capture snapshots of vegetation from a particular year. Thus for annual crops, a map produced several years ago cannot predict which fields will contain which crop in a different year. In addition, no publically accessible records exist of what will be grown, and where, in the current or future years. To overcome these problems, a two-stage approach was carried out to select fields.

Logistical issues and differences between sampling sites led to slight differences in the selection procedures used in 2010 and 2011. The process for 2011 is described initially, followed by the differences of the 2010 process. A graphical overview of the process for 2011 is shown in figure 2.1 and that for 2010 in figure 2.2.

In the first stage, circular landscape sectors of 1km radius were chosen using past land cover data. At this scale the relative proportions of crops and other vegetation, and its spatial complexity are likely to be sufficiently constant between years to be informative for planning purposes. In the second stage, visits were made to locate wheat fields within the chosen sectors, and the relevant landowners were contacted.

The two stage approach was implemented as follows. Using GIS, a grid of points was created spaced 1 km apart, forming the centres of candidate landscapes, for a moving-window analysis of the entire study area. In a 1km circular buffer around each point three variables of interest (VOI) were quantified which, while not being used for post-hoc analysis due to the lack of *a priori* knowledge of the exact locations of study fields, nevertheless provided a pragmatic way to introduce variation in uncorrelated aspects of landscape composition and configuration of relevance to aphid and natural enemy dynamics. The variables chosen represent logically different ways in which managed countryside can differ: i) the percentage of arable land; ii) the density of field boundaries (*eudist*), and iii) a linear combination of the mean area (*AREA_MN*) and shape complexity (*SHAPE_MN*) of patches which summarises the degree of aggregation of arable land. See table 2.1 for definitions of italicised variable names.

A custom-made land cover map based on Ordnance Survey MasterMap (MM) (Ordnance Survey, 2011) was used data to supply the three landscape context variables. MM is spatially accurate, includes common linear features of arable land such as hedges and ditches, and provides vegetation descriptions for land parcels. However, it does not distinguish between different types of agricultural land use. So, for MM agricultural parcels Land Cover Map 2000 (LCM) vector data was used to assign to them a type of agricultural land use, depending on what category in the LCM layer lay beneath the centroid of the MM parcel. Due to the large number of vegetation descriptions in both datasets, a coarser but more generalisable classification was devised. It consisted of 8 classes (abbreviations used henceforth given in brackets) : i) arable land (“*arable”*); ii) agricultural grassland (“*ag_grass*” – included pasture and silage/hay meadows); iii) rough grassland (“*rough_grass*” – non-woody vegetation which isn’t grazed or cut); iv) mixed woody and non-woody vegetation (“*mixed*”); v) gardens (“*garden*”); vi) deciduous and coniferous woodland (“*woodland*”); vii) water bodies (“*water*”); and viii) buildings, roads and other non-vegetated surfaces (“*other*”).

With this new land cover map for the study area, the three VOI were evaluated for each circular sector, then the sector was categorised as a “low” (0th – 33rd percentile), “medium” (34th – 67th percentile) or “high” (above 67th percentile) value. A subset of sectors were carried forward which had either low or high (i.e. no “medium”) values of the three treatment variables, to maximise variation between study sites. These sites therefore belonged to one of 8 (all combinations of low and high for three variables = 2^3) treatment combinations.

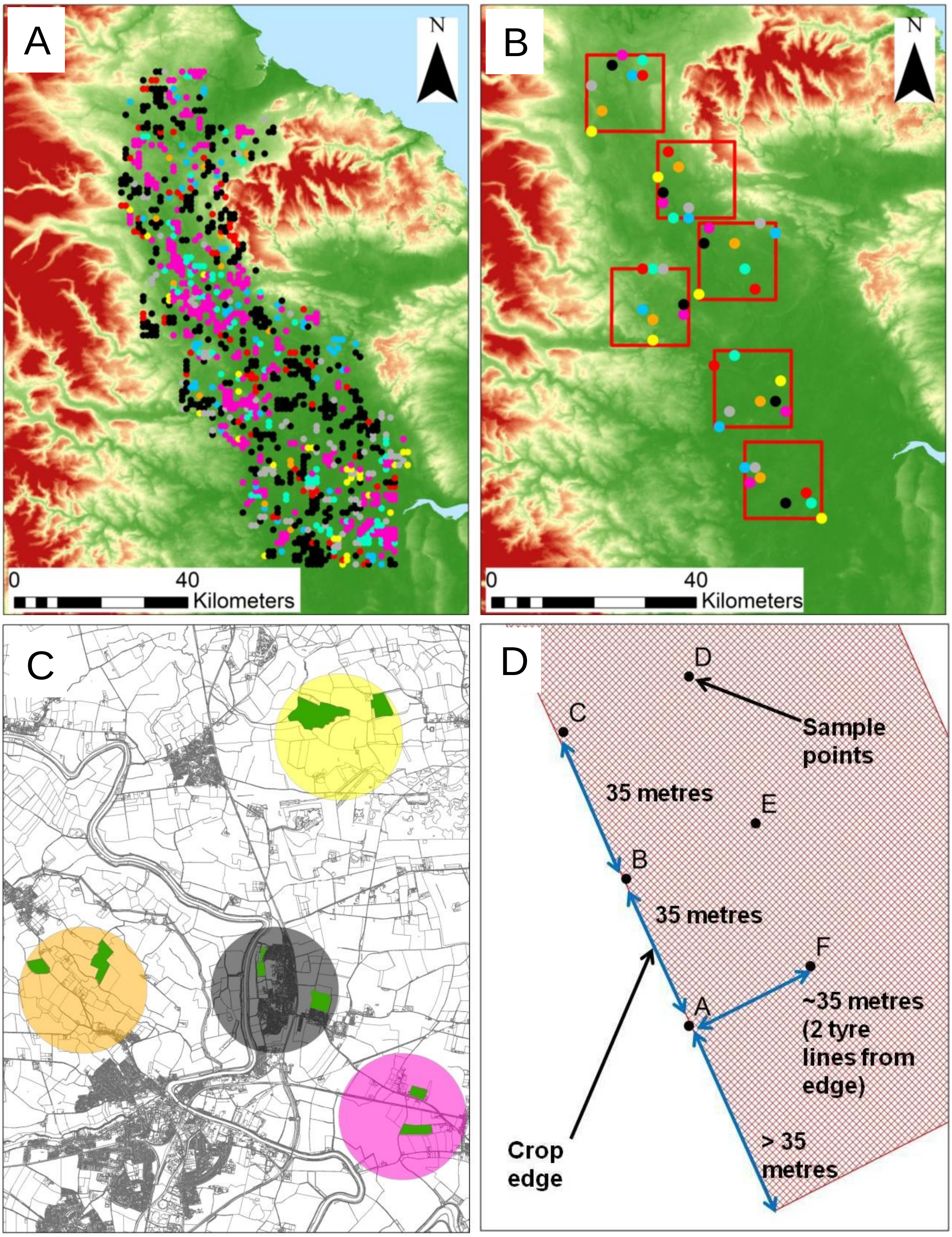

Figure 2.1: Maps to illustrate the site selection process for 2011 (A – C) and sampling design for both years (D).

A: Classification of each 1km radius circular sector into one of 8 treatment combinations (shown as different point colours), based on the three variables of interest, making up the first stage of site selection in 2011. Points are shown over an elevation model of the vale of York, to give geographic context. Clustering of the treatment combinations is apparent here. B: The six 15 by 15 km regions (red squares) containing all 8 combinations, used to ensure dispersion of sectors of the same treatment combination. Points shown are the chosen sectors. C: Example of four sectors (translucent colours), with 2 fields chosen in each (green fill). Background line-map is OS Mastermap data. D: Schematic of the sampling scheme in an example field. The red-hatched area is the crop itself. Edge sampling points were roughly 1m into the crop. On subsequent visits, sampling took place on a different set of 10 stems, but within 1m of the previous set. All maps created using ArcGIS 9.2 (ESRI (UK) Limited, 2006).

The next step was to choose a further subset of sectors where the VOI were uncorrelated with one another, and were not correlated with other confounding environmental variables. Appendix 1 shows how the VOI were related to environmental gradients before and after site-selection. Spatial clustering of treatment combinations is also undesirable, because the effects of unmeasured spatially structured environmental variables, spatially restricted events (such as thunderstorms) and spatial biological processes (such as dispersal) can introduce spatial autocorrelation in response variables (e.g. Beale et al., 2010).

To ensure spatial dispersion of sectors with the same treatment combination, the study region was first divided up into a series of overlapping 15 km by 15 km squares, and then selected those squares containing examples of all 8 treatment combinations. In each square, two Euclidean distances were then calculated between every pair of landscape sectors: the geographic distance between the central points; and a multivariate “environmental” distance incorporating standardised values of 12 variables describing the topography (Copyright University of Manchester/University College London Year 2001), climate as the first two axes of a principal component analysis of 10 climate variables (Met Office, 2010), agricultural suitability and ES participation (Copyright Natural England, 2011), percentage of urban area, and crop diversity (Shannon index) (EDINA National Data Centre, 2009) within each sector. The set of 8 sectors (1 of each treatment combination) from each square was chosen which maximised the dispersion of sectors having the same high/low category for individual VOI (e.g. sectors having a high proportion of arable land) in geographic and environmental space (“dispersion”), and minimised the mean environmental distance between all sectors (“matching”). Finally, six 15 km by 15 km squares were chosen which had the best combined rank of matching and dispersion, and which did not overlap.

This process supplied 48 landscape sectors, in each of which 2 winter wheat fields were chosen, with the condition that they were not adjacent. In one sector, no permission was obtained, leaving 94 fields in total. The efficacy of the selection procedure in achieving its aims is evaluated in appendix 1.

The site selection process in 2010 differed from that described above in a few key respects. Firstly, the initial moving window analysis was carried out across all of lowland England, but using a much less detailed dataset - the LCM data only – and a 4km square analysis window rather than a 1km radius circle. The matching criteria for environmental similarity of windows were as above, but only one VOI was used to provide variation in landscape composition. The length of “relevant border” - that between arable land and non-crop vegetation, per unit area of arable land – was calculated. This gave a combined measure of both the proportion of arable land and its aggregation. Each 4km by 4km square was then categorised, as above, into “High” or “Low” based on its relevant border value. Next, 11 visually environmentally homogeneous regions (same rock type and topography) were identified, where both High and Low squares were present. From these 11 sets, High/Low pairs of squares were chosen to give the best environmental match. Finally, four wheat fields were chosen in each square, rather than to two. The site selection in 2010 thus resulted in a much more clustered design than did the 2011 process, with 22 clusters of four fields spread over a much larger geographic area.

2.2.2 Field sampling

Field sampling took place in 88 winter wheat fields across lowland England in 2010, and 94 winter wheat fields in the Vale of York in 2011 (see figure . Live aphids, mummified aphids (hereafter referred to as “mummies”) and Syrphid larvae (relevant for other chapters) were counted in each field on 4 occasions between ear emergence and harvesting (2010: 6th June - 29th July; 2011: 3rd June – 29th July), at approximately 14 day intervals. Although counts of mummies underestimate aphid parasitism, the scale of sampling precluded dissection or aphid rearing. Visits progressed from the most southerly sites northwards, to minimise phenological differences due to sampling date. At each visit, counts were made at 6 points in the field; 3 points were spaced 35 m apart along one margin, 1 m into the crop (“edge” samples), and 3 points parallel to these approximately 35 m into the crop (“centre” samples; see figure 2.1 D for schematic). The exact distance of centre samples from the margin was determined by the location of the linear tyre tracks (a consideration to minimise trampling) but 35 metres was the target distance. The margin chosen for sampling was that nearest to an access point. At every point the leaves, stem and ears of 10 blindly chosen tillers were visually searched. Mummies were collected in gelatine capsules, and emerged adult parasitoids identified to genus in the laboratory, using the key of Powell (1982). When more than 5 mummies were present at a sample point, the first 5 were taken as a sample of the species present. Permission from landowners was obtained before commencing sampling, and data on insecticide applications to study fields was sought through correspondence with the relevant farmers or contractors. Insecticide application information was obtained for 75 of the 94 fields. On the last visit, the final crop height, and the number of stems in a 0.44 m^2 quadrat were recorded. Finally, the boundary type along which sampling took place was recorded, as the presence or absence of a grass strip, hedgerow, or trees.

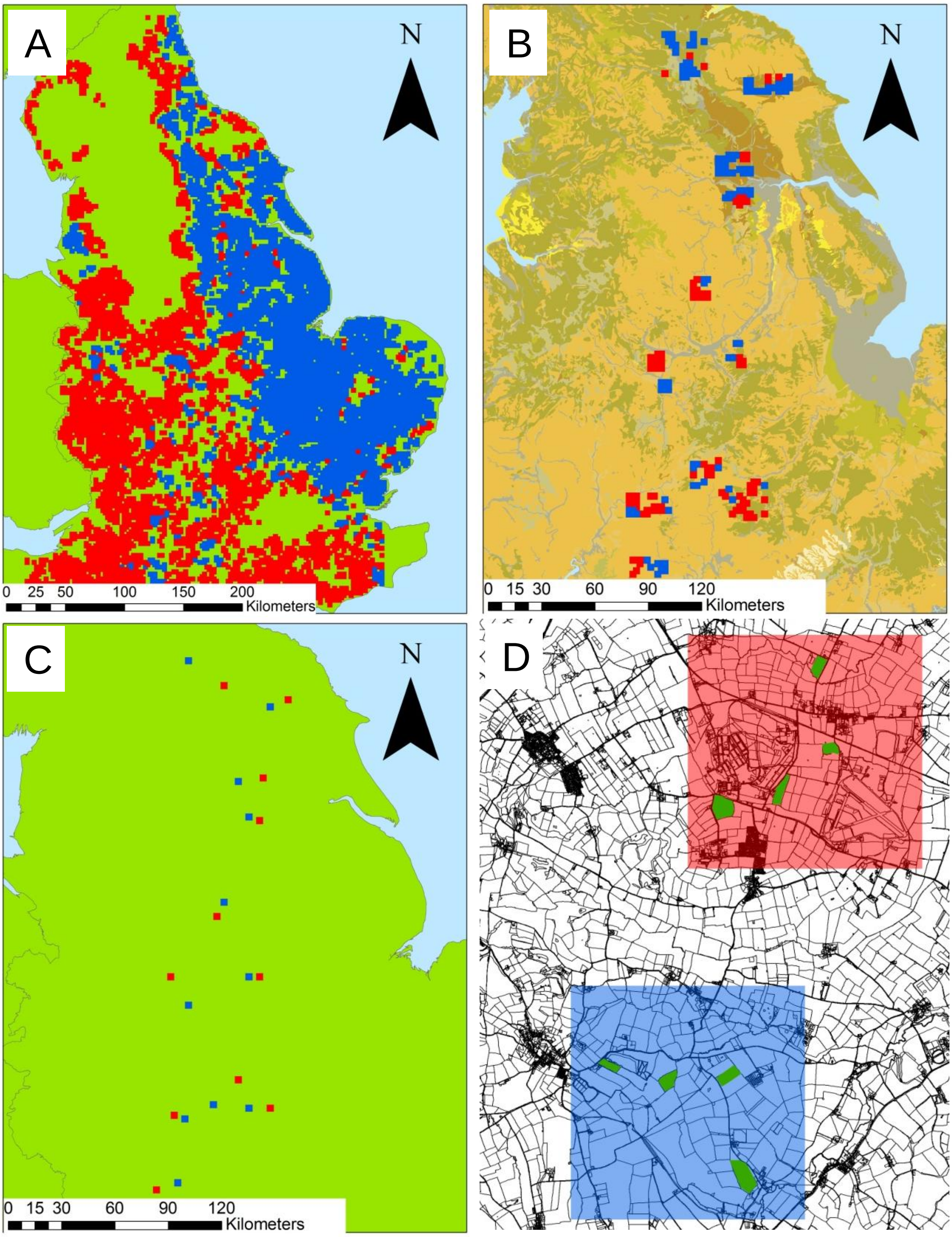

Figure 2.2: Maps outlining the site selection process for 2010.

A: Distribution of "High" (red) and "Low" (blue) categorised 4km by 4 km squares (according to "relevant border" – see main text) used as the first stage of site selection in 2010. A broad East-West separation is apparent, but a strip through Yorkshire and the Midlands contains squares of both categories in close proximity. B: Clusters containing both High and Low squares, on relatively homogeneous land. Map underneath shows superficial geology. C: Chosen High/Low pair of squares, according to environmental matching. D: Example High/Low pair, showing 4 chosen study fields in each (green fill), over OS Mastermap data. All maps assembled in ArcGIS 9.2 (ESRI (UK) Limited, 2006).

2.2.3 Quantification of landscape context

Metrics of landscape composition and configuration were quantified in circular buffers of 6 different radii around each sampling point: 200m, 500m, 1000m, 1500m, 2000m, and 2500m. This range of scales reflects a compromise between those found to be important in other studies, and computational feasibility. First of all, new land cover data was made for the largest buffer sizes, using MM data as a basis and the simplified classification scheme outlined above. Parcels classed as *ag_grass* and *arable* were digitised at the coarsest scales after inspection of the most recent satellite images available from Google Earth (© 2011 Infoterra Ltd. & Bluesky), and for smaller radii by reference to maps made during field sampling. The landscape level metrics calculated were the mean parcel shape complexity (*landSHAPE_MN*); the area-weighted mean patch area (*landAREA_AM*); the interspersion and juxtaposition index (*landIJI*), the patch type richness (*landPRD*), and the field boundary density (*eudist*).

Table 2.1: Definitions of landscape metrics

The metrics described below are used in this and subsequent chapters. All metrics except for “eudist” were calculated as below in Fragstats v3.3 (McGarigal, 2002), from which the codenames were taken. The field boundary density - eudist - was calculated in ArcGIS. Codenames in the text are often prefixed with the class name (e.g. “ag_grass”) or “land” to specify the level at which the metric is being applied. The suffixes “_MN” or “_AM”, to indicate the mean or area-weighted mean of the metric across patches in the class/whole landscape, and another to show the spatial extent (radius from focal point, in metres) at which the metric has been measured (e.g. “_1500”) are also added, where applicable. For possible variable ranges, “Inf” refers to infinity and ⌀ to the largest dimension of the analysis extent – the diameter in this case.

Metric codename and definition	Description	Range
$\boldsymbol{AREA = a_{ij}\left(\frac{1}{10000}\right)}$	Area, *a*, of patch *j* in class *i*, in hectares (ha).	0 < ***AREA*** < Inf
$\boldsymbol{PLAND = \frac{\sum_{j=1}^{n} a_{ij}}{A}(100)}$	Percentage of landscape. Sum of the area of all patches *j* of class *i,* divided by total landscape area *A*, converted to a percentage.	0 < ***PLAND*** ≤ 100
$\boldsymbol{SHAPE = \frac{p_{ij}}{4\sqrt{a_{ij}}}}$	Shape complexity. Perimeter of patch *j* of class *i* divided by the perimeter of a maximally compact (square) shape of equal area.	1 ≤ ***SHAPE*** < Inf
$\boldsymbol{IJI = \frac{-\sum_{k=1}^{m}\left[\left(\frac{e_{ik}}{\sum_{k=1}^{m} e_{ik}}\right)\ln\left(\frac{e_{ik}}{\sum_{k=1}^{m} e_{ik}}\right)\right]}{\ln(m-1)}(100)}$	Interspersion and Juxtaposition Index. The diversity of edge types *e* between patch types *i* and *k,* summed across all patch types*,* divided by the maximum possible value for *m* patch types.	0 < ***IJI*** ≤ 100
$\boldsymbol{PRD = \frac{m}{A}(10{,}000)(100)}$	Patch richness density. Total number of patch types *m,* per 100 ha of the total landscape area *A*.	0 < ***PRD*** < Inf
$\boldsymbol{eudist = \frac{\sum_{c=1}^{n} d_c}{n}}$	Euclidean distance *d* to the nearest linear feature for each cell *c* in a raster, averaged over all cells *n.* Proxy for field boundary density; denser boundaries = smaller distance on average.	0 ≤ ***eudist*** < ⌀

For each land cover class, the percentage cover of the buffer (*PLAND*) and the mean parcel shape complexity (*SHAPE_MN*) were evaluated. This set was chosen from among 42 metrics available from *Fragstats* because of the low correlation between metrics (maximum r = 0.459), and because each metric embodies a heuristically different aspect of landscape context (see table 2.1 for definitions). Metrics were not calculated for the “water” and “other” classes, as they were deemed unimportant for the present analysis. *ArcGIS* 9.2 (ESRI (UK) Limited, 2006) and *Fragstats* v3.3 (McGarigal, 2002) were used for all GIS operations.

2.2.4 Estimating explanatory variable importances

All statistical procedures were carried out using R version 2.14.0 (R Development Core Team, 2011). Random forests were constructed using the `cforest` function in the R package “party” (Hothorn et al., 2006), which produces models not biased against categorical predictors, unlike the alternative `randomForest` function. This was done for every response variable separately, with the sampling location being the unit of response. The variables making up the set of predictors were: *PLAND* and *SHAPE_MN* for every land cover class and the *IJI*, *SHAPE_MN, PRD*, *AREA_AM*, and *eudist* for pooled classes at each scale from 200m – 2500m (102 variables); the position of the sample in the field (edge plot or centre plot, “edge_cent”; 1 variable); the crop height and stem density (2 variables); the occurrence or not of spraying between the focal visit and the one previous (1 variable); the field boundary type (3 variables); and the numbers of aphids, parasitoids, syrphid larvae and hyperparasitoids at the previous visit (visits 2-4 only; 3-4 variables). For aphids, these last variables consisted of the abundance of conspecific aphids and all parasitoids and syrphid larvae; for parasitoids this included conspecific parasitoids, all hyperparasitoids and all aphids. By including the past aphid and parasitoid and syrphid larval numbers as predictors, temporal correlation of populations and effects of natural enemies are accounted for. The effects of other variables (for visits 2-4) therefore represent their influence on numbers over the period between the focal visit and the previous one, independent of the previous populations. Sampling date was also included to control for phenological effects. The overall number of variables was 112 (for aphids) or 113 (for parasitoids).

Due to the large difference in magnitude of populations between visits, using random forests of regression trees only would not have been suitable for all response variables. To cope with this, two different forests were made for each predictor, the first predicting the presence or absence (0/1) of individuals (step A1 in figure 2.3), and the second predicting the abundance where individuals were present (A|P; step A2).

Average variable importance (PVI) measures were then calculated from 50 repeats of the `cforest` algorithm (step B1 and B2) to smooth over the inherent randomness, with 500 trees per run, and $\sqrt{p}$ (for 0/1) or $p/3$ (for A|P) variables out of p sampled at each split of every tree. The raw PVI scores were divided by their standard deviation to give a "z-score" importance (ZI), which has the same meaning for 0/1 and A|P models. Averaging scores over 50 repeats increases the reliability of the estimates, because the number of trees per forest was restricted due to computational limitations. I then combined the ZI measures from the 0/1 and A|P models for each response variable, using a weighted average of the two (step C). If the response values across samples were mainly 0 or 1, then the 0/1 model weighed most strongly, whereas for larger abundances and few absences the A|P model dominated the average.

This procedure gave a single set of ZI measures for each response variable, comparable between taxa and time points. Figure 2.3 shows a graphical overview of the analysis.

An important aspect of the importance measures extracted from random forests to bear in mind, is that the variables receiving the highest scores may not be the most biologically likely causal agents, because variables strongly correlated with these will also have high scores. This is an advantage in so far as that correlated variables do not "steal" importance from one another, as occurs in linear models. However, it does mean that although overall patterns of similarity over all predictors may be informative, the identity of the most important predictors (as shown in tables 2.2 and 2.3) should be interpreted with caution.

2.2.5 Comparison of explanatory variable importance measures between visits and species

Several methods were applied to compare variable importance sets across different response variables, appropriate to each of the main questions.

Firstly, to compare the relative contribution of between-taxa and temporal variation to differences in predictor variable importances (question 1), response variables of interest were grouped into a table (step E in figure 2.3), with a column for each response and a row for each explanatory variable. The elements were then chord transformed, which results in the multivariate distance between response variables reflecting the difference in *relative* ZI of each predictor, rather than the absolute ZI (Legendre and Gallagher, 2001). This was done to remove the confounding effect of visit number on absolute ZI scores. With the chord-transformed table, permutational multivariate ANOVAs were performed to partition the sources of variation, using the `adonis` function in the R package “vegan” (Oksanen et al., 2010). This is a more robust alternative to a traditional MANOVA.

Secondly, to assess the change in the importance of broad categories of drivers over time (question 2) the predictor variables were grouped into five subsets, representing different sorts of influence: landscape effects, within field dynamics, boundary type, crop height and density, and position in the field. Each category was then given an importance score for predicting aphids and parasitoids as two grouped variables, using the maximum score of any of its constituent explanatory variables (step D). Using the maximum score prevents upward or downwards biases from using the sum or mean of the variables in each class, because the classes contained very different numbers of variables. Finally, the relative score for each class (shown in figure 2.7) was calculated, as the class score divided by the sum of all class scores.

Thirdly, in order to show differences in importance of individual explanatory variables (question 3) and the relative similarity of responses simultaneously, a principal component analysis (PCA) was applied to the chord-transformed table described above. The results of the PCA were then used to prepare biplots for graphical interpretation (see figure 2.8). To estimate effect size and direction of response is problematic due to the high degree of colinearity. For a very simple guide, linear mixed models were created using √transformed abundance for each response, including the explanatory variables shown in tables 2.2 and 2.3 for aphids and parasitoids respectively. The aphid and parasitoid populations at the previous visit were also added (as in the `cforest` models) to control for temporal correlation. These models were only intended as a very rough guide, as no validation was carried out, and large colinearity was present among the predictors.

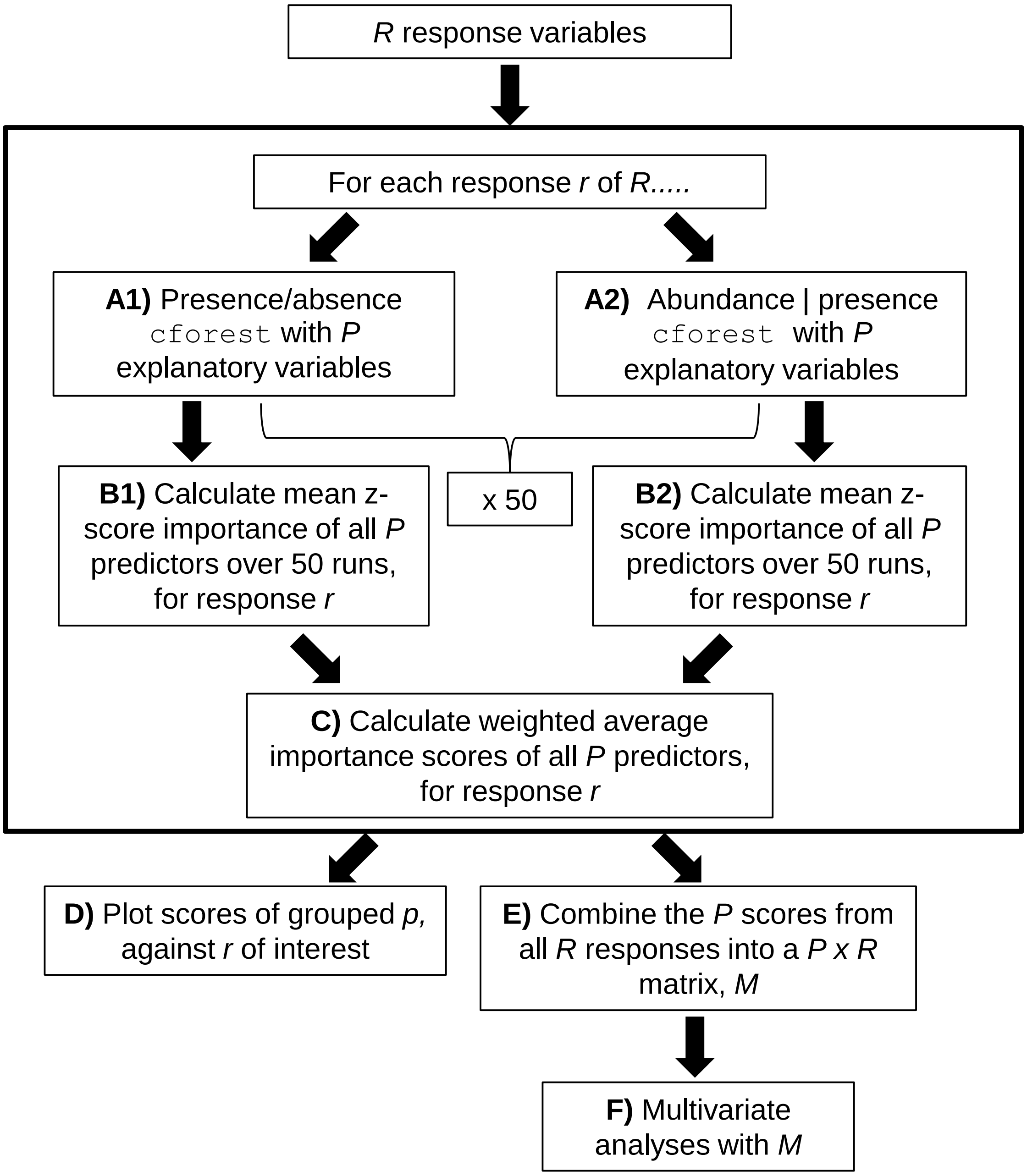

Figure 2.3: Workflow diagram of the methods used to compare the importance of explanatory variables in predicting different response variables.

See text for explanation of the steps. For steps E – H, only sets of response variables modelled with identical sets of predictor variables were used to create matrices for multivariate and distance analysis. Aphids and parasitoids were therefore treated separately. A visual representation of the matrix *M* is partially shown (for selected explanatory variables only) by tables 2.2 and 2.3, with the importance score represented by the depth of shading.

2.3 Results

2.3.1 Field observations

In 2010 (2011) a total of 108,318 (262,417) aphids were counted, of which 79% (78.5%) were *Metopolophium dirhodum*, 19.8% (18.5%) *Sitobion avenae* and 1.2% (3%) *Rhopalosiphum padi.* Mean aphid density increased to a maximum in the third round of visits (figure 2.4 A and B) in both years (2010: 4th to 16th July, 2011: 3rd to 14th

July) of 13.6 (29.5) aphids per tiller, but there was large among-field variation (range = 0.6 – 46.7 (0.4 – 185.8), s.d. = 7.25 (27.4)). Only six out of 64 fields, for which information was obtained, were sprayed with insecticide in summer 2010, compared to 24 out of 75 in 2011, when aphids were more numerous.

In 2010 (2011) 748 (5,747) parasitised aphids were collected, with much higher parasitism rates in 2011. The taxonomic composition of parasitoids reared from collected mummies was very similar for both years; 80.8% (82%) were *Aphidius sp.*, 10.8% (13%) *Praon sp.*, 7.8% (4.5%) *Ephedrus sp.* and 0.4% (0.5%) *Aphelinus sp* (figure 2.4 C and D).

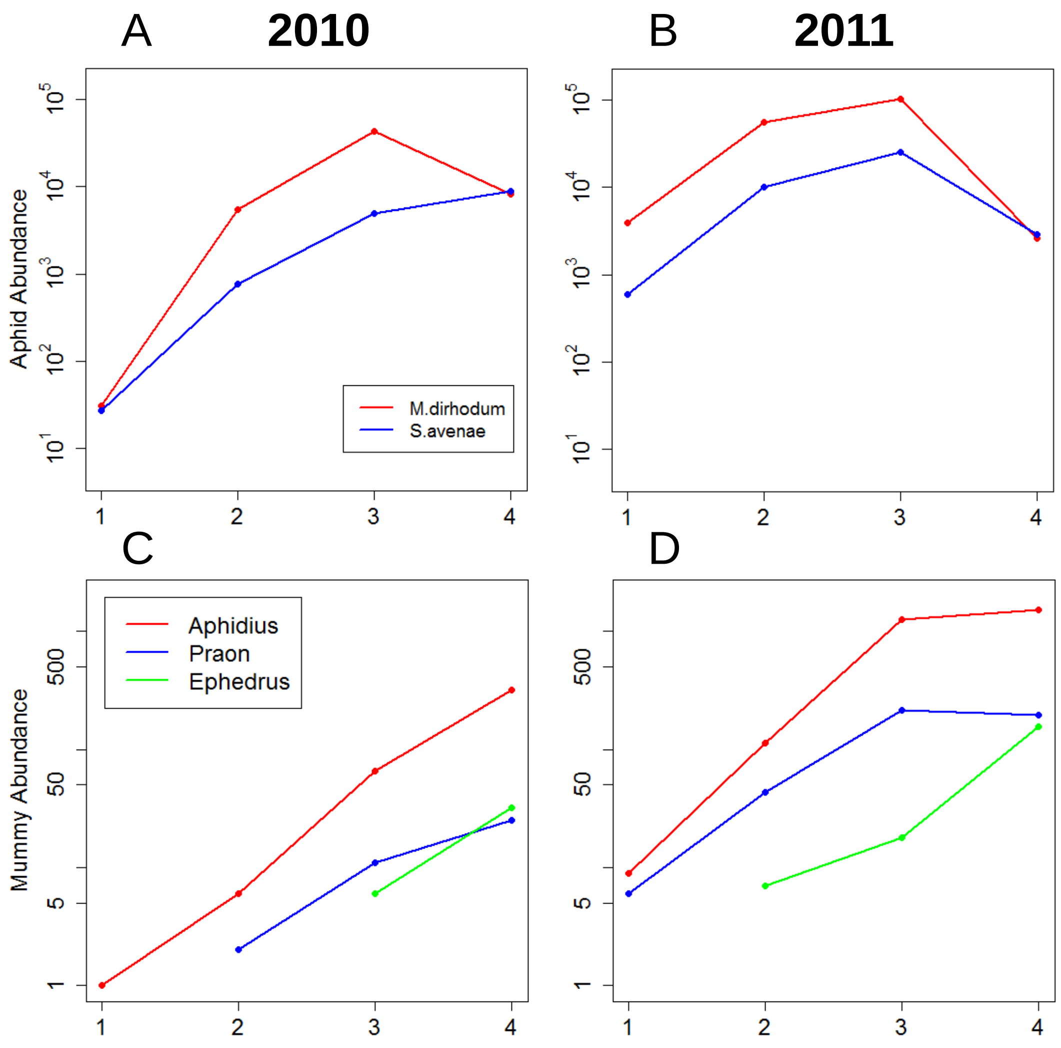

Figure 2.4: Temporal changes in aphid and parasitoid abundance and species composition.
Plots of abundance of the two most frequent aphid species (A and B) and the three most common primary parasitoid genera (C and D) versus the sampling occasion. Figures are the grand total of all fields.

2.3.2 What are the relative contributions of annual, seasonal and taxonomic variation in the importance of predictor variables, to overall differences?

For aphids, between-visit (seasonal) variation explains 30% of the overall difference in predictor importance between responses; much more than between species or inter-annual variation (figure 2.5). Twenty-two percent of total variation is attributable to the interaction between aphid species and visit, where the chord distance of variable importance sets between *S.avenae* and *M.dirhodum* becomes smaller later in the season. This pattern was observed in both 2010 and 2011 (figure 2.6 A). A smaller amount (12.5%) is contributed by the Year: Visit interaction, which shows a decrease in the inter-annual distance (within species) later in the season (figure 2.6 C), but because `cforest` models could not be made for the first visit in 2010 due to insufficient numbers, this source of variation may be underestimated here.

For parasitoids, seasonal (16%), annual (15%) and taxonomic (10%) variation contribute similarly to the total. The largest contribution comes from the Taxon: Visit interaction (31%), again showing a decrease in the between-taxon chord distance later in the season, in both years (figure 2.6 B). Sixteen percent of variation also arose from the Year: Taxon interaction, which shows that the between-year difference was lower for *Aphidius* than for *Praon.*

Overall, for both aphids and parasitoids, within-taxon seasonal differences dominated, with a convergence of taxa in variable importance space over time. This pattern is also visible in figure 2.8.

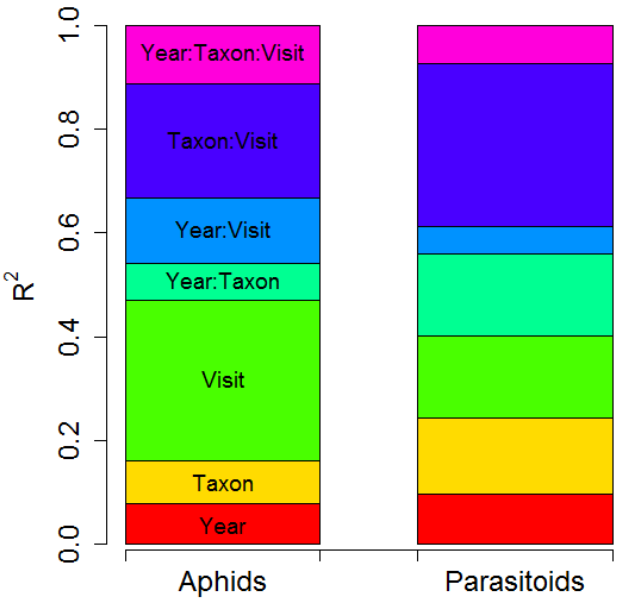

Figure 2.5: Variation in variable importance scores attributable to season, year and taxon. Bar plot showing the breakdown of variation in sets of variable importance scores between response variables, among inter-annual (Year), inter-visit (Visit) and inter-taxon (Taxon) differences, and their interactions. Results are shown from permutational multivariate ANOVAs carried out with aphids and parasitoids separately. Colours in the parasitoid bar represent the same variable as those in the aphid bar.

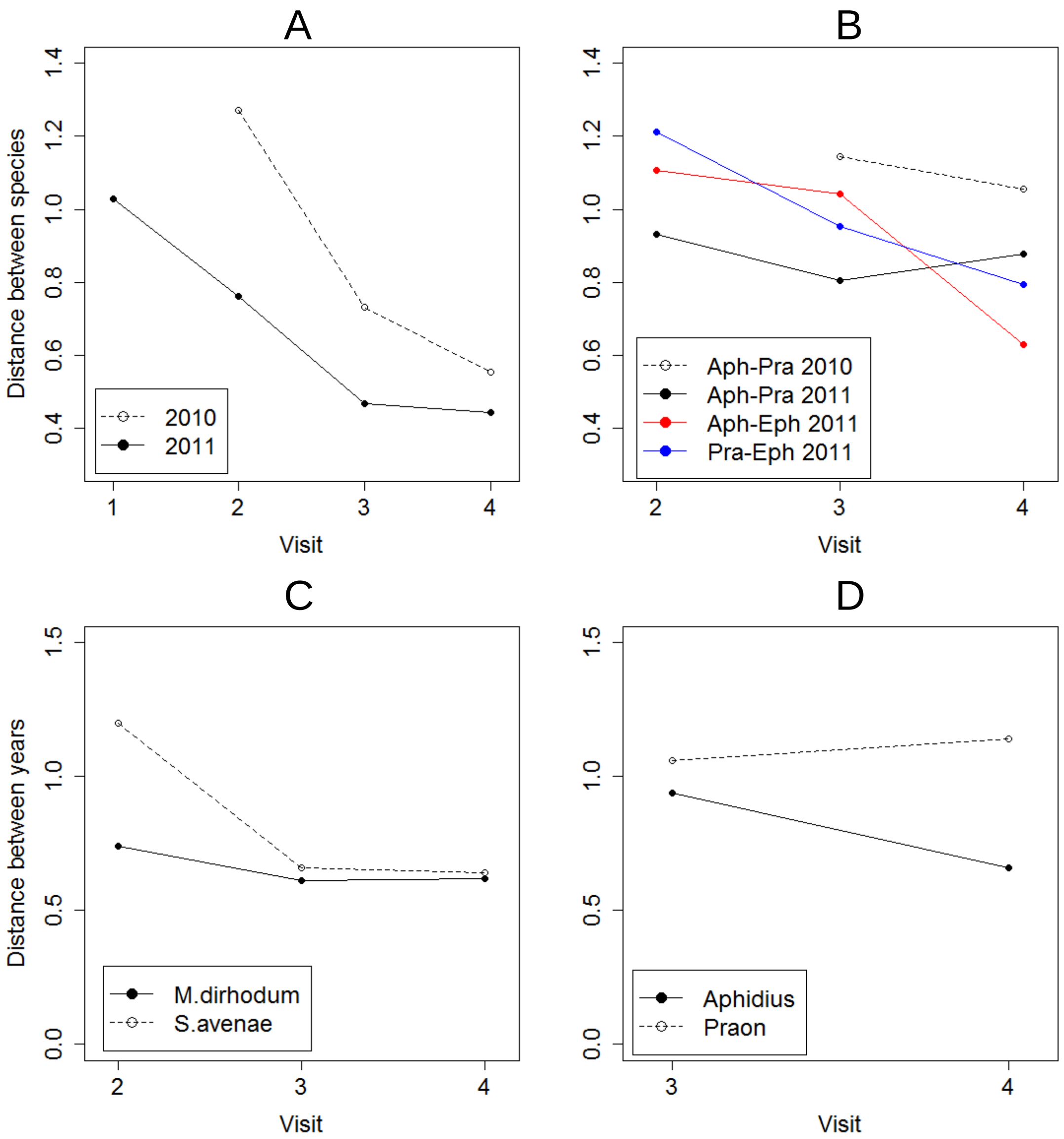

Figure 2.6: Differences between taxa and between years in sets of variable importance scores.
Plots show the chord distance in variable importance space between response variables. Panels A and B show the between-taxa distances for aphids and parasitoids respectively, plotted against the sampling occasion to show trends over time. In panel A, points represent the distance between *M.dirhodum* and *S.avenae.* In panel B, “Aph” = *Aphidius sp*., “Pra” = *Praon sp*., and “Eph” = *Ephedrus sp*. Panels C and D show the between-year distance for each taxon plotted against sampling occasion (except for Eph, as this was only present at visit 4 in 2010. Where sampling occasions are not shown, this was due to insufficient abundance of that response for a `cforest` model to be fitted. Absolute distance values are not important, only the trends.

2.3.3 Is landscape context dependence of aphid and parasitoid abundance greater earlier in the season, relative to other kinds of driver?

There is no evidence from this analysis that landscape context effects diminish in their importance for aphids or parasitoids as the season progresses, relative to other sorts of predictor. For aphids as a group in 2011, the best landscape predictor rose in importance relative to other classes from the second to fourth visits, with an early bias towards central locations declining over time (figure 2.7 A and C). The influence of aphid and parasitoid numbers at the previous visit was strongest for the third visit, declining at the fourth.

For parasitoids as a group in 2011, the effect of the best landscape predictor was most influential at the third visit, but still more important at the fourth visit than the second. Parasitoid distribution was centre biased from visit 2 onwards, but only matched the bias in aphid distribution after visit 3 (figure 2.7 C), producing less predation pressure on aphids further into the field in the early season, but more even pressure later.

Grouped importance for the first visit is not shown, as by definition, the relative effect of previous aphid and parasitoid abundance could not be accounted for. This should be borne in mind when interpreting these results. For example, no large trends are apparent in the importance of edge type or crop structure variables in figure 2.7, but table 2.2 shows that the presence of boundary trees is important for *M.dirhodum* abundance at the first visit in 2011.

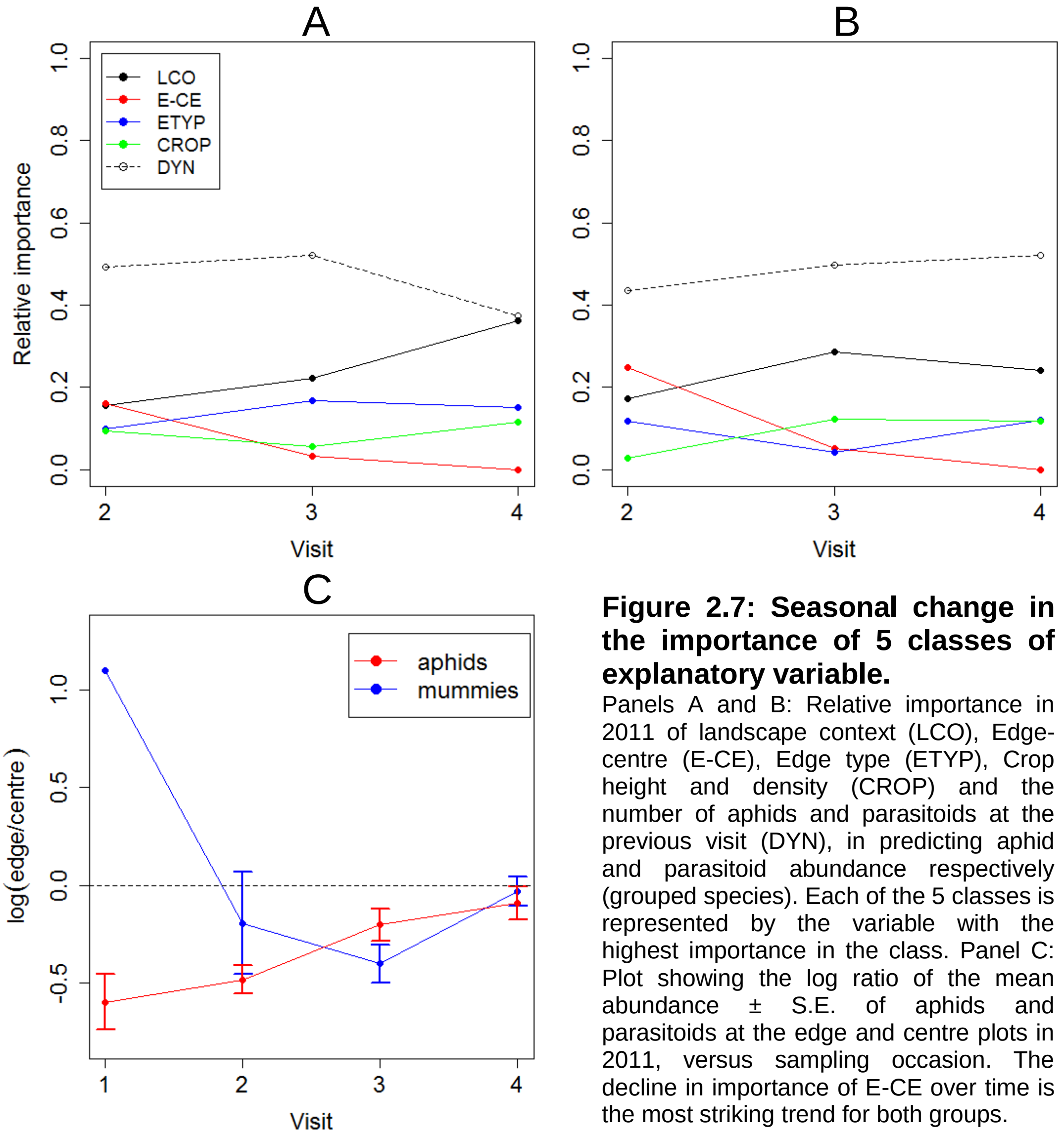

Figure 2.7: Seasonal change in the importance of 5 classes of explanatory variable.
Panels A and B: Relative importance in 2011 of landscape context (LCO), Edge-centre (E-CE), Edge type (ETYP), Crop height and density (CROP) and the number of aphids and parasitoids at the previous visit (DYN), in predicting aphid and parasitoid abundance respectively (grouped species). Each of the 5 classes is represented by the variable with the highest importance in the class. Panel C: Plot showing the log ratio of the mean abundance ± S.E. of aphids and parasitoids at the edge and centre plots in 2011, versus sampling occasion. The decline in importance of E-CE over time is the most striking trend for both groups.

2.3.4 *How do the identities of the most important predictor variables change within a season?*

Contrary to the hypothesised pattern, for aphids there was no sign of a shift from dependence on non-crop to arable related measures later in the season. Trends in the relative importance of individual predictors are evident (Figure 2.8 A and B; table 2.2) however.

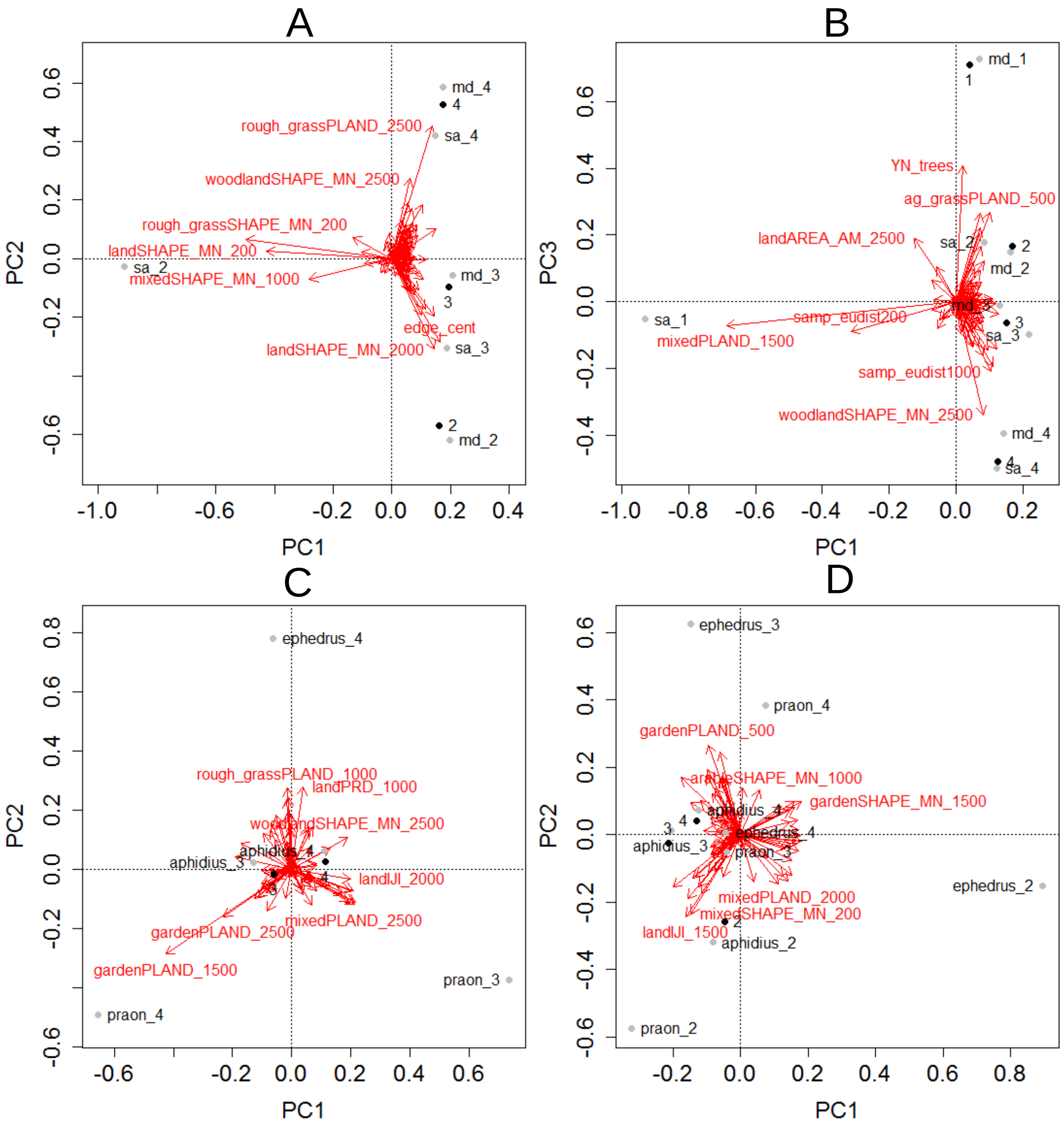

Figure 2.8: Biplots showing seasonal change in predictor importance
Biplots present the scores from a PCA of predictor variables as red arrows and labels, and the response variables as grey points and black labels. Points labelled e.g. "sa_2" or "md_3" stand for the score for *S.avenae* at visit 2 and *M.dirhodum* at visit 3 respectively. Black points and single digits are the projection of the scores for all aphids or all parasitoids at that visit. Panels A and B are biplots for aphid abundances in 2010 and 2011 respectively. Panels C and D are biplots for parasitoid abundances in 2010 and 2011. The PCA was carried out on a chord-transformed table, so the distances between variable points approximate the chord distance between them. The direction and length of an arrow shows how much the importance of that predictor variable changes along that axis; arrow length is not proportional to absolute importance.

Table 2.2: Summary of variable importances by species and visit for Aphids

SA = *S.avenae*, MD = *M.dirhodum*. Year and visit number (2-4 in 2010, 1-4 in 2011) above each column indicate the response modelled in each case, with `cforest`. The depth of cell shading is proportional to the chord transformed ZI of the corresponding variable in modelling that response (white = low, black = high). Predictor variables shown are those with the highest ZI of their class (see question 2) for any one of the responses. Red "+", blue "-" and green "+/-" signs summarise the effect direction and magnitude from simple mixed models of the response against the explanatory variables in the table, in addition to numbers of aphids at the previous visit. Important variables with "+/-" can be involved in an interaction, or non-monotonic relationship with the response, rather than having no effect. Symbols intended only as a guide.

Variable	MD 2010			SA 2010			MD 2011				SA 2011			
	2	3	4	2	3	4	1	2	3	4	1	2	3	4
landSHAPE_MN_2000	-	+/-	+/-	+/-	-	-	-	+/-	+/-	+/-	+	+/-	+	+/-
landIJI_1500	- -	-	+/-	-	-	-	+	+	+/-	+	+	+	-	+/-
landPRD_500	+/-	+	-	+	+	-	+	+	+	+	+	+	+	+/-
samp_eudist1000	- -	-	+/-	-	-	-	+/-	-	-	+/-	+	-	-	+/-
rough_grassPLAND_2500	+	+/-	+ +	+/-	+/-	+ +	-	-	+/-	+	+	-	+/-	+/-
rough_grassSHAPE_MN_200	+/-	+/-	+/-	-	+/-	+/-	+/-	+/-	+/-	+	+/-	+/-	-	+/-
mixedPLAND_1500	+/-	+/-	-	+	+/-	-	-	+/-	-	-	+/-	+/-	-	+
mixedSHAPE_MN_500	+	+	-	+/-	+	+/-	+	+	+/-	+	+/-	+/-	+	+/-
mixedSHAPE_MN_1000	-	+/-	+	-	+/-	+/-	+/-	+	+	- -	-	+	+	-
mixedSHAPE_MN_2500	-	+	-	+/-	+	+	+	-	+	+	+/-	+/-	+	+/-
ag_grassPLAND_500	+/-	-	+	+/-	-	+/-	+	+	- -	-	+	+	-	-
woodlandSHAPE_MN_2500	+/-	+/-	+	-	+/-	+	+/-	-	-	+	+/-	+	+/-	+ +
Density	+/-	+/-	-	-	+/-	+/-	+/-	-	+/-	+/-	+/-	-	-	+/-
Height	+	+/-	+	+/-	-	+/-	+	+	+/-	+/-	-	+/-	+/-	+/-
edge_cent	- -	-	+	-	-	-	- -	- -	+/-	+	-	+/-	-	+/-
YN_trees	- -	+ +	+	- -	+ +	+ + +	+ +	-	+	+/-	+/-	-	-	+/-
YN_grass	-	+ +	- -	+/-	+	+/-	+	+ +	+ + +	+ +	+/-	+/-	+ +	+
YN_hedge	-	+	+/-	+	+/-	+	-	+ +	+	+ +	+	+/-	+ +	+

Table 2.3: Summary of variable importances by species and visit for Parasitoids

Format is the same as above. Aph. = *Aphidius sp*., Pra. = *Praon sp.*, Eph = *Ephedrus sp.*

Variable	Aph 2010		Pra 2010		Eph 2010	Aph 2011			Pra 2011			Eph 2011		
	3	4	3	4	4	2	3	4	2	3	4	2	3	4
landSHAPE_MN_2000	+	-	-	+/-	-	+/-	-	+/-	+/-	-	-	+/-	-	+/-
landIJI_1500	-	+/-	+/-	-	- - -	+/-	-	+/-	+	+	+ +	+	+	+/-
landIJI_2000	+	+	+	+	+ + +	+	+	+	-	-	-	-	+/-	+
landPRD_1000	+/-	-	-	+/-	-	+	+	+/-	-	+/-	-	+/-	-	+/-
landPRD_2500	+/-	+/-	+/-	-	+/-	-	- -	- -	+	+	+	+	+	-
samp_eudist1500	+/-	+/-	+/-	+/-	-	-	-	-	+	+/-	-	+	-	-
arableSHAPE_MN_1000	-	+/-	+/-	+/-	+/-	+	+ +	+	+	+/-	+	+/-	+/-	+
gardenPLAND_200	+/-	+/-	-	+/-	+/-	+/-	+/-	+/-	+/-	+/-	+	+/-	+/-	+/-
gardenPLAND_1500	+/-	-	+/-	+	+ +	+/-	+	+	+	+	+/-	-	+	+
gardenPLAND_2500	+	+/-	+/-	-	- -	-	+	+	-	-	-	-	- -	+
mixedSHAPE_MN_200	-	-	+/-	+/-	+	+/-	+	+	+/-	+/-	+/-	+	+/-	+/-
woodlandPLAND_200	+/-	+/-	+/-	-	+/-	+	+/-	+/-	+/-	+	+/-	-	+/-	+/-
Density	+/-	+/-	+	+/-	+/-	-	-	+/-	+/-	-	+/-	+/-	+/-	+/-
Height	+/-	+/-	-	-	+/-	+/-	-	-	+/-	+/-	+/-	-	+/-	+
edge_cent	+/-	+/-	-	+	-	- -	-	-	+/-	+/-	+	-	+/-	+/-
YN_trees	+ +	+	-	+	- -	+/-	- -	-	+ +	+ +	+	+	-	-
YN_hedge	-	+/-	+	-	+/-	-	-	+/-	-	+/-	-	-	-	+
YN_grass	+	+/-	-	+	-	-	-	+/-	-	-	+	-	-	+

In 2010, local shape complexity influences *S.avenae* strongly initially (table 2.2), thereafter showing similar patterns to *M.dirhodum. M.dirhodum* abundance responds to larger scale shape complexity and edge-centre effects early on, then positive effects of larger scale area of rough grassland later on. In 2011 *S.avenae* is again is very different to *M.dirhodum* at the first visit, responding to the area of mixed vegetation at medium scales, and positively to the presence of boundary trees respectively. At the final visit, both species abundances positively correlate with large scale availability of woodland.

For their parasitoids however there is some evidence of non-crop to crop shift in predictor importance. In 2011 the large scale interspersion of vegetation types is dominant for *Aphidius* and *Praon* initially, but both taxa are then influenced by the shape complexity of arable land at medium scales later on. *Praon* also shows an influence of garden availability later in the season, in both years.

2.4 Discussion

This chapter presented a novel method to compare the environmental correlates of many different response variables, with landscape context being characterised by several different aspects of complexity. High seasonal variability in the importance of predictors was observed for both aphids and parasitoids. Landscape context had an important influence at all time points observed in the study, but the identity of the most important aspects changed over the season for each species. Furthermore, measures of the shape complexity and interspersion of vegetation patches were among the most important variables. These findings are discussed in more detail below, for aphids and parasitoids in turn.

2.4.1 Annual, seasonal and taxonomic variation in the importance of predictors: Aphids

For aphids, between visit variation was far more important than between species variation, and there was also a trend for reduced between species difference at later visits. The first result supports the notion that from the perspective of a single aphid species, the kind of landscape which augments abundance in a focal field changes through the season, when the effect of past aphid and natural enemy populations are accounted for. The second result in effect shows that the correlation in numbers of *M.dirhodum* and *S.avenae* increases later in the season.

These patterns could occur when the most suitable vegetation types for sustaining aphid growth, and therefore sources of alate colonists, shifts over the course of a season from spring hosts to summer hosts. Because both aphid species feed on cereals in summer, if continued movement occurs, the sources of colonists for the two species will become more similar. For aphids, it was hypothesised that predominantly non-crop overwintering sites would provide immigrants to early-maturing crops such as winter barley and early-sown winter wheat, but that these crops themselves would constitute better sources of new colonists for late-sown winter wheat than non-crop vegetation. If this is the case, given that the crucial period between wheat flowering and milk-ripening where feeding damage is most serious is relatively short, the landscape characteristics influencing crop damage through aphid movements (i.e. not mediated through natural enemies) are likely to differ according to the timing of this vulnerable period.

The result presented in figure 2.7 shows that the most important landscape effect does not become weaker relative to other predictors later in the season. Östman et al. (2003) and others have characterised aphid population dynamics as two distinct phases; an establishment phase, then a growth phase. The results of my second question however, which asked whether the importance of landscape effects wanes over the course of the four visits, suggests that movement of aphids between vegetation patches influences abundance throughout the season, rather than only during a brief initial period. A stable or increasing relative importance of the landscape category could, in theory, arise even as the absolute importance decreases, if all other categories decrease in concert due to aphid numbers being unrelated to any of the predictor variables included. Preliminary analyses showed this not to be the case however, with absolute importances overall remaining stable or even rising. A caveat to note here though is that although my sampling periods were likely to have spanned initial colonisation of *S.avenae* individuals, for 2011 in particular *M.dirhodum* was already established in many fields by my first sample, and so early landscape context effects may have proved much more important for this species if earlier sampling had occurred.

The evidence of a switch in the source of migrating aphids from non-crop to crop vegetation was not well supported when the identity of predictor variables having the greatest importance (table 2.2), or the largest change in importance (figure 2.8 A and B) was compared between visits. Arable related factors were not among the most important variables later in the season in either year. Instead, in later visits for both years, there seems to be a tendency for the large scale shape complexity of woodland and area of rough grassland to become important. If this is a real effect, it suggests that non-crop sources of aphids continue to be important in the later season. Landscape structure may interact with aphid movements through short-range re-distribution of aphids after long-range migration, causing perimeter-dependent immigration into attractive patches (Hamback et al., 2007), in addition to local dispersal. The importance of shape-complexity measures early in the season, as observed for *M.dirhodum* in 2010, may reflect this effect. There is some evidence that the dominant dispersal behaviour of aphids changes from long to short distance migration from spring to summer (Loxdale et al., 1993), which could explain the change in landscape effects over the season, without the need to invoke changes in the role of different vegetation types as aphid sources.

In earlier visits, there was more difference between years than in later visits (figure 2.6 C). This could be due to inter-annual variation in the importance of different sources of aphid colonists, in addition to the seasonal changes mentioned previously. For example, Vialatte et al. (2007) showed that migrants from local sources contributed proportionally more to establishing populations than long-distance migrants when aphid numbers were high. *M. dirhodum* in this study were far more numerous in 2011 than in 2010 (figure 2.4 A and B), and for this species shape complexity at the largest spatial scale was most important early on in 2010, compared to non-arable land within 500 metres in 2011.

Effects of boundary trees and edge-centre differences were present in both years for aphids. The edges of fields often receive smaller inputs of fertiliser and growth regulators than further in, so wheat can sustain higher aphid population growth in field centres (Ruggle and Holst, 1995). Later in the season however, edge-centre differences tend to even out and aphids become more uniformly distributed (Taylor and Taylor, 1977). Boundary trees can act as wind-breaks which encourage the precipitation of aphids from aerial planktonic dispersal in the lee of the boundary (Lewis and Stephenson, 1966), but also shade field edges, prolonging the period suitable for aphid feeding in these areas. Differences between the edge and the centre of fields can have consequences for the efficacy of biological control if natural enemy distribution does not match that of the aphids (Krauss et al., 2011).

2.4.2 Annual, seasonal and taxonomic variation in the importance of predictors: Parasitoids

For parasitoids, the most obvious feature to emerge was the variation between response variables contributed by the interaction between seasonal and taxonomic effects. This can be looked at in two ways; figure 2.6 B emphasises decreasing between-species differences later in the season, whereas when response variable scores are presented as a biplot (figure 2.8 C and D) it highlights the difference in between-visit distances for the different parasitoid taxa. Figure 2.7 B shows that this trend is largely driven by the difference in important predictors between *Ephedrus* and the other two genera over time. *Ephedrus* abundance in wheat fields tended to increase later than that of the other two genera in both years (figure 2.4 C and D), which could reflect dispersal sources of Ephedrus becoming more similar to those of *Aphidius* and *Praon* towards the end of the season. Early season differences between genera may stem from differing specialisation of the constituent species. The dominant Aphidiine was *Aphidius uzbekistanicus*, which Stary and Havelka (2008) found only attacking S.avenae on grasses in the Czech Republic, whereas *Praon volucre* and *Ephedrus plagiator* (the likely identities of most specimens in the other two genera) are rather more generalist/switching specialist in feeding habit, parasitizing aphids on a wide variety of plant families and habitat types. However, no particular association of *Aphidius* with grassland early on was evident.

The importance of landscape context did not decrease throughout the season for parasitoids, as for aphids. When considering the mechanisms of landscape context effects on mobile natural enemies such as parasitoids, it is more widely accepted that continual aerial dispersal occurs throughout the season, in contrast to apterous aphids where landscape effects are less widely recognised (Chaplin-Kramer et al., 2011). The dispersal of parasitoids into fields from alternative hosts on other vegetation has been widely studied (e.g. Langer and Hance, 2004, Langer, 2001, Müller and Godfray, 1999, Muller and Godfray, 1997), and its role in increasing pest suppression evaluated. What has been less widely studied is the role of crop fields to act as sources of parasitoids (but see Lu et al., 2012, Vorley and Wratten, 1987, Pons and Starý, 2003). During peak aphid densities on cereals, these fields are likely to be the largest sources of emerging parasitoids in arable dominated landscapes, especially from crops with similar plant volatile profiles to the crop of interest, when considering the learned olfactory preferences common in aphid parasitoids (see section 1.7.4 in the general introduction).

In contrast to the pattern for aphids, the identity of important landscape variables predicting parasitoid abundance did show a shift towards arable-related measures later in the season in 2011, but not in 2010. The interspersion and juxtaposition of vegetation types in the surrounding 1500 - 2000 metres (landIJI) appeared to be important for the abundance of both *Aphidius* and *Praon* early in the season, perhaps because this tends to reduce the spatial separation of alternative resources. While this remains important for *Praon*, for both genera the shape complexity of arable land in the surrounding 1km becomes more important later on. Whilst not constituting evidence of any causal relationship (see below), this does suggest that greater edge length over which parasitoids can disperse from nearby arable fields increases the immigration into the focal field. Noticeable also is the importance of garden availability, particularly for

Praon. Gardens are recognised as excellent resources for pollinators, due to their consistency and diversity of resource provision (Osborne et al., 2008). The same may also be true for parasitoids, whose fecundity and longevity are increased by floral nectar sources found in gardens (Simpson et al., 2011, Wäckers et al., 2008), and alternative aphid hosts are available there, particularly for generalist species such as *Praon volucre*.

If variable importances affecting parasitoid pressure on aphids change through the season, management should target increasing parasitoid abundance at the time that it can do the most to suppress aphid populations. As was the case for aphids however, the timing of the critical period for crop damage is dependent upon sowing dates and rates of maturation of particular fields, so the landscape effects favouring parasitoid immigration into early maturing cereal fields might be different to those increasing abundance in later maturing fields. Given the more convincing evidence for a role of crops as sources for parasitoids than for aphids, what constitutes a beneficial landscape context for parasitoid immigration may vary more within a season than the landscape factors influencing aphid immigration rate. Landscapes favouring parasitoid dispersal into fields in both the early and late seasons may be compatible however, if they both benefit from greater interspersion of different vegetation types (as seems to be the case here). If only proportional area based metrics had been included in analysis, this possibility would not have been evident. If the optima for providing early and late biocontrol (or for two different crops) are not compatible, compromises should be sought which maximise overall return. Nevertheless, dependence among the proportion and shapes of different habitat types make trade-offs and synergies non-trivial to predict. This issue will be explored in chapter 4.

2.4.3 Perspectives on the use of the variable importance framework

The models of species abundance in this chapter are based on correlations, and there was no way to account for residual spatial autocorrelation in the response variable. Inference of causal mechanisms should therefore be drawn with caution, and results should rather indicate areas for more focused future research.

Correlation between aphid and parasitoid taxa at later visits (figure 2.6) could arise from causal agents not included as explanatory variables, which happen to be correlated with those that were, to produce artefactual results. Insecticide spraying would synchronise populations of all species in a field, but the effect of this was accounted for in the analysis. Nevertheless, other variables, such as microclimate and the effect of natural enemies not recorded in the survey (such as entomopathic fungi) could be correlated with some of those included. If this were the case, “landscape effects" need not involve any interaction of aphids or parasitoids with landscape context through dispersal late in the season, but could arise through overfitting of `cforest` models to extreme values of aphid abundance, with variation purely arising through differences in growth rate and mortality.

The use of different sets of study sites, with aphid numbers varying over large spatial scales, introduced variation into the data which may have been wrongly modelled with some explanatory variables included. In 2010 it is likely that there was more variation among explanatory variables than in 2011 due to the wider geographic spread of fields, which may have resulted in some important variables from 2010 not being found to be so in 2011.

In its defence, `cforest` is designed to be robust to idiosyncratic features of a dataset, due to the bootstrapping scheme used to create each tree in random forests, and because trees are not grown maximally, but until no new split passes a threshold of significance (Hothorn et al., 2006). Some statistical intuition is helpful here. For example, if a pattern occurs in both years, or when average abundance of the response variable is greater, it is less likely to be a statistical artefact.

2.4.4 Conclusions and future directions

This chapter presented a novel method of representing response variables in terms of the importance of predictor variables explaining them, and used this method to explore temporal and taxonomic differences in variables affecting aphid and parasitoid abundance. Metrics describing the spatial configuration of land cover were important, and suggested mechanisms of landscape context influence which would not have been evident without their inclusion. Machine-learning algorithms enabled the comparison of the importance of many predictors across different response variables, and in doing so permitted the consequences for inference of considering the year and the season during which a study took place to be uncovered. This chapter presented evidence that aphids themselves interact with landscape structure, raising the possibility manipulating aphid populations through "geographic control", in addition to biological control. It has also shown shifts in the importance of different landscape context metrics for initial and later season abundance of parasitoids. "Optimal" landscape planning is thus likely to be a compromise between the benefits to crops with differing phenologies.

Equally, the analysis has demonstrated where improvements could have been made to provide more solid conclusions. Sampling more frequently, and with more effort would help elucidate seasonal changes more effectively, but this was beyond the means of this study due to the large number of fields sampled. In addition, mapping of crop types and management over large areas would enable more specific hypotheses about movements of insects. Being able to distinguish early and late-sown cereals would be a particular advantage for studying spill-over between crops, both for post-hoc analysis and for initial study field selection. More precisely, perhaps functional characterisation of crop fields according to their herbivore induced volatile organic compound profile and maturation timing, may provide a more powerful way to study the shifting role of different patches as sources of parasitoids for a focal field, compared to agronomic distinctions. Again, this was not feasible here, but could be implemented using real-time aerial or satellite photography where available (Bradter et al., 2011, Pena-Barragan et al., 2011).

Finally, the use of random forest importance measures in this framework comes with two drawbacks, which if addressed, would increase the power of this sort of analysis considerably. Firstly, there is no way (to the author’s knowledge) of accounting for correlation in the response variable caused by grouping in space or otherwise by inclusion of random variables. This would go some way to mitigate the problems associated with inference in the presence of spatial dependence (Keitt et al., 2002). Secondly, the ability of the PVI scores to identify individual important predictors is decreased by the high scores given to variables only incidentally correlated with them (Strobl et al., 2008). The `cforest` model also allows computation of a “conditional variable importance” measure, which does not suffer this problem. However, the computational demands of the conditional importance calculation increase enormously as the number of predictor variables rises, and was therefore impractical for use in this analysis.

The random forests PVI is not well suited to the purpose of finding a parsimonious set of causally important variables. Nor are random forests very useful for determining the form of the relationship between explanatory and response variables, due to the lack of a single consensus tree model. Rather a more parsimonious parametric modelling approach should be taken to fulfil these purposes, and this will be the aim of the next chapter.

3. Modelling scale dependent influences on an aphid – natural enemy system

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Abstract

Recent research has linked the abundance of crop pest insects and their natural enemies to the complexity of the surrounding landscape, but measures of landscape complexity have been simplistic. The proportional area, shape complexity and interspersion of vegetation types, in addition to field boundary density, may have differing effects on abundances of pests and their natural enemies, but considering these measures, at multiple spatial scales, raises problems for statistical analysis.

This chapter aimed to discover which local and landscape-scale variables best predict the abundance of cereal aphids in winter wheat crops, and two functional groups of aphid predators: parasitoid wasps and hoverfly larvae. Insect counts were made in 75 fields on four occasions between June and July 2011, in Yorkshire, UK. A novel variable selection procedure using the Random Forests algorithm was developed, to objectively find a small number of strong predictors from a large number of candidates with a high degree of colinearity.

Aphids and their parasitoids were more abundant in landscapes with high shape complexity within 1km, and parasitoids benefited from high interspersion of land cover types in a 2.5 km radius. In contrast, hoverfly larvae were more influenced by the proportion of arable land within 1.5 km and rough grassland at the smallest spatial scale, with configuration being of less importance. Aphids were more abundant in the centre of fields than at the edges, and this difference was influenced by field margin vegetation, but neither parasitoid nor hoverfly larval abundance, per aphid, showed edge to centre trends.

The importance of configurational aspects of landscape complexity suggest that the supply of migrants from local alternative habitats may be a more important determinant of aphid and parasitoid abundance than for hoverfly larvae, whose local density is probably limited by access to floral resources.

The novel variable selection procedure may be adapted to tackle other ecological problems with many, colinear candidate predictors.

3.1 Introduction

Land use change driven by agricultural intensification has been widely implicated in the erosion of the ability of natural enemies to suppress pest populations in crop fields. Conversely, deliberate manipulation of land use patterns to increase natural enemy (NE) abundance, promote diversity, and facilitate dispersal into crop fields has been suggested as strategy for increasing natural biological control potential (Kremen et al., 2007, Marino and Landis, 1996, Tscharntke et al., 2008). To do this effectively requires knowledge of the responses of pest insects and their natural enemies to changes in specific aspects of the surrounding landscape.

Aphids are consumed by a large range of polyphagous and specialist arthropods, but the interactions of species or functional groups with the composition and spatial structure of the surrounding landscape varies according to species traits. Among the most important are body size (Borthagaray et al., 2012), capacity for directed and passive dispersal (Bilde and Topping, 2004), non-prey resource needs (e.g. Wäckers et al., 2008), and reproductive rate. Thus, different aphid predators will respond individualistically to changes in agricultural landscapes, whether intended for conservation biocontrol or not. Hymenopterous parasitoids and syrphid larvae are two of the most common aphid natural enemies in English winter wheat fields, and differ markedly in many aspects of their biology which may affect the characteristics of landscape and the spatial scale which are most important to them (see section 1.7.4 and 1.7.5 in Chapter 1 for more detail). It is useful therefore to model the patterns of parasitoid and syrphid larval abundance to be better able to predict the outcome for overall natural enemy pressure in this study system, and by studying co-occurrence patterns, estimate how similarly the two groups might respond to landscape changes.

Studies have previously recorded patterns for more than one group of natural enemy (e.g. Thies et al., 2011), but have generally quantified landscape “complexity” very simply, as the proportion of semi-natural or arable land. As discussed in section 2.1.1 of the previous chapter, if a better understanding of the effects of land use change on biological control by multiple natural enemies is sought then the shapes of vegetation patches and their spatial relationship with other patches should not be ignored, vegetation should not be lumped together as “semi-natural” or “agricultural” land cover categories, and variables should be measured over several spatial scales.

By demanding this level of thematic resolution and diversity of metrics however, the number and colinearity of potential explanatory variables and interactions is inflated to a degree that makes model fitting and simplification in a traditional linear modelling framework very difficult. In chapter two the random forests algorithm was used to explore how the importance of explanatory variables changes when predicting the abundance of different species, in samples taken at different time points. Random forests are able to handle more explanatory variables than observations without overfitting (so called (“large *p* – small *n*” problems), and to implicitly model non-linear relationships and interactions among predictors through its constituent tree models (see the introduction to chapter 2 for more details) (Breiman, 2001, Cutler et al., 2007). These strengths make random forests a very useful tool to incorporate the desired broader definition of landscape composition and structure when modelling the abundance of species at focal sites.

3.1.1 Drawbacks of random forests for model interpretation

Unfortunately, the flexibility of the random forests algorithm comes at the expense of interpretability. Unlike single tree models, random forest produces no single “consensus” tree whose structure can be explored. Partial dependence plots can be used to show the mean of the response at different values of single explanatory variables (Cutler et al., 2007), but interactions are difficult to visualise. The large number of variables involved, and the absence of parameters describing the sign and magnitude of the relationship of predictor and response make inference rather bewildering and perhaps somewhat arbitrary. Additionally, spatial autocorrelation of species abundances introduced through unmeasured extrinsic drivers or intrinsic dispersal and aggregation cannot be accounted for in random forests, which could lead to invalid conclusions being drawn (Keitt et al., 2002, Lennon, 2000). The dataset of aphid and parasitoid abundances used for the previous chapter were widely spread in geographic space, introducing large scale spatial trends in response variables. The identities of truly important predictor variables from that analysis were uncertain, and variables merely correlated with these or with stochastic spatial variation may have been given high importance scores. Conditional variable importance, which would have been more reliable in picking out truly important predictors, could not be calculated due to computational restrictions.

3.1.2 Advantages of parametric regression

In contrast to random forests, traditional parametric (or semi-parametric) regression models using a much smaller number of explanatory variables are more suitable tools for describing relationships clearly. There are numerous methods to account for spatial autocorrelation in species abundances available for parametric models (Dormann et al., 2007), and the model equation can be used (with care) to interpolate or extrapolate predictions to new environmental conditions (Guisan and Zimmermann, 2000). Furthermore, the importance of explanatory variables in parametric models is inherently conditional on the effects of other variables in the model, so superfluous correlated predictors are penalised by goodness-of-fit criteria.

For better interpretation of the effects of individual variables describing landscape context on the abundance of cereal aphids and their natural enemies, parametric models will be used in this chapter. The relationship of aphid abundance in focal fields will be modelled, as a function of landscape context at several spatial scales and field-scale variables. Then the response of the numbers of parasitoids and aphidophagous syrphid larvae to aphid abundance will be investigated, and how this is itself influenced landscape and field-scale variables. The aim will be to find a small set of strong, uncorrelated explanatory variables to model each response variable, from among the many possible candidates.

3.1.3 Reducing the number of predictors

Parametric regression models, and selection procedures based upon them, perform poorly in the case of large p – small n problems, and when there is multicolinearity between predictors (Graham, 2003, Carrascal et al., 2009). The broad set of landscape composition and configuration metrics quantified at several spatial scales, used in the previous chapter, will also be used here as candidate variables for a model selection procedure. However, doing so results in both large p and colinearity. With a large number of variables and interactions, model selections in multiple regression based on stepwise procedures are unstable (Burnham and Anderson, 2002), and all-subsets approaches quickly become unfeasible due to a “combinatorial explosion” as the number of predictors rises. In addition, curved relationships and interactions need to be specified explicitly in linear models, further adding to the complexity of model selection.

Due to these problems, before multiple regression is carried out it is common to undertake preliminary exclusion of variables, to reduce the colinearity and overall number of potential predictors. Diagnostic tools such as variance inflation factors can guide researchers as to which variables are collinear, but biological intuition is important when deciding which of a set of correlated variables to omit (Zuur et al., 2009). A useful alternative to variable pre-selection involves re-casting the predictor variables as sets of orthogonal linear combinations, using principal components regression (Jolliffe, 2002) or partial least squares regression (Carrascal et al., 2009), but both of these methods implicitly assume linear relationships between the response and the predictors with no interactions. Landscape effects on insect abundance may however readily involve non-linear or threshold responses, and interactions between different landscape metrics, or large and local scale variables.

Here once more, random forests may be a useful tool, able to model non-linearity and interactions implicitly for a large number of variables, in order to pre-select strong, uncorrelated predictors for entry into multiple regression models. When all predictors could potentially be of importance and there is no *a priori* reason for choosing one variable over another, a rule-based procedure is preferable to arbitrary judgement. The variable importance measure used in the previous chapter has been shown to give high scores to all members of sets of collinear predictors (Genuer et al., 2010, Strobl et al., 2008), and therefore stepwise deletion or addition procedures based on variable importance (e.g. Diaz-Uriarte and de Andres, 2006, Bradter, 2010) would not effectively minimise colinearity. Rather, a novel backwards elimination procedure using random forests based on a goodness-of-fit criterion is presented, which aims to yield a smaller set of variables with minimal colinearity.

3.1.4 Modelling at the functional group level

An important decision to make before trying to model an ecological system for interpretation or prediction is which level of organisation to attempt to describe, be it individuals, species, functional groups, or ecosystem processes. Grouping species into functional types (e.g. Medvigy and Moorcroft, 2012) or averaging over temporal variation make models much more tractable, but ignoring heterogeneity will inevitably result in loss of information and precision (Evans et al., 2012).

In this chapter the abundance of aphids, parasitoids, and aphidophagous syrphid larvae will be modelled at a functional group level, pooling abundance across sampling occasions to give a seasonal total. The seasonal total of aphids is correlated strongly with peak numbers, which is in turn highly correlated with wheat yield loss (Rabbinge and Mantel, 1981). While this approach ignores the temporal and taxonomic variation in responses to landscape context, in this case it may be more effective to model at a coarser level. This decision does involve an element of pragmatism; the species and temporally specific data in this study are relatively sparse, making it difficult to find appropriate error distributions for regression models, and the uncertainty surrounding parametric models of each species at each time point would be large. If these separate responses are combined *ex post* to predict patterns at a functional group level, these errors will combine to make conclusions very tentative indeed. By looking for patterns at a functional group level directly, abundances become large enough for robust statistics to be used, and there is less uncertainty around predictions under similar conditions. The approach in this chapter is accordingly not to infer mechanistic species-specific processes, but rather describe important patterns between field-scale and landscape context factors and the abundance of groups involved in an economically important interaction.

3.1.5 Objectives

Summarising all of the points discussed above, this chapter aims to answer the following main questions:

1. From a large pool of candidate variables describing different aspects of landscape context and field conditions, which are the most important influences on the abundance of aphids, parasitoids and syrphid larvae as functional groups?

2. What is the functional form of each relationship?

3. What is the appropriate spatial scale of measurement?

4. How do landscape or field-scale predictors interact with aphid abundance to determine the numbers of parasitoids and syrphid larvae?

5. Are the abundances of parasitoids and syrphid larvae positively correlated? In other words, do similar environments support high numbers of both natural enemy groups?

3.2 Methods

The data used in this chapter are the same as those used in chapter 2, except that this analysis is restricted to observations made in 2011. The data represent 6 ten-stem samples from seventy five fields for which full records of management were obtained (450 observations in total), spread over a 100 km by 40 km region of Yorkshire. Four visits were made to each field between early June and late July 2011. A full explanation of study field selection, sampling and landscape quantification procedures is provided in sections 2.2.1 – 2.2.3 of chapter 2. Here, only the statistical methodology unique to this chapter is described.

3.2.1 Creating statistical models of abundance

The main goal of statistical analysis was to find parsimonious, interpretable models of the relationship between field-scale and landscape context variables and the abundances of cereal aphids, their parasitoids (referred to as "mummies" henceforth), and aphidophagous syrphid larvae (SL henceforth). A two-stage approach was adopted, where as discussed above, an initial variable pre-selection using random forests was carried out, followed by model selection using multiple regression. The following process was performed for each response variable separately. Figure 3.1 presents a flowchart of the procedure.

For the first step, random forests were created using the `cforest` function in the R package "party" (Hothorn et al., 2006). The original random forest algorithm is biased towards inclusion of variables with many potential cut points, or categories (Strobl et al., 2008), which was undesirable as several of the candidate variables were binary. The `cforest` algorithm is not biased in this way.

Observations were pooled across species within groups, and across visits, to give the total abundances of aphids, mummies, and SL as groups for the season. Initially, 102 landscape metrics (6 classes × 2 metrics × 6 scales + 5 landscape level metrics × 6 scales), the position (edge/centre) of the sample in the crop, the presence/absence of field margin features, the final height and stem density of the crop, and the occurrence of spraying were considered as potential predictors for all responses. Sampling date of the first visit was included to control for phenological trends Aphid abundance was included as a covariate for mummy and SL models, which offers two advantages over using parasitism rate (PR) and SL per aphid (SLPA) as responses: i) the shape of the relationship between aphid abundance and that of the two NE groups can be modelled; and ii) the effects of other predictors on NE abundances in interaction with aphid abundance (i.e. affecting PR and SLPA), and independently (i.e. additively) can be disentangled. The number of predictors in total (*P*) was thus 112 for aphid abundance and 113 for mummies and SL. All abundances were first √transformed so that residual error from random forest models was approximately normally distributed.

Beginning with all variables, `cforest` models were made where each predictor was omitted in turn, with 20 repetitions of each model to average over the randomness inherent in the algorithm. Each forest contained 500 trees, with *P/3* randomly chosen predictors available as candidates at every bifurcation. Each time, a "pseudo-AIC" score was calculated. This was based on AIC (Akaike's Information Criterion; Akaike (1974)) with the number of parameters being taken as the size of the pool of available variables for each model (step A in figure 3.1). The complexity penalty inherent to AIC helped remove predictors correlated with important variables, but with low unique explanatory power.

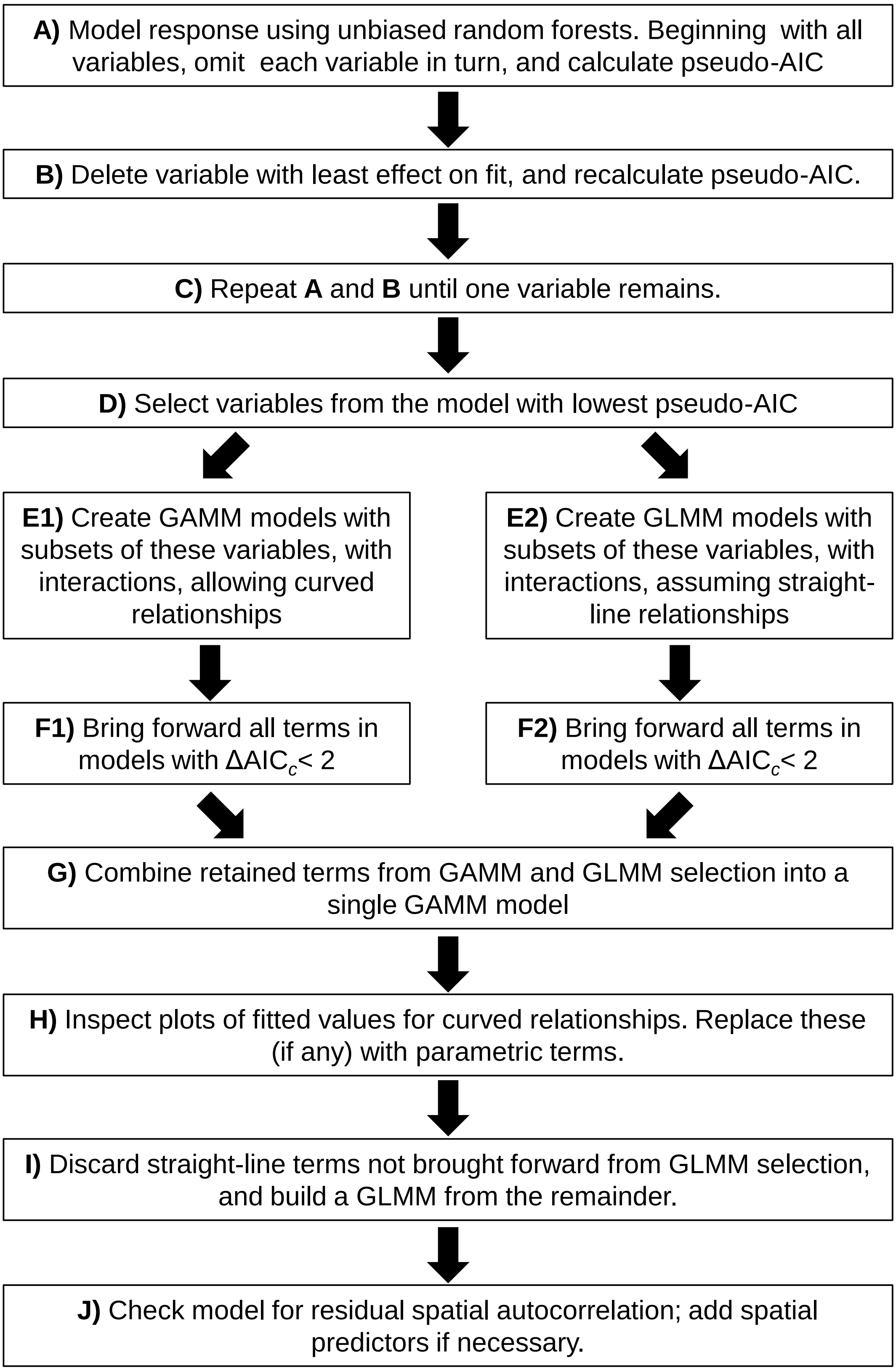

Figure 3.1: Flowchart outlining the variable selection procedure used to choose statistical models for each of the three response variables.

GAMM = generalised additive mixed model, GLMM = generalised linear mixed model. See text for definition of pseudo-AIC.

The variable whose omission caused the largest decrease (or smallest increase) in pseudo-AIC was deleted (step B).This process was repeated until a single variable remained. The variables present in the model with the lowest pseudo-AIC were taken forwards to the next step. This comprised 24, 12 and 12 variables for aphids, mummies and SL respectively. These sets were expected to contain all important predictors as the deletion of these would have led to an increase in AIC, but it is likely that some less important ones could have remained.

Many of the variables carried forward at this point could have been important only through non-linear and interactive relationships, which linear models without interaction terms would not identify. Therefore for the next step, subsets of the variables remaining were entered into generalised linear (GLMM) and generalised additive (GAMM) mixed models with up to 5 variables at a time, including all two-way interactions (step E1 and E2). Aphid and mummy abundance were square-root transformed to meet Gaussian assumptions in a global model, and SL was fitted with a poisson error distribution (log-link). Aphid abundance was log transformed to maintain the relationship between aphids and SL. It was important to employ the random factor of “field ID” at this stage to account for non-independence of samples within the same field, resulting from unmeasured field-specific conditions (e.g. wheat variety) or spatial processes, which could significantly affect the outcome of variable selection (e.g. Keitt et al., 2002, and from preliminary analysis of the data here excluding the random effect of field ID).

The subset models were ranked according to AIC_c, the AIC corrected for small sample sizes (Hurvich and Tsai, 1989), and the terms found in models with strong support ($\Delta AIC_c < 2$) were carried forward to the next step (step F). Models other than the top ranked one were considered because model selection bias and uncertainty make the identity of the best model very contingent on individual datasets and selection procedures. Using only variables from the top model, when several have strong support, would inevitably have left out some important terms (Burnham and Anderson, 2002). This was considered here more important than the loss of parsimony incurred by inclusion of extra variables. Relative variable weights (w_{+j}) were calculated at this stage as the sum of Akaike weights (w_i) of the models in which each variable j appeared, across the whole set of subset models.

All variables carried forward to from steps F1 and F2 were then combined into a single global model, in order to visualise the form of any non-linear relationships and to assess whether any residual spatial autocorrelation remained. The fitted relationship of the response with each explanatory variable was plotted, and if a curve had been fitted, an appropriate parametric function was tried instead. If the model fitted better with curvilinear terms than with only straight-lines according to AIC_c, they were retained (steps G and H). Only the square-root aphid abundance, as a covariate in the mummy model, showed a curved response, and this was replaced by a cubic term ($\sqrt{}$aphids + aphids + aphids$^{3/2}$). Plots were also used to discard any variables in straight-line relationships carried through from the GAMMs but not from the GLMMs (step I).

The resultant global models were then assessed for residual spatial autocorrelation, not accounted for by the random effect of field ID (step J), which could severely affect parameter estimates and standard errors (e.g. Beale et al., 2010). Moran's I was calculated for the residuals, using a neighbour weighting of $1 - (d_{ij}/d_{max})$ for the distance d between samples i and j, and compared to a permuted null distribution. At $\alpha = 0.05$, no significant autocorrelation remained in any of the three models. Standard errors and confidence intervals for coefficient estimates were obtained from running the model with standardised continuous predictors on 999 bootstrap samples (that is, sampling with replacement) of the observations, and the explanatory power of the final models and individual variables were estimated using Nagelkerke's generalised R^2 (Nagelkerke, 1991). Explanatory power of fixed-effects alone were calculated by creating predicted values from the fixed-effect regression coefficients only, then calculating Nagelkerke's R^2 from a generalised linear model of the observed data versus these predictions.

3.2.2 Co-occurrence of parasitoids and syrphids

Studying the important variables selected for the models of mummy and SL abundance, and their coefficients, would not be very informative when trying to predict their co-occurrence, due to high positive and negative dependency between metrics of landscape context. Instead, as a simple alternative, the Pearson correlation coefficient was calculated between the numbers of aphids, mummies and SL at the whole-field level (rather than by sample location as above). This demonstrates the observed co-occurrence of the two natural enemy groups. The partial correlation of SL and mummies was also calculated, which shows the relationship controlling for their joint dependence on aphid abundance. A permutation test with 999 samples was then carried out to assess the significance of any observed correlations or partial correlations.

All statistics were carried out using R version 2.14.0 (R Development Core Team, 2011). Linear mixed models were carried out using the `lmer` function in the R package "lme4" (Bates et al., 2008), and additive mixed models with the `gamm` function in the "mgcv" package (Wood, 2011). Spatial weightings and Moran's I were calculated using the `moran.mc` function in “spdep” (Bivand et al., 2012). Partial correlations were carried out using the `cor2pcor` function in “corpcor” (Schaefer et al., 2012).

3.3 Results

A total of 262,417 aphids, 5,747 mummies and 728 SL were counted across the four sampling occasions. From field identification, the main species of syrphid present was *Episyrphus balteatus,* with *Scaeva pyrastri* also common. Species composition of aphids and mummies is given in section 2.3.1 of chapter 2.

3.3.1 Aphid abundance

Both landscape context and field-scale variables were selected for the final model of aphid abundance (table 3.1), and interactions among them received strong support.

There was good evidence that aphids were more abundant when the shape complexity of arable land in the surrounding 1km was higher, with the effect being greater for central samples than those at the edge (figure 3.3 A). A similar, but less well supported effect of the area of woodland within 1500 m was apparent, whereby the difference between edge and centre samples was greater with more woodland (figure 3.3 B).

Table 3.1: Coefficients and variable weights for the aphid abundance model. Coefficients obtained from the composite model of √aphid abundance incorporating all of the terms below. Continuous predictors were standardised to aid comparison. The last column shows the decrease in Nagelkerke’s R^2 of the model (fixed effects only), when that variable is dropped from the model, as a percentage of that of the full model. The variables “YN_grass” and “YN_hedge” represent the presence or absence of a grass strip or hedge in the field boundary (coefficient: present – absent). “Edge_cent” is the position of the sample at the edge or centre of the field (coefficient: edge – centre). For definitions of other variable names, see table 2.1 in chapter 2.

Variable	Coefficient	S.E.	Lower C.I.	Upper C.I.	W_{+j}	% total R^2
woodlandPLAND_1500	1.58	1.06	-0.74	3.38	0.36	1.65
arableSHAPE_MN_1000	2.90	0.80	1.13	4.32	0.29	17.20
YN_hedge	-1.66	0.73	-3.09	-0.26	0.11	41.25
YN_grass	1.09	1.78	-2.07	4.86	0.57	59.58
edge_cent	-2.38	0.54	-3.45	-1.33	1.00	22.88
woodlandPLAND_1500*edge_cent	-1.11	0.65	-2.20	0.26	0.36	1.59
arableSHAPE_MN_1000*YN_grass	0.38	0.87	-1.33	1.98	0.06	0.39
arableSHAPE_MN_1000*edge_cent	-1.02	0.48	-1.88	-0.01	0.28	1.71
YN_hedge*YN_grass	11.40	1.12	9.34	13.60	0.10	35.82
YN_grass*edge_cent	-2.69	1.09	-4.83	-0.70	0.56	2.07

Interactions between field-scale variables were also important. The best supported interaction term in the model (table 3.1) showed that aphids were more common in the centre of fields than at the edge, and that this difference is amplified by the presence of a grass strip at the field boundary (figure 3.3 C). A striking interaction between the presence of a hedge and a grass strip was also observed, with far higher aphid abundance when both were present (figure 3.3 D). However, this interaction was not present in many of the best models, as judged from its w_{+j} score (table 3.1).

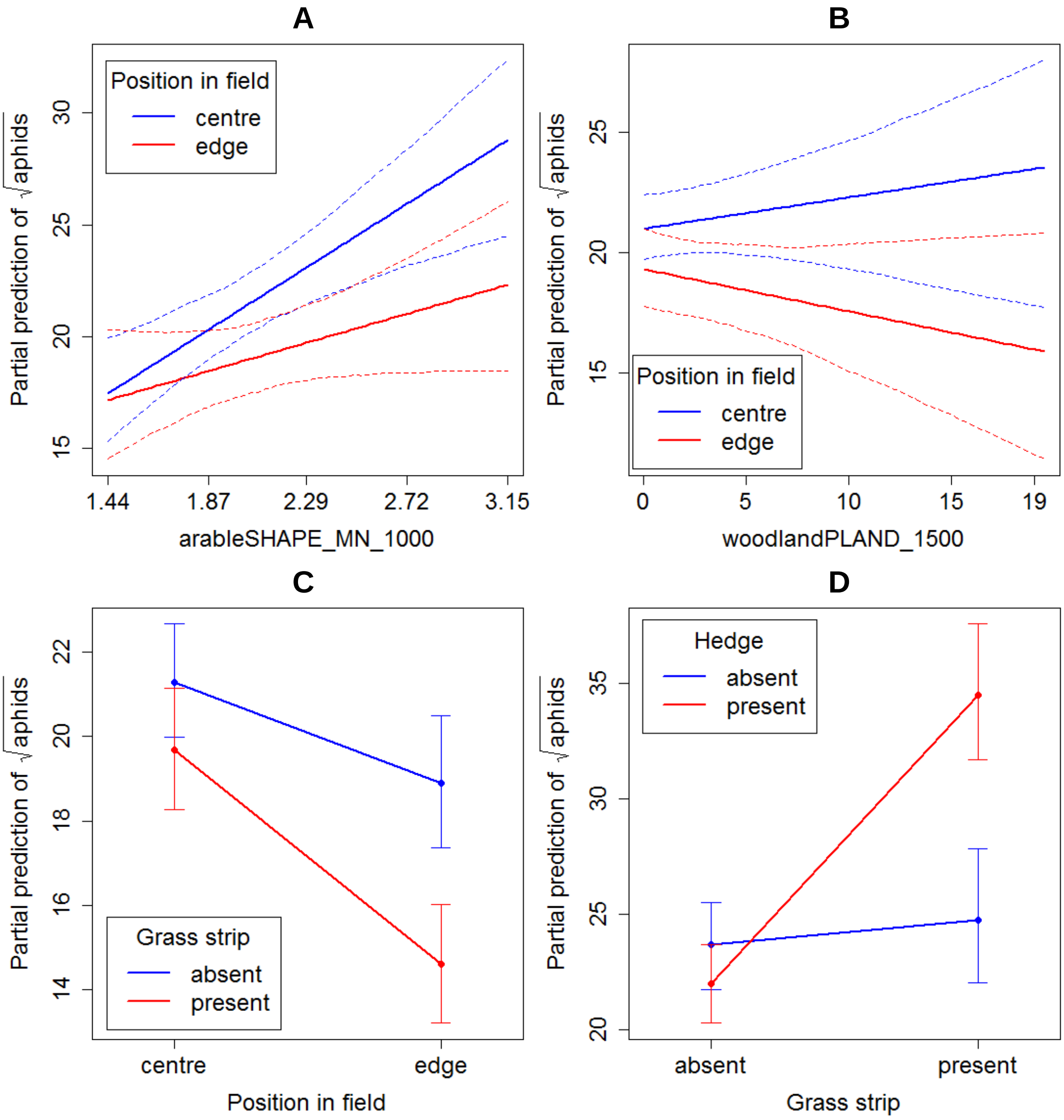

Figure 3.3 Plots of important terms from the final model of (square root) aphid abundance.

Partial response plots of √aphid abundance versus important interactions between variables in the final model of √aphid abundance. Bold lines show fitted aphid abundance, and dashed lines (A, B) and bars (C, D) represent the 2.5% and 97.5% quantiles of predictions from 999 bootstrap repeats of the model. Relationships shown were those with a t-value of >1.5. Partial response plots (Faraway, 2006), are derived by computing predictions from the coefficients of the variables of interest only, helping to visualise their relationship with the response variable. Residual points (present in figures 3.4 and 3.5) are defined as the partial prediction plus the residual from the full model for each observation.

Patterns of aphid abundance not explained by field-scale variables or landscape context contributed significantly to the model fit. In the final model of aphid abundance, fixed effects alone explained 23% of the total variation (Nagelkerke's R^2), but with the effect of field ID to account for random between-field variation, this rose to 56%.

3.3.2 Mummy abundance

The identities of important predictors in the model of mummy abundance were much more certain than was the case for aphids, with the same set of main effects being present in virtually all of the best supported models (as measured by w_{+j} ; table 3.2).

Mummy abundance, not surprisingly, was most strongly positively related to aphid abundance, but showed signs of saturation at high aphid numbers (figure 3.4 E). Aphid abundance was however also involved in interactive effects with other landscape context and field-scale variables, so its effect alone is difficult to interpret.

Table 3.2: Coefficients and variable weights for the mummy abundance model. As table 3.1. The polynomial terms for √aphids are given a weight of NA, as these were added after the calculation of w_{+j}. The weight of √aphids thus applies to all of the parts of the polynomial.

Variable	Coefficient	S.E.	Lower C.I.	Upper C.I.	w_{+j}	% total R^2
√aphids	1.09	0.99	-0.87	2.95	0.99	3.01
arableSHAPE_MN_1000	0.29	0.04	0.22	0.37	0.99	10.31
landIJI_2500	0.27	0.04	0.19	0.34	0.99	8.56
Height	-0.19	0.05	-0.27	-0.09	0.93	5.00
aphids	0.41	3.86	-6.87	8.06	NA	0.08
aphids$^{3/2}$	-1.13	4.02	-9.39	6.19	NA	0.36
√aphids:arableSHAPE_MN_1000	0.05	0.05	-0.04	0.14	0.27	0.22
√aphids:landIJI_2500	0.03	0.53	-0.94	1.15	0.85	0.01
√aphids:Height	-0.11	0.05	-0.22	-0.04	0.73	0.84
√aphids:aphids$^{3/2}$	0.09	0.38	-0.63	0.86	NA	0.11
arableSHAPE_MN_1000:landIJI_2500	0.06	0.04	-0.03	0.14	0.36	0.28
landIJI_2500:Height	0.01	0.04	-0.06	0.10	0.24	-0.01
landIJI_2500:aphids	-0.14	1.24	-2.82	2.22	NA	0.01
landIJI_2500: aphids$^{3/2}$	0.34	0.88	-1.39	2.29	NA	0.05

Parasitoids were more common at high values of the interspersion and juxtaposition of vegetation types at the largest scale (landIJI_2500), and once again when the shape complexity of arable land in the surrounding 1km was high. Both of these variables also showed well supported positive interactions with aphid abundance, meaning that at high values, the number of mummies rose more steeply with aphid abundance than at low values (figure 3.4 B and C). There is also evidence for a weak positive interaction (small coefficient in table 3.2) between these two variables (figure 3.4 D).

The maximum height attained by the crop was the only field-scale variable to be included in the final model. In taller crops, mummy abundance has a shallower relationship with aphid abundance than in shorter crops, indicating reduced parasitism rates (figure 3.4 A).

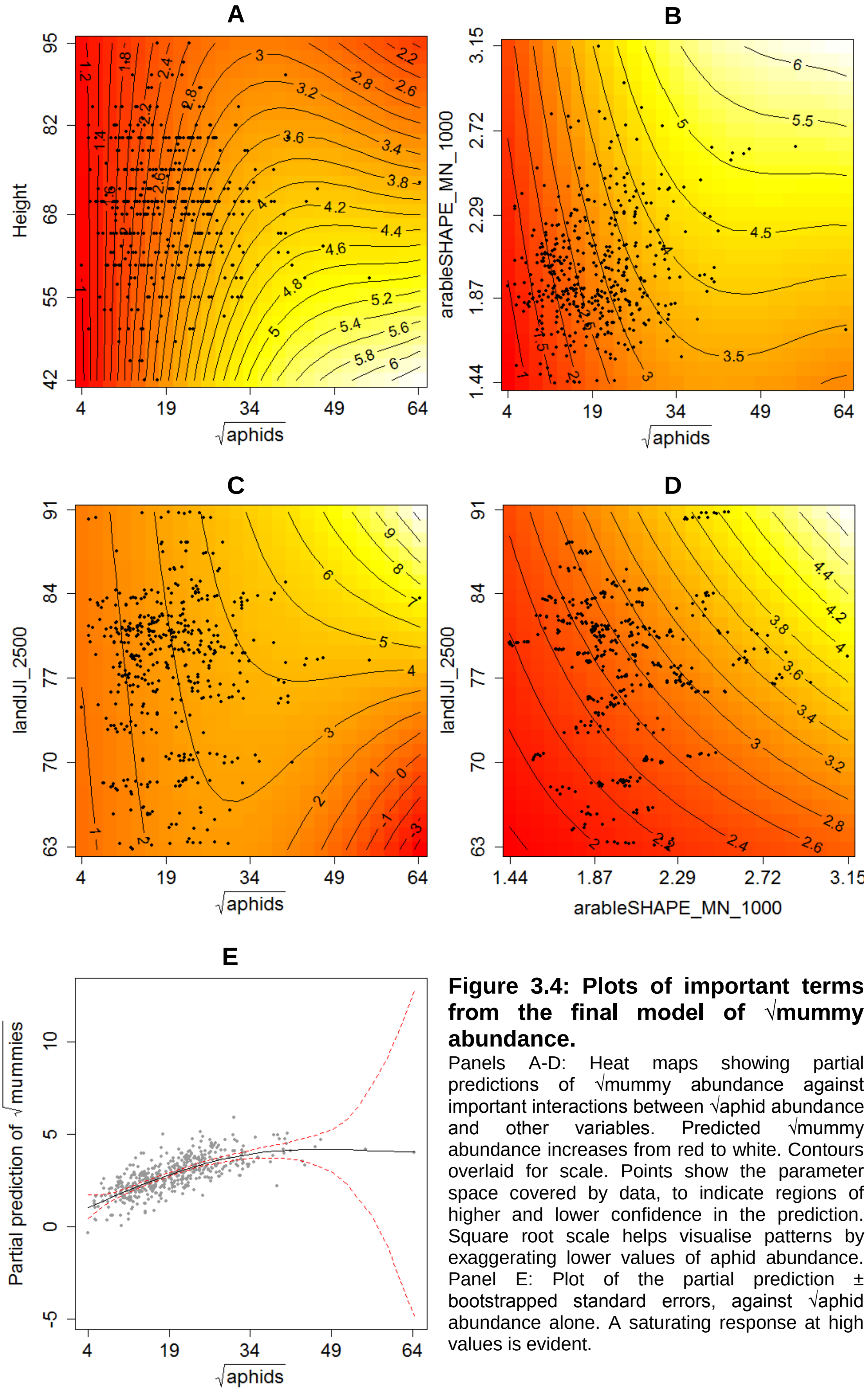

Figure 3.4: Plots of important terms from the final model of √mummy abundance.

Panels A-D: Heat maps showing partial predictions of √mummy abundance against important interactions between √aphid abundance and other variables. Predicted √mummy abundance increases from red to white. Contours overlaid for scale. Points show the parameter space covered by data, to indicate regions of higher and lower confidence in the prediction. Square root scale helps visualise patterns by exaggerating lower values of aphid abundance. Panel E: Plot of the partial prediction ± bootstrapped standard errors, against √aphid abundance alone. A saturating response at high values is evident.

In contrast to the model of aphid abundance, environmental variables accounted for most of the explained variation in mummy abundance. Nagelkerke's R^2 with fixed effects alone was 0.63, compared to 0.66 with the random effect of field ID.

3.3.3 *Syrphid larval abundance*

There was considerably more uncertainty over the identity of the best predictors of syrphid larval abundance than was the case for mummies. Aphid abundance, and the proportion of arable land in the surrounding 1500 m were the two predictors with strong support, but many of the main effects and interactions were present in only a small proportion of the highest ranked models.

Table 3.3: Coefficients and variable weights for the syrphid larval abundance model.
Format as for table 3.1.

Variable	Coefficient	S.E.	Lower C.I.	Upper C.I.	W_{+j}	% total R^2
log_aphids	0.30	0.06	0.19	0.43	0.99	33.06
rough_grassPLAND_200	0.05	0.09	-0.13	0.21	0.26	16.48
arablePLAND_1500	-0.23	0.05	-0.35	-0.15	0.99	29.45
ag_grassSHAPE_MN_1000	0.10	0.07	-0.03	0.27	0.09	-0.58
rough_grassSHAPE_MN_1000	0.09	0.06	-0.02	0.20	0.17	1.62
woodlandSHAPE_MN_1000	-0.15	0.06	-0.29	-0.04	0.14	9.71
arableSHAPE_MN_1500	0.05	0.06	-0.08	0.18	0.19	5.01
gardenSHAPE_MN_2000	0.00	0.07	-0.12	0.13	0.21	0.12
landAREA_AM_200	0.02	0.06	-0.10	0.14	0.05	1.18
Density	0.02	0.05	-0.08	0.12	0.59	0.72
log_aphids:rough_grassPLAND_200	0.06	0.09	-0.12	0.27	0.12	0.71
log_aphids:arablePLAND_1500	0.00	0.06	-0.09	0.13	0.22	-0.03
log_aphids:rough_grassSHAPE_MN_1000	-0.01	0.07	-0.14	0.11	0.05	0.00
log_aphids:woodlandSHAPE_MN_1000	-0.07	0.06	-0.22	0.03	0.10	-0.25
log_aphids:arableSHAPE_MN_1500	-0.04	0.07	-0.17	0.10	0.05	0.55
log_aphids:gardenSHAPE_MN_2000	-0.01	0.07	-0.13	0.13	0.05	0.10
log_aphids:landAREA_AM_200	-0.07	0.07	-0.21	0.06	0.04	1.13
log_aphids:Density	0.00	0.06	-0.11	0.12	0.13	-0.02
rough_grassPLAND_200:arablePLAND_1500	0.22	0.08	0.09	0.42	0.18	5.77
rough_grassPLAND_200:woodlandSHAPE_MN_1000	-0.20	0.11	-0.40	0.01	0.05	5.35
rough_grassPLAND_200:arableSHAPE_MN_1500	-0.17	0.09	-0.36	-0.02	0.03	2.90
rough_grassPLAND_200:Density	0.07	0.08	-0.08	0.21	0.02	0.62
arablePLAND_1500:ag_grassSHAPE_MN_1000	-0.07	0.07	-0.22	0.04	0.07	-0.95
arablePLAND_1500:rough_grassSHAPE_MN_1000	0.02	0.07	-0.11	0.16	0.04	0.04

Syrphid larval abundance, was positively related to that of aphids, but less tightly so than mummy abundance (figure 3.5 C). There were more syrphid larvae in fields with a low proportion of arable land in the surrounding 1500 m (arablePLAND_1500). Although an interaction between log(aphids) and arablePLAND_1500 is most strongly weighted, the effect size is almost zero in the final model (table 3.3; figure 3.5 A).

There is also weak evidence that the response of syrphid larvae to arablePLAND_1500 is reversed to a positive relationship when there is a high proportion of rough grassland within 200 m of a sample (figure 3.5 B).

Reflecting the uncertainty over the most important variables, syrphid larval abundance was the least well explained of the three functional groups by environmental variables. In contrast to the model of mummy abundance, random variation between fields accounted for most of the total explained variation (Nagelkerke's R^2 fixed-only: 0.18, fixed plus random: 0.89).

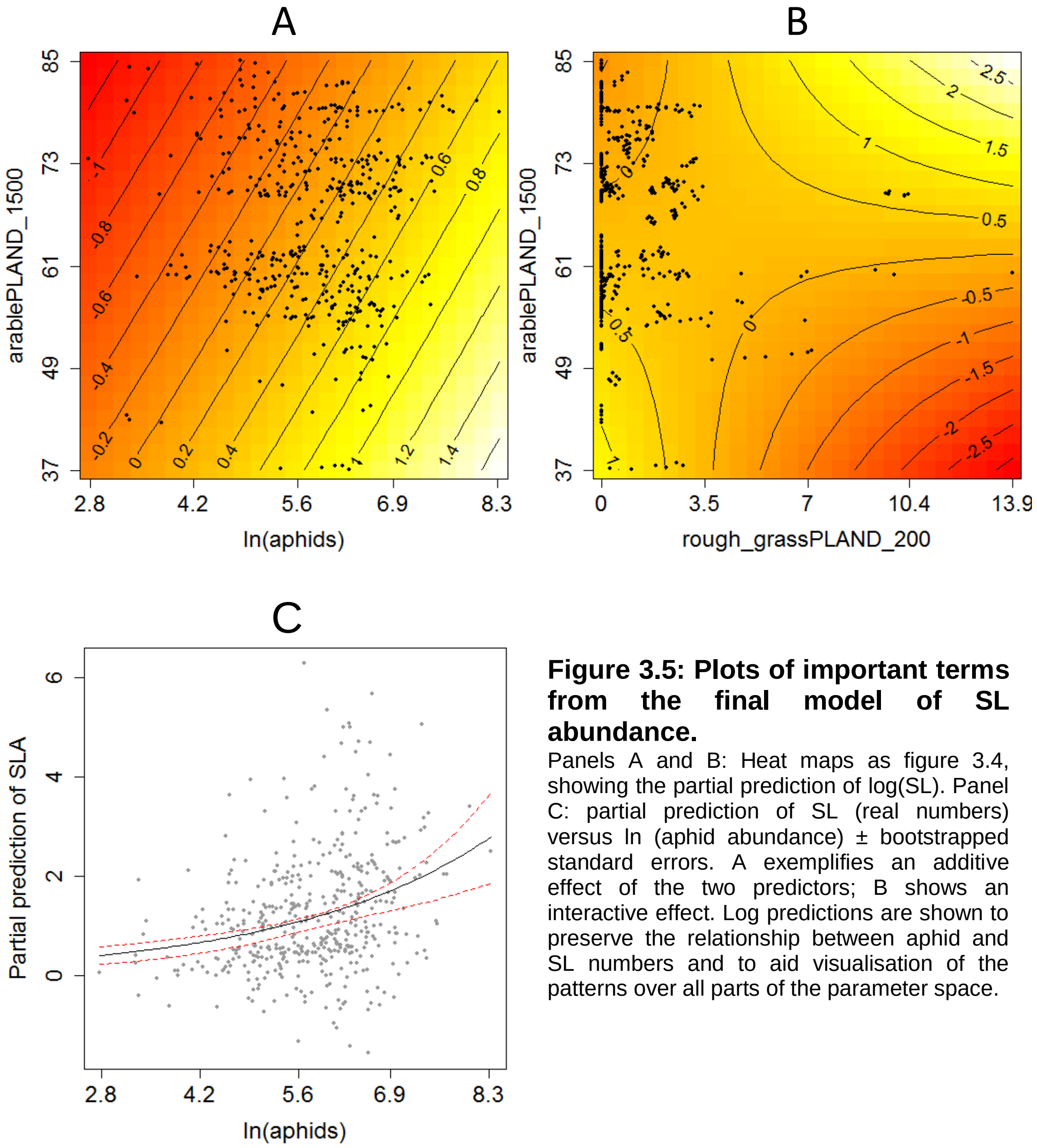

Figure 3.5: Plots of important terms from the final model of SL abundance.

Panels A and B: Heat maps as figure 3.4, showing the partial prediction of log(SL). Panel C: partial prediction of SL (real numbers) versus ln (aphid abundance) ± bootstrapped standard errors. A exemplifies an additive effect of the two predictors; B shows an interactive effect. Log predictions are shown to preserve the relationship between aphid and SL numbers and to aid visualisation of the patterns over all parts of the parameter space.

3.3.4 Co-occurrence of natural enemy functional groups

Mummy and SL abundance, when measured at the whole-field level, had a correlation coefficient of 0.34 (bootstrapped 95% interval 0.14 to 0.50) indicating a positive association. However, when the partial correlation was used to account for the confounding effect of their joint correlation with aphid abundance, the figure fell to 0.007, which was not significantly different from zero (bootstrapped 95% interval -0.22 to 0.20). This result was confirmed graphically by comparing a scatterplot of the two abundances (figure 3.6 A), and one of residuals from separate linear models with aphid abundance as a covariate (figure 3.6 B).

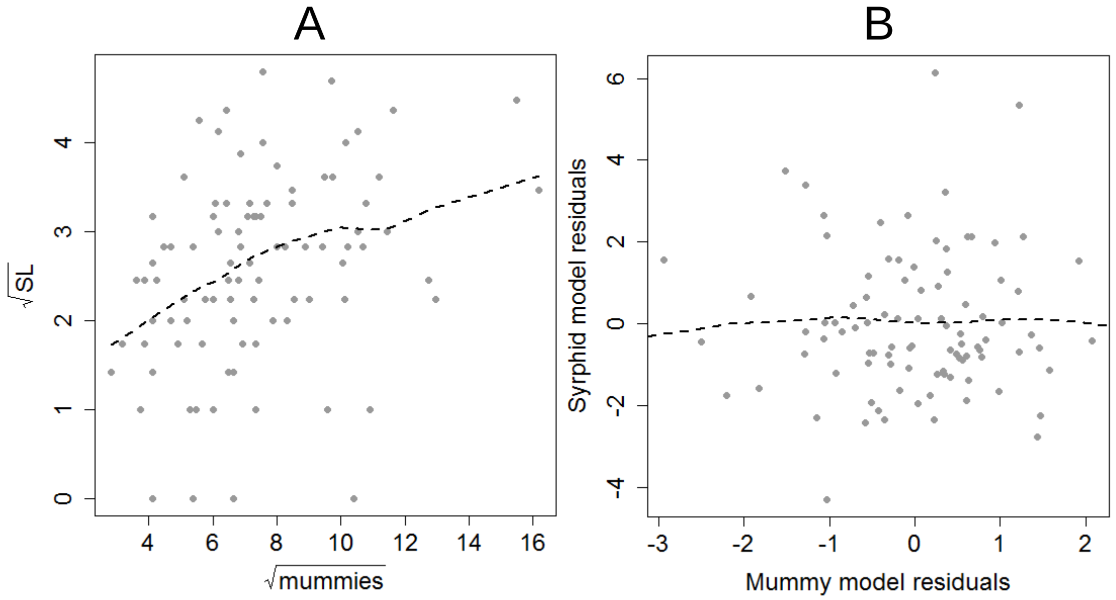

Figure 3.6: Illustration of the absolute and partial correlation of mummy and SL abundance.
Panel A: Scatterplot of √ transformed abundances of both groups at the field level, showing a positive association. Panel B: scatterplot of the residuals from linear models created of √ transformed abundances of each enemy group against √ aphid abundance (also at the field-level), revealing no residual correlation. These two plots are visually analogous to the absolute (A) and partial (B) correlation of mummies and SL. Dashed lines show a lowess smooth through the points.

3.4 Discussion

The objective of this chapter was to discover which characteristics of the study fields and the surrounding landscape best explain the abundance of aphids, parasitoids and syrphid larvae, at what spatial scale, and in what manner. A novel variable selection procedure using random forests allowed a large pool of candidate predictors, describing several aspects of landscape complexity, to be reduced to a number and independence amenable to regression modelling, without excluding variables involved in non-linear or interactive effects. All three functional groups were influenced by shape complexity or configurational aspects of landscape context, and for aphids and parasitoids, to a greater extent than by measures of proportional area. Interesting statistical interactions were also retained in the final models, which would not have been apparent without the modelling approach taken here. The remainder of this section discusses the interpretation of the three individual models in more detail, evaluates the modelling approach, and suggests further research.

3.4.1 Aphid abundance

Aphid abundance in a field is a function of the *in situ* growth and mortality rates, and the number of immigrants and emigrants moving to and fro. The most convincing landscape context pattern was the higher aphid density when arable land in the surrounding 1000 metres had high shape complexity. Assuming that plant nutritional quality for aphids was uncorrelated with landscape context, this pattern lends support to the argument for relatively local landscape context influencing aphid movement. Despite many studies demonstrating long distance travel of cereal aphids (e.g. Hardy and Cheng, 1986), colonisation from local sources may be numerically far more important (Loxdale et al., 1993), particularly in years where aphids are abundant (Vialatte et al., 2007). The longer the length of perimeter of arable land for a given area, the easier migration to and from fields becomes, especially if dispersal is perimeter-dependent (Hamback et al., 2007). This could affect focal field aphid abundance in three ways: i) higher densities of cereal aphids on winter hosts in the vicinity could be maintained from which colonists of the focal field arise; ii) dispersal from other crops in the surrounding arable land to the focal field is promoted, or iii) if the shape of the focal field dominates the shape complexity metric, then a long field perimeter may increase aphid immigration from less suitable surrounding vegetation. Further analysis and fieldwork would be necessary to distinguish these possibilities.

More strongly supported than the influence of arable shape complexity however, were the effects of field boundary type, and the difference in density between the edge and centre of fields. Aphid density was lower at the edge than the centre sampling plots, and this difference was greater in fields where a grassy strip (>2m wide) was present (figure 3.3 C). This could reflect decreases in inputs of fertiliser and herbicides near the edges of fields from practical considerations, making wheat here less nutritious for aphids. When a grass strip is present, farmers are encouraged to reduce inputs near to the margin, perhaps augmenting the edge-centre difference in plant quality. Alternatively, this interaction could be partly due to natural enemy pressure being higher near the margin, particularly a grassy one (Krauss et al., 2011). Neither parasitoid nor SL abundance was higher near the edge, but other natural enemy groups not recorded could have produced the effect.

The relatively good support for interactions between landscape context and the edge-centre density disparity is intriguing. The positive effect on aphid density of arable shape complexity within 1000 m seems to be greater in the field centre than at the edge (figure 3.3 A). This may however be a numerical artefact; if a constant ratio of aphids in the edge and centre samples is maintained due to relative plant attractiveness, a whole-field increase in aphid density would result in a larger numerical difference. The pattern of increasing aphid density with higher proportional area of woodland within 1500 m for central samples, but slightly decreasing density at edge samples, is more difficult to interpret however (figure 3.3 B). The confidence intervals for this interaction are wide, but if the effect is real, one possibility is that woodland both supplies aphid immigrants, and supports natural enemies acting predominantly at the field edge.

3.4.2 Mummy abundance

Mummy abundance was tightly associated with that of aphids, but with good evidence that the influence of arable shape complexity, interspersion of patch types and crop height modify with the aphid-mummy relationship. These four variables all received very high Akaike weights (table 3.1), which suggests that none of them are redundant.

There were interactions between all three environmental variables included, and aphid abundance, in the final model. The predominance of interactive effects could be due to the functional response of individual females, whereby immigrants attack more hosts over their lifetime at higher host densities (Van Alphen and Jervis, 1996 and references therein). An environmental variable influencing the number of immigrants will therefore affect parasitism rate, rather than only absolute numbers of parasitised hosts. Alternatively, there is evidence that high aphid abundance increases the olfactory attractiveness of a field to parasitoids (Kaplan, 2012 and references therein), perhaps amplifying landscape effects on immigration. In reality, both of these processes probably play a part. Plant height appeared to influence parasitism rates (figure 3.4 A), which again may reflect an effect on parasitoid functional response, through decreased foraging efficiency (Gingras et al., 2008).

As was the case for aphids, the shape complexity of arable land within 1000 m had a positive effect on mummy abundance (figure 3.4 B). This may be due to similar reasons to those proposed for the aphid response above. Inter-annual population build up of parasitoids has been shown on non-crop vegetation surrounding fields, when a large area of a particular crop is grown nearby (Thies et al., 2008), and increased edge-length will likely promote greater crop to non-crop spillover. Equally, given observations of between-crop movement of parasitoids (e.g. Pons and Starý, 2003, Lu et al., 2012) and the strong learned preference of parasitoids for olfactory cues similar to those found in their natal environment (Powell et al., 2003, van Emden et al., 1996), greater influx of colonising parasitoids from other crops may be a more likely means by which increased arable boundary length affects focal field abundance. This second mechanism does however assume perimeter-dependent dispersal. The interspersion of patch types in the surrounding 2500 m (landIJI_2500), which also has positive effects on parasitoid abundance (figure 3.4 C and D), may perhaps reflect once more abundance in the landscape as a whole being promoted by decreased resource separation, when parasitoids must use host on different vegetation types or non-prey resources (Banks et al., 2008). Unfortunately, due to logistical constraints, all arable crops were represented by the same category in the quantification of landscape context, so landIJI does not represent interspersion of crop types. The mapping of specific crop types (e.g Pena-Barragan et al., 2011) deserves more attention in conservation biocontrol research, given the potential importance of crop-crop interactions.

Overall then, these results show that parasitoid abundance per aphid seems to be enhanced by the shape complexity and interspersion of patch types, rather than by a high proportion of semi-natural vegetation *per se*.

3.4.3 Syrphid larval abundance

The abundance of syrphid larvae (SL) increased with aphid density, as for mummies, and this again received a high weighting (figure 3.5 C and table 3.3). The relationship is less clear than that for mummies; SL were far less numerous and this could reduce the correlation at the sample scale (but see section 3.4.5 regarding sampling scale considerations). In contrast to mummies however there was no evidence of saturation of SL numbers at high aphid densities, indicated by the better fit of a straight line for modelling the between log(aphids) and log(SL) than any curved line during the fitting of GAMMs.

The other strongly weighted effect was the association of high SL abundance when the percentage of arable land within 1500 m (arablePLAND_1500) was low. Although an interaction of this variable with aphid density received moderate support from its Akaike weight (table 3.3), the interaction coefficient is small in the final model resulting in an effectively additive relationship (figure 3.5 A). An additive relationship implies that, unlike for parasitoids, the process that causes the SL response to high aphid density is separate from that which drives their response to arable proportional area. The area of arable land may be pertinent for syrphids either because: i) as inferred by other authors (e.g. Haenke et al., 2009), a low area of arable land means larger areas of other land cover, which may provide better nectar resources for adult syrphids, increasing fecundity and population density in the whole landscape; ii) egg laying adults might initially be spatially diluted when a larger area of crops with aphids surrounds the focal field (sensu Otway et al., 2005), and the number of syrphid generations occurring in the productive wheat fields is insufficient for initial dilution to be reversed to a concentration effect by the end of the season (Ankersmit et al., 1986). These possibilities are not mutually exclusive however; adult female syrphids need to alternate repeatedly between feeding on nectar and pollen, and oviposition (Almohamad et al., 2009), so in flower poor landscapes may preferentially oviposit near to the isolated floral resource patches. This hypothesis is supported by other studies, which have found higher numbers of adult aphidophagous syrphids in more arable dominated landscapes (Gabriel et al., 2010, Haenke et al., 2009), if the adults are caught using attractive water traps or on floral margins, when females are likely to be feeding rather than ovipositing. The proportion of rough grass very close to the field modifies the effect of arablePLAND_1500 (figure 3.5 B), though the effect is only weakly supported (w_{+j} = 0.18). Rough grass area within 200 metres increases SL abundance in the focal fields more at high arablePLAND_1500 (or equally, arable PLAND has a positive effect on SL density when surrounded by a lot of rough grassland). If rough grassland as classified in this study contains floral resources for adult syrphids, it may serve to attract them near to the focal field from a large area of arable land, encouraging preferential oviposition there. In turn, when no particularly attractive floral resources are adjacent to the focal field, adults may be attracted to other fields closer to such resources. A redistribution effect towards resource-rich rough grassland is the main mechanism proposed above, but increased floral resource availability has been shown to increase the longevity and oviposition rate of female *E.balteatus*, and also increase the overall likelihood of oviposition near to an aphid colony (Laubertie et al., 2012). Thus, increased fecundity of females near to floral resource patches may also explain some of the variation in syrphid larval abundance in this study.

3.4.4 Co-occurrence of natural enemy functional groups

Co-occurrence of natural enemies is of relevance for conservation biocontrol for two reasons. Firstly, it can be argued that management (field or landscape-scale) which promotes the abundance of several types of natural enemy is more likely to encourage effective pest control, provided that intra-guild predation or interference is not too strong (Straub et al., 2008, Denoth et al., 2002). Secondly, the temporal and spatial stability of ecosystem function has been linked to functional redundancy and response diversity of the species involved (sensu Laliberté et al., 2010). Management for syrphids and parasitoids, given their accepted role as effective aphid antagonists and their different life-history traits, may provide both benefits.

The finding that the partial correlation between mummy and SL density (i.e. when aphid abundance has been accounted for) at the field level is essentially zero, is interesting with regard to management recommendations: strong positive correlation would suggest that both groups would either benefit or suffer from similar changes; negative correlation would imply low compatibility of requirements or negative interactions. Zero correlation suggests that certain conditions produce “win-wins”, and others trade-offs in the abundance of the two groups. Determining which changes will produce a given response is very different from interpreting existing patterns however, and dependencies among landscape metrics make extrapolations far from trivial. This will be the subject tackled in the next chapter.

3.4.5 Evaluation of the modelling approach

There are several cautionary notes to stress when interpreting the results of the models presented above.

First and foremost, statistical models were based on the correlations between abundance and environmental variables, rather than experimental manipulation with controls. The site selection procedure helped to remove possible effects of confounding environmental variables by ensuring treatments were not clustered in geographic or environmental space, but nonetheless predictors found to be important here may still only be correlates of underlying, unmeasured drivers.

Secondly, the models were static, i.e. did not attempt to model population dynamics, because the sparse data for early time points and coarse temporal scale of observations (see section 3.1.4) would have been problematic. Consequently, although aphid numbers could be considered as a covariate for models of natural enemy abundance, the feedback of natural enemy abundance on aphid population change was bundled up in the effect of landscape on aphids, so separation of direct landscape effects and those mediated through natural enemies isn't possible. Chaplin-Kramer et al. (2011) argued that studies of conservation biocontrol should model pest population trajectories, rather than point abundances or summed abundance (as here), but doing this requires much greater sampling intensity and smaller intervals, which for this study would have sacrificed the spatial replication of sampling.

Thirdly, by summing abundances of groups over all sampling occasions, temporal resolution was lost. Moreover, the summation was effectively weighted towards the occasion where the abundance for a particular group was highest. In the previous chapter the change in the importance of predictors between the four sampling occasions was explored, and demonstrated significant trends; for example, field scale edge-effects for *Aphidius sp*. were most pronounced in initial visits then declined later on (see table 2.3 in chapter 2). In the analyses above, the variables being included (for aphids and parasitoids) therefore are most likely to represent those having most influence on abundance at visits 3 and 4, when abundance of aphids and parasitoids peaked. Variables affecting abundance at visits 1 and 2 only on the other hand were weighted down, explaining the absence of edge effects for parasitoids, or boundary trees for aphids as predictors in the models here. Other authors have found that variation in natural enemy abundance early in the season is a better predictor of pest outbreaks than later in the season (Ekbom et al., 1992, Ostman et al., 2001), suggesting that the variables found in this chapter to affect total abundances of natural enemies over the season might not be the same as those driving their abundance at the time most crucial for aphid control. A more intensive early-season sampling regime than was undertaken here is necessary to address this issue.

Lastly, when interpreting the strength of the observed patterns, the absolute explanatory power of each model must be taken into account (the Nagelkerke's R^2 value), in addition to the relative importance of each predictor in the model (the w_{+j}). The proportion of variation explained by environmental variables was highest for parasitoid abundance, with little extra explained by the random effect of field ID. In contrast, environmental variables explained far less variation in aphid or SL abundance, but the random effect of field ID explained a large proportion. Thus, there is more confidence in using the parasitoid model for predicting new observations than there is for the other two, because random effects cannot be extrapolated or interpolated – there is nothing in the model which can predict the random offset of the intercept for a field which has not previously been sampled. The reasons for the poor explanatory power for aphids and SL may be many. Both groups have been observed to travel long distances by active and passive means (Loxdale et al., 1993, Tenhumberg and Poehling, 1995) for instance, so perhaps the spatial extent of landscape context measurement did not capture the most important scales. Alternatively, and perhaps more likely, within-field variation was larger for these two groups than for parasitoids. Aphid distribution is often very aggregated and ephemeral in wheat fields (Winder et al., 1999), and SL abundance at the sample level may be poorly related to aphid abundance at that sample due to the rapid and localised predatory impact of SL on aphids. Perhaps modelling field-level abundance would have found stronger links with environmental variables, but this would not have enabled edge – centre comparison or accounted for distant samples having quite different landscape context, especially at the 200m or 500m extent. One important variable for SL that was not measured, but may have explained a large amount of variation, was floral abundance. Quantifying this in the wider landscape may be possible from remotely sensed images, and would allow much better inference of the spatial scale over which oviposition by adult syrphids in aphid colonies is related to the availability of floral resources. In general, mapping of floral resources and vegetation type and palatability (for aphids), would enable a more functional mapping of landscape context tailored to the requirements of syrphid species as adults and larvae. This should be a target for future studies investigating the spatial scale at which mobile organisms and their resources interact to provide ecosystem services.

3.4.6 Conclusions and future directions

The findings presented above help to vindicate calls for landscapes to be characterised in a more comprehensive way in ecological studies, dealing with several aspects of complexity in order to improve our understanding (Fahrig et al., 2011). As demonstrated here, statistical methods are available to deal with the analytical problems that doing this inevitably brings.

Despite parasitoids and syrphid larvae being the two most common aphid natural enemy groups observed in this study, others may be more dominant when using different sampling techniques and working in other study regions (Thies et al., 2011). The modelling approach presented in this chapter could therefore be extended to functional groups such as coccinellid beetles, neuropteran larvae and arachnids.

Finally, a major constraint to confident inference in this analysis was the poor thematic resolution achieved for classifying land cover. In particular, arable land was represented by a single category, despite the potential importance of between crop interactions (Pons and Starý, 2003). Elucidating the role that the spatial arrangement of different crop types may play for pest and natural enemy abundance will require crops to be mapped over large extents, and applied to insect abundance data collected over the same period. This is currently challenging, but would greatly advance the knowledge underpinning our ability to manage landscapes for biological control.

4. Trade-offs and synergies between multiple natural enemies with land use change: a simulation approach

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Abstract

Landscape context can influence populations of insect crop pests, operating directly on pest species, and indirectly through predation by their natural enemies. Pests are often prey for multiple species of natural enemy, each interacting with landscape context in different ways, making predicting the overall effect of land use change on pest populations challenging.

In this chapter a novel, map-based simulation of land use change was used to identify potential win-wins, lose-loses and trade-offs were identified between the populations of cereal aphids, and two aphid natural enemy groups; parasitoid wasps and hoverfly larvae. Statistical models were used to evaluate the effect of 90 different changes in landscape composition (i.e. the relative area of different vegetation types), aggregation of vegetation types, and field boundary density on the abundance of the three groups in 8 focal winter wheat fields in differing initial landscape context.

Changes in landscape composition had the strongest influence on the direction and consistency of responses for all three groups, with aggregation and boundary density alterations having less influence. Replacing non-crop vegetation with arable crops over 10% of the landscape, in an aggregated way, produced undesirable results for all three groups (aphids increased, natural enemies per aphid decreased). There was less agreement on win-win scenarios however; replacing arable land with non-crop vegetation benefited parasitoid and syrphid larval abundance, but did not result in decreased aphid abundance. These results suggest that avoiding further loss of non-crop habitat to arable crops would be beneficial for control of cereal aphids.

The effects of simulated land use change on aphids and their natural enemies also differed among the 8 fields studied. This indicates the importance of considering specific contexts, rather than taking a one-size-fits-all approach, to assess the impact of land use change drivers.

This chapter was the first study to use a simulation approach to study the effects of land use change on a pest-natural enemy system, but would be improved by using future political and economic storylines to objectively predict land use changes.

4.1 Introduction

4.1.1 Inter-specific differences and conservation biological control

Predicting the outcome of changes in land use for populations of crop pest insects and their natural enemies is a key challenge for designing effective conservation biological control strategies. The task is made more difficult by the multiple ways in which landscape context can influence crop pest–natural enemy systems, operating on each species or species group both directly, and indirectly through trophic interactions. For example, there is evidence that the availability of local overwintering sites and spring hosts influences aphid colonisation of crops directly (Chapters 2 and 3 in this volume; Loxdale et al., 1993, Vialatte et al., 2007, Roschewitz et al., 2005), but also that aphid suppression is enhanced by natural enemies in heterogeneous landscapes which facilitate access to alternative prey or non-prey resources (Bianchi et al., 2006, Gagic et al., 2011, Langer and Hance, 2004, Langer, 2001, Roschewitz et al., 2005, Thies et al., 2011, Tscharntke et al., 2008).

Moreover, many pests are preyed upon by a large range of natural enemies, with varied trophic, life-history and dispersal traits. These biological differences are reflected in the individualistic responses of pest and natural enemy species or functional groups to landscape context, with the importance of different characteristics and different spatial scales varying widely. For instance, Schmidt et al. (2008) found that spiders could respond either positively or negatively to the proportion of semi natural habitats, and at scales ranging from 100 metres to 3 kilometres, depending on the species.

Consequently, the challenge of evaluating the outcome of landscape-scale alterations for conservation biocontrol is one of predicting which changes will result in “win-win” situations among the responses of the organisms involved, and which will produce trade-offs or “lose-lose” outcomes, from the perspective of the farmer. Favouring management that increases species diversity of the predatory assemblage is one possible strategy, and doing so is likely to increase the long-term stability of pest control, through the insurance effect of increased functional redundancy, and higher diversity of responses to environmental stochasticity (Macfadyen et al., 2012, Tscharntke et al., 2012). However, often the magnitude of pest suppression is more strongly linked to the presence of a few, effective natural enemies, than diversity *per se* (Denoth et al., 2002, Straub and Snyder, 2006, Swift et al., 2004). Additionally, the risk of intraguild predation, detrimental to pest suppression, may increase with species diversity (Costamagna et al., 2008, Meisner et al., 2011, Traugott et al., 2012).

Therefore, it may be most effective for conservation biocontrol management to aim to promote the “right” kind of diversity (sensu Straub et al., 2008); increasing the abundance of several groups of effective natural enemies to improve immediate pest suppression, whilst also maintaining a level of response diversity to foster temporal stability. In practice, adopting this approach requires that statistical or mechanistic models of the individual responses of species or functional groups to their environment be combined, to make predictions of the overall effect of a deliberate or unplanned change. This is especially useful when the identities of pest species or the most effective natural enemies vary geographically, precluding general recommendations (Thies et al., 2011).

4.1.2 Problematic features of landscape studies

Hymenopterous parasitoids and syrphid larvae were the two most common natural enemy groups attacking cereal aphids in the winter wheat crops studied in the previous chapters. There was no residual correlation in abundance of these two groups, once the effect of aphid abundance had been removed (section 3.3.4 and figure 3.6 in chapter 3), suggesting that both synergies and trade-offs in their response to landscape changes are possible, depending on their nature.

Understanding of the response of organisms to change can arise from manipulative experiments, long-term datasets documenting historical “natural experiments” (sensu Diamond, 1983), or study of spatial variability (“space-for-time substitution”). However, landscape manipulations on an appropriate scale and with sufficient replication are rarely feasible (McGarigal and Cushman, 2002), and long term datasets are patchy (Pickett, 1989). As a result, space-for-time substitution is often the only practical option for generating predictions. In chapter 3, parametric statistical models were created, linking the abundance of aphids, parasitoids and syrphid larvae to metrics describing landscape context. However, there are features of analyses involving spatial predictors which make naïve interpretation of regression coefficients from these models insufficient for predicting responses to changes, or for envisaging landscapes producing optimal outcomes.

Firstly, in real landscapes, attributing spatial trends in the abundance of a species to existing environmental variation is very different to predicting the effects of a change in the environment (McArdle, 1996). The patterns used to model abundance are averages across all study sites, whereas changes are applied to individual landscapes, with idiosyncratic initial conditions and constraints. The effect of a given change could thus vary widely from location to location.

Secondly, the metrics used describe landscape configuration and shape complexity in the previous two chapters summarise spatially explicit patterns as single numbers, which is useful for statistical modelling but also adds a level of abstraction to the resultant models. Translation of these indices back into spatial patterns once more is much more challenging.

Thirdly, and perhaps most fundamentally, metrics of landscape context are highly interdependent. It is difficult to predict, *a priori*, what effect increasing the proportional area of arable land, for instance, will have on its shape complexity or the interspersion of patch types in a landscape. When organisms respond to multiple aspects of landscape context, as was observed in previous chapters, their response to a change in one variable will be difficult to predict. This interdependency also renders many combinations of landscape metric values impossible, and furthermore it may not be possible in real world landscapes to predict in advance exactly which combinations are possible and which are not. A search of the parameter space used for model creation, in order to find optimal values, is therefore unlikely to produce a realistic answer.

4.1.3 Map-based simulations

Simulations offer a solution to all three of the issues hampering prediction discussed above. They enable landscape scale experiments to be carried out *in silico,* by manipulating digital maps representing the values of environmental variables or distribution of particular habitats. Models linking the spatial patterns of vegetation depicted by the map to the abundance and distribution of an organism can then be used to make predictions of the outcome. Maps are intrinsically spatially explicit, so deal automatically with dependency among predictors and initial conditions, and provide a way to translate simple alterations into the units of landscape metrics, with which models were parameterised in the previous chapter. For these reasons, map–based simulation will be the approach used in this chapter to predict responses in abundance to land use change.

This type of approach has been used in varied fields; for example in finding optimal landscapes for conservation of several species with differing habitat requirements (Holzkämper and Seppelt, 2007a), and for predicting synergies and trade-offs in the value of ecosystem services, commodities and conservation in a large valley (Nelson et al., 2009). Map-based simulation has the potential to be applied to any multi-objective problem where the competing responses are linked to variables expressed by the map, and thus could contribute significantly to planning sustainable agricultural systems.

As discussed in section 1.5.3 of the general introduction, there are existing spatial analysis software tools which allow the user to input land cover maps, then to map the production and use of multiple ecosystem services across the area. ARIES (**AR**tificial **I**ntelligence for **E**cosystem **S**ervices) (Villa et al., 2009) and InVEST (**In**tegrated **V**aluation of **E**cosystem **S**ervices and **T**rade-offs) (Natural Capital Project), are two well-developed examples of this, which feature built-in functions for evaluating many ecosystem services. Conceptually, exploring trade-offs and synergies between natural enemy and pest populations is just a more focused version of doing this for separate ecosystem services, and so these tools could be usable for the issue being addressed in this chapter. However, the advantage of having built-in ecosystem service functions in ARIES and InVEST is a hindrance in this case, as neither possesses a tool designed specifically for pest control, or one that can model tri-trophic interactions. More importantly, both frameworks rely on process-based models to evaluate ecosystem services provided by mobile agents which, as discussed later in this chapter, are a beneficial attribute when the necessary parameters are available. Ecosystem services in InVEST and ARIES are modelled as being produced by land parcels of one type, and used by parcels of another type, with a strength governed by distance decay functions. The statistical models developed in chapter 3 linking aphid and natural enemy populations in focal fields to the surrounding landscape are unfortunately incompatible with this process-based approach. Although the influence of the proportion of woodland within 1500 metres in the statistical model of aphid abundance (section 3.3.1) could in theory be used to ascribe a positive production value to woodland within that range, it is difficult to see how the same conceptual inversion could be achieved for configurational measures such as shape index.

Bespoke statistical models such as those developed in chapter 3 can be used in an existing spatial optimisation framework called LUPOlib (**L**and **U**se **P**attern **O**ptimisation **lib**rary) (Holzkämper and Seppelt, 2007b). However, optimisation of landscapes using LUPOlib relies on the network of parcel boundaries remaining fixed, and this is an aspect of landscape structure which if changed would have profound influence on the possible spatial configurations of land cover patches. Furthermore, LUPOlib is restricted to converge on single, optimal solutions, which does not allow the evaluation of a variety of user-defined land cover maps.

For these reasons, in this chapter a new land-use simulation and evaluation procedure will be developed that can simulate change in land cover classes, alterations to the land parcel structure of maps, and predict the consequences of land-use changes on pest and natural enemy populations using existing statistical models.

4.1.4 Objectives

The aim of this chapter is to present an extensible map-base simulation method, and link this to the statistical models developed in chapter 3 in order to predict the numbers of aphids, parasitoids and syrphid larvae (SL) resulting from a wide variety of land use change scenarios. This will enable trade-offs and synergies between these multiple outcomes to be identified.

The goal of the simulation in this chapter is not to seek globally “optimal” land use patterns through an automated process (cf. Holzkämper and Seppelt, 2007b). Optimisation of landscapes for specific objectives may yield objective guidance when the importance of goods and services desired from a landscape is dominated by a small minority, and when a landowner has complete control over land at the relevant spatial scale. In lowland UK landscapes however, as in many other parts of the world, landscapes are the emergent product of decisions by many small landowners, and a large range of goods and ecosystem services must be produced from them. Knowing the optimal landscape composition and configuration for aphid biocontrol control in this situation cannot therefore be used as a prescriptive guide, as it would be unlikely to be optimal for other variables (e.g. food production, species conservation, pollination, water quality etc.) not accounted for, and because it would be difficult to control the actions of many separate actors. Optimisation also does not allow exploration of which land use changes would be undesirable for all objectives (“lose-loses”), which is arguably important if these adverse changes are a realistic possibility. Therefore, though completely objective, optimisation is not well suited to the purpose of this chapter.

An increasing use of land use simulation is to assess the impact on ecosystem services and other aspects of society of a range of potential economic, climatic and political storylines (“human drivers”), such as those developed by the ATEAM (Rounsevell et al., 2005) and ALARM (EU project code: GOCE-CT-2003-506675) projects, or in response to proposed policy reforms such as the upcoming “greening” of the Common Agricultural Policy (EFRA, 2012). The link between human drivers and land use change is made via models of landowner decision making, based upon theories of rational choice (Parker et al., 2003). These are often stochastic and agent-based, being run many times to allow uncertainty in land use change to be incorporated (e.g. Nelson et al., 2008). This approach has the advantage that the realisations of land use change stem from a small, objective set of likely alternative human drivers. However, this method would involve a considerable investment in time, and the small set of land use scenarios produced would make it more difficult to reveal win-wins, lose-loses and trade-offs between the three response variables.

Instead, in this chapter I will prescribe directly a subjective, but large variety of changes in the proportion of different land cover classes, to the degree of aggregation or fragmentation of land cover classes, and to the length of field boundaries. These will be implemented to a small number of template maps, covering a large part of the variation in landscape structure observed around the winter wheat fields studied for this thesis.

Specifically, the analysis will try to answer the following questions:

1. Which scenarios predict win-wins, lose-loses, and trade-offs between the predicted outcomes for aphid abundance, parasitoids and syrphid larvae?

2. How do configurational and field boundary changes modify the effect of changes in proportional area?

4. How do the results of questions 1 and 2 depend on the character of the original landscape?

4.2 Methods

Details of the methodology for planning and carrying out data collection can be found in sections 2.2.1 – 2.2.3 in chapter 2. The procedure for creation of the statistical models used to evaluate the outcome of landscape simulations, and details of the models themselves, are described in sections 3.2.1 and 3.3.1 – 3.3.3 of the previous chapter. Only the methods unique to this chapter are presented below.

4.2.1 Selecting template landscapes

The simulations were carried out on several different landscapes in order to study how the effects of changes vary according to starting conditions. The primary consideration in selecting template maps was to represent as much variation in landscape composition and configuration as possible, in a small enough number of examples to allow direct comparison, and to keep computational demands within reasonable bounds.

Initially, parts of the Ordnance survey Mastermap (MM) topography layer (Ordnance Survey, 2011) were obtained for the area within 2500 metres of each of the 94 fields sampled in 2011 (roughly 2000 ha). MM is vector format data assigning a thematic identity to land parcels (“polygons” hereafter) covering the whole of the UK. Each polygon was reclassified into one of eight aggregated cover classes, as described in sections 2.2.1 and 2.2.3 in chapter 2, becoming either “arable”, “ag_grass”, “mixed”, “woodland”, “rough_grass”, “water” or “manmade”.

The composition and configuration of each map sector was then quantified at the 2500 metre radius scale, using the open-source software *Fragstats version 3.3* (McGarigal, 2002). The mean patch shape complexity (*landSHAPE_MN*); the area-weighted mean patch area (*landAREA_AM*); the interspersion and juxtaposition index (*landIJI*), the patch type richness (*landPRD*), and the field boundary density (*eudist*) were calculated for the landscape as a whole. For every relevant land cover class (i.e. excluding "water" and "other"), the percentage cover (*PLAND*) and the mean patch shape complexity (*SHAPE_MN*) were calculated. See table 2.1 in chapter 2 for details on the calculation and meaning of the metrics.

With each landscape now defined by a set of metrics, a principal components analysis was carried out (after first standardising all variables) in order to determine the primary gradients in landscape context present, so that examples of landscape maps from each part of the gradients could be chosen. Five components had eigenvalues >1, but because a small number of selected templates was desired only the first two were used for the next step, contributing 32% and 16% of the overall variation respectively. The area and shape complexity of gardens, the area of rough grassland, and the richness of patch types are positively loaded on the first principal component, while the second component relates most strongly to increasing area of agricultural grassland and field boundary density (table 4.1).

Next, the scores of landscape maps on components 1 and 2 were categorised into either "low" (0 – 33rd percentile), "mid" (34th – 66th percentile) or "high" (67th – 100th percentile) groups. Thus, each landscape map now belonged to one of nine (3 groups for PC1 x 3 groups for PC2) combinations of groups.

As the final selection step, a set of landscape maps, one from each of the nine combinations, were chosen so that the Euclidean distance (in principal component space) between nearest neighbour maps was as large as possible. There was one combination – "low" on component 1 and "high" on component 2 - to which no maps belonged, so the selection process produced 8 landscape maps representing much of the variation of the first two principal components (figure 4.1).

Table 4.1: Loadings of landscape metrics on the first two principle components describing variation in landscape context.

Landscape metrics	Loadings	
	PC1	PC2
landSHAPE_MN	-0.23	-0.16
landAREA_AM	-0.25	-0.12
landIJI	0.21	-0.32
landPRD	0.37	0.08
eudist	-0.16	-0.35
ag_grassPLAND	-0.04	0.53
ag_grassSHAPE_MN	0.12	-0.18
arablePLAND	-0.25	-0.32
arableSHAPE_MN	-0.22	0.05
gardenPLAND	0.36	0.01
gardenSHAPE_MN	0.35	-0.10
mixedPLAND	0.19	-0.29
mixedSHAPE_MN	0.06	0.11
rough_grassPLAND	0.31	-0.21
rough_grassSHAPE_MN	-0.33	-0.22
woodlandPLAND	-0.07	-0.21
woodlandSHAPE_MN	0.21	-0.26

4.2.2 Simulating changes

Land use change scenarios were derived by (a) stochastically manipulating the classification of polygons corresponding to land parcels such as fields and woodlands, to produce changes in the proportional area of different land classes; (b) doing so in three different spatial manners - aggregated (“agg”), random (“ran”) and dispersed (“dis”) (figure 4.2 B), and (c) altering the field boundary structure of the maps, which changed both the field boundary density and also the tapestry of parcels over which class changes could be made.

Ten different proportional area modifications were defined, altering the classification of 200 ha (~ 10%) of the landscape area in each case. These comprised combinations of increase, stasis, or decrease in the area of arable, ag_grass, and non-crop vegetation (table 4.3 shows all 10 combinations), implemented by conversion of individual polygons.

Polygon conversion was implemented using an iterative algorithm that in each iteration randomly selected one polygon belonging to a class whose area was set to decrease (“target” polygons), and decided whether or not to alter its class and what to change it to, with probabilities determined by the other conditions of the simulation. After every iteration the cumulative area converted was checked, and the algorithm repeated until the desired area of land was reached. Polygons classed as “manmade”, “water”, and “garden” were not included in the simulation, so their area and spatial configuration remained constant. The field at the centre of the map in which sampling had taken place was also exempt from change.

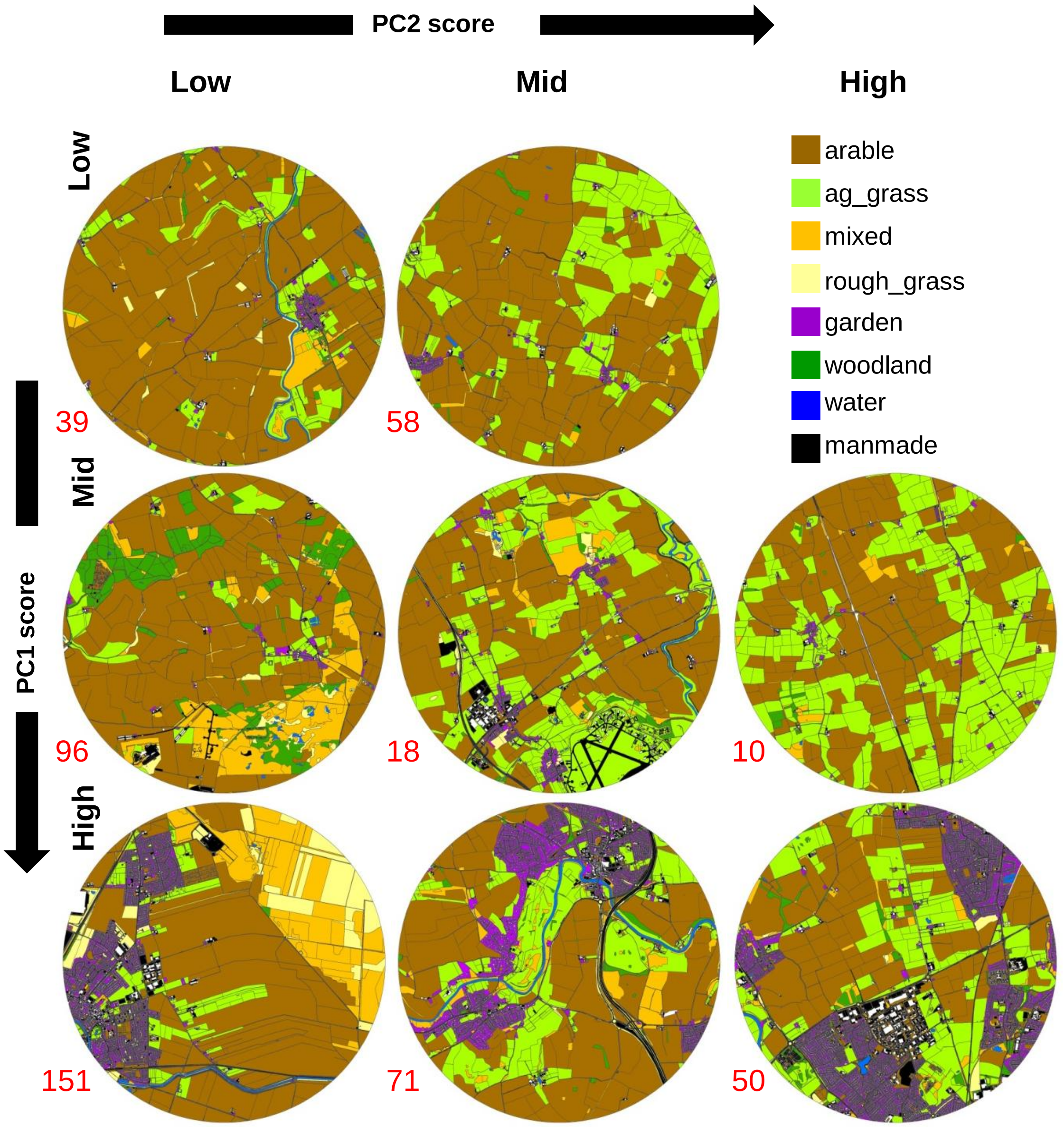


Figure 4.1: Template maps selected for the simulation procedure
Images of the 8 chosen landscape maps resulting from the selection procedure described above, arranged according to their categorisation on components 1 and 2 from the PCA of landscape metrics. Land cover class is indicated by colour, defined in the key at the top right. No landscapes fell into the “Low-High” combination. Red numbers indicate the landscape ID, used in tables 4.4 to 4.9 in appendix 3. Maps were created with ArcGIS 9.2 (ESRI (UK) Limited, 2006).

The three spatial variants of proportional area change were carried as follows (figure 4.2 B). In the aggregated case, the probability that a selected target polygon would be changed was greater when it was adjacent to a polygon of a class set to grow in area. The dispersed case reversed this, making conversion more likely when not adjacent to a polygon of a growing class. For the random case, the probability of conversion was equal (0.5) for all target polygons, independent of their spatial situation. When the area of more than one land cover class was set to increase, the probability that any one of the growing classes would be chosen as the new class of a target polygon was proportional to its initial area in the random case, or the length of its border with the target polygon in the aggregated or dispersed cases.

Boundary manipulations involved either adding or removing 30 km of field boundaries (figure 4.2 A). Boundary line removal was implemented by merging neighbouring polygons of the same class. Addition was achieved by finding the centroid of a polygon, identifying the nearest point on the boundary to the centroid, creating a new line joining the two and projecting it to the opposite boundary. The original polygon was then split along this line. As for proportional area changes, One set of proportional area manipulations was also carried out on the original boundary pattern, so three different boundary treatments were used in total.

The three factors varied in simulations (proportional area change, manner of change and boundary manipulation) were combined in a crossed-factorial design, producing 90 (10 x 3 x 3) unique scenarios of land use change in total.

The manner in which real land cover changes occur is dependent on many small decisions by multiple land owners, so the simulations were designed to produce stochastic changes based on probabilities rather than deterministic functions, to reflect this real-life unpredictability. To account for the variability in how a particular desired scenario might play out in the simulation, each was repeated ten times, resulting in 900 simulation runs being carried out in total from each template landscape.

The manipulated vector maps were translated into changes in landscape metrics by first converting them to a raster format, then calculating the new landscape metric values using *Fragstats*.

The simulation algorithms were written in R 2.14.0 (R Development Core Team, 2011), making use of functions from the packages “rgeos” (Bivand and Rundel, 2012), “sp” (Bivand et al., 2008), and “maptools” (Lewin-Koh and Bivand, 2012). The R code for the map manipulation algorithms is provided in appendix 2.

4.2.3 Statistical model choice and validation

In order to link simulated changes in land cover maps to outcomes for the abundance of aphids, parasitoids and syrphid larvae, appropriate models must first be chosen. In chapter 3, both random forest and generalised linear mixed models were fitted, which have very different structures bringing concomitant strengths and weaknesses (sections 3.1.1, 3.1.2 and 3.2.1 in chapter 3). Random forests (fitted with the function `cforest` from the R package "party" (Hothorn et al., 2006)) can model complex variable interactions and non-linearities allowing them to fit their training data very well, but are thus vulnerable to overfitting. This is especially likely as methods to account for grouping and spatial autocorrelation are lacking, meaning that this variation may be modelled (wrongly) with predictor variables.

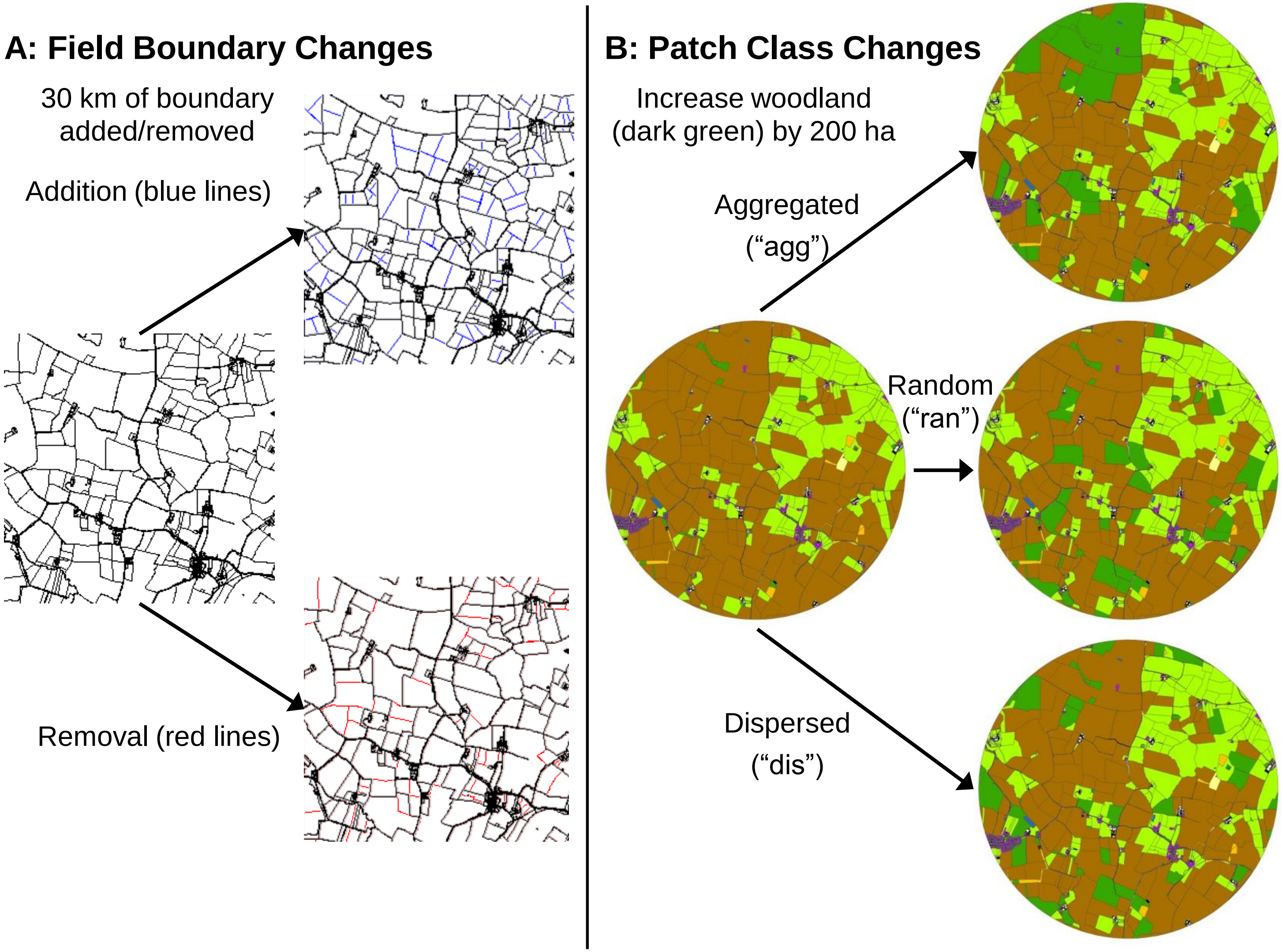


Figure 4.2: Illustration of the map manipulations used to simulate land use change. Panel A shows an example of a map section, showing the effect of removal and addition of boundaries on the field pattern and boundary density. Red lines show boundaries that have been removed, blue lines added boundaries, from the original layout at the left. Only arable and ag_grass polygons were merged or split. Panel B illustrates the results of polygon conversion with an example template (original on the left), showing the differences produced by aggregated, random and dispersed increases. The original field layout was used. In this case, woodland is increasing by 200 ha, at the expense of arable land, which was not one of the scenarios used in the analysis, but illustrates clearly the results of the manipulation.

In contrast, the generalised linear mixed-models (fitted with `lmer` in the package “lme4” (Bates et al., 2008)) incorporate random effects, but their simpler structure means that they explain a lower proportion of the data to which they are fitted.

The task required of models here was to make predictions for new data, so the models’ performance in this respect was most important consideration. The predictive accuracy of both types was assessed by internal validation using bootstrap samples of the 2011 samples (following Efron and Tibshirani, 1994), and cross-validation using data from 2010. The internal validation fitted the same model structure to 1000 bootstrap samples of the 2011 observations, and calculated the mean goodness of fit of models to the bootstrap samples, minus the mean fit to the original data. This is a measure of the “optimism” of explanatory power; how contingent the fit is on the idiosyncratic training data. For cross-validation, the goodness-of-fit was calculated for models predicting the response variables in 2010. Nagelkerke’s R^2 (Nagelkerke, 1991) was used to assess model fit. Only the fixed effects parts of mixed-models were used to assess performance, as random effects cannot be predicted for new covariate values.

Linear models were deemed more appropriate than random forests to use for making predictions from the simulations. They had higher predictive power in cross-validation for parasitoids and syrphid larvae, and showed lower optimism, indicating that their explanatory power reduced to a lesser degree when predicting from new covariate sets (table 4.2).

Table 4.2: Results of internal and external model validation

Fit of the fixed effects part of linear mixed effects models (“Linear”) and unbiased random forest models (“cforest”) on training (2011) and test data (2010). “Response” pertains to the abundance of the group in the units of the model response. Optimism is the difference in fit predicting a subsample only compared to predicting the whole dataset, when models are trained on the subsample. Larger optimism values indicate poorer performance on new data from the same population. Fit for 2010 data indicates generality of the model to a new population (different year and location).

Response	Model	Optimism	Nagelkerke's R^2 2011	Nagelkerke's R^2 2010
Aphids	cforest	0.120	0.787	0.007
Aphids	Linear	0.016	0.228	0.003
Parasitoids	cforest	0.099	0.782	0.104
Parasitoids	Linear	0.032	0.627	0.125
Syrphid larvae	cforest	0.284	0.616	0.005
Syrphid larvae	Linear	0.068	0.184	0.009

4.2.4 Evaluating outcomes

The new landscape metrics calculated from each scenario were combined with the original field-scale variables (not changed during simulations), and fed into the linear models (see tables 3.1 – 3.3 for identity of variables and parameter estimates) to predict sample-level abundance of aphids, parasitoids and syrphid larvae. Because the abundance of aphids was an important covariate in the models for both natural enemy groups, aphid abundance was predicted first and this new estimate used in natural enemy models. To account for parameter estimate uncertainty, each linear model was fitted to 500 bootstrap samples of the 2011 data, yielding 500 sets of coefficients. Each scenario was then evaluated using all 500 variants of the models. The difference in the outcome between samples within fields was not the focus of the analysis, so samples were treated as further replication to account for small-scale variation. Multiplied by the 10 replications of each simulation, 30,000 predictions in total were generated for every scenario.

If linear models are used for extrapolation beyond the range of covariate values to which they were fitted, they are unlikely to give sensible answers (Evans et al., 2012). This is especially the case for log-linear models, such as the model of syrphid abundance in chapter 3. However, given the uncertainty associated with the course of each simulation, and that of parameter estimates in the linear models used for prediction, the reliability of absolute estimates is questionable.

Instead the replication introduced to account for uncertainty was harnessed, to predict the consistency of the direction of change, over all 30,000 quantitative predictions. This allowed predictions to be quantitative in a different way, avoiding the issues associated with extrapolation. A consistency index (C-index) was devised, to summarise the change in aphid abundance (“Aphids”), in parasitoids per aphid (“PPA”), and in syrphid larvae per aphid (“SLPA”). The C-index was calculated by first reducing the differences between the quantitative predictions and the original values to their sign (-1 or 1). Then, the 30,000 signs were summed (giving a number between -30,000 and 30,000), and divided by 30,000 to yield a number between -1 and 1. A value of -1 therefore indicates a reduction in all cases, 1 an increase in all cases, and near 0 a mixture of increases and reductions. “Win-wins”, “lose-loses” and trade-offs between the aphid abundance, PPA and SLPA were assessed by addition of the individual C-indices.

4.3 Results

4.3.1 Consensus patterns in scenarios producing best and worst-case predictions

Clear separation between the scenarios resulting in the most beneficial and most detrimental outcomes for all measures of interest was observed, particularly when considering changes in the proportional area of land cover classes (figure 4.3 A).

For most templates, increases in the proportion of non-crop land at the expense of arable land produced increased parasitoids per aphid (PPA; figure 4,3 A and 4.5).

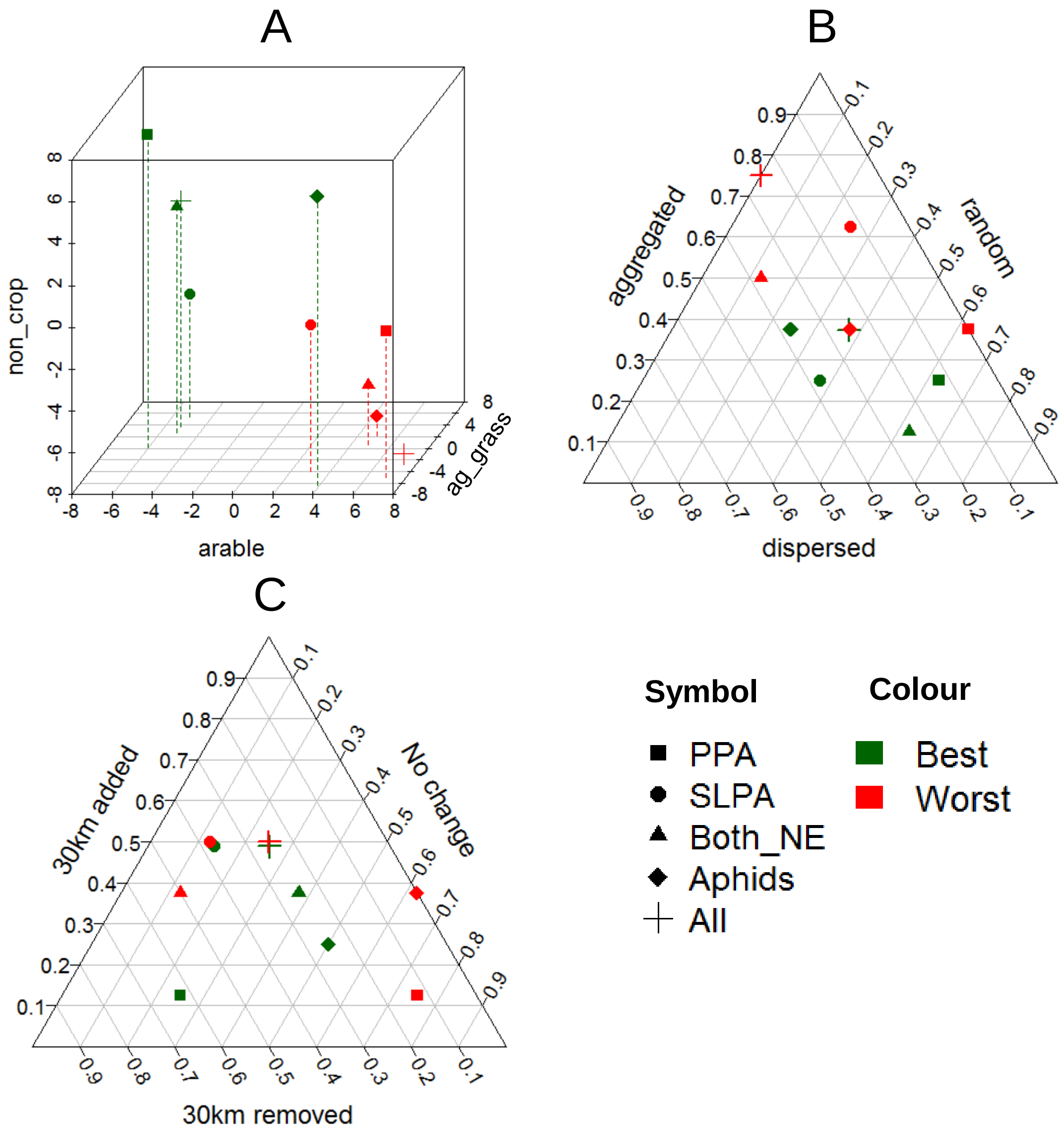


Figure 4.3: Summary of the scenarios causing good and bad outcomes for different target measures

Plots describing which values of proportional area change (A), manner of change (B) and boundary change (C) produced the best or worst results. Five different results of interest are shown: “PPA” = parasitoids per aphid, “SLPA” = syrphid larvae per aphid, “both_NE” = combination of parasitoids and syrphid larvae per aphid, “aphids” = aphid abundance, “all” = combination of all three responses. “Best” refers to a decrease in aphid abundance, but to an increase when considering the other four measures. Panel A: 3d scatterplot showing how outcomes were affected by a proportional area change. Axis scores show how many templates underwent an increase (+) or decrease (-) in area of that class to produce the best (or worst) result, corresponding to the “overall” scores in tables 4.4-4.9 in appendix 3; i.e. a score of -8 indicates that a decrease was the best/worst for all templates, 8 an increase was good/bad for all templates, and around 0 no consensus. Best outcomes for most measures of interest were usually promoted by increasing non-crop land at the expense of arable, indicated by high and low scores on those two axes respectively. Panels B and C are ternary plots showing the fraction of the 8 landscape templates where specific configuration (B) and boundary changes (C) produced the best or worst outcomes. Best outcomes were more often promoted by dispersed and random patterns than aggregated ones, shown by the low score on the “aggregated” axis.

Increases in arable area were part of most worst-case scenarios for PPA (figure 4.3 A), and on average caused declines (figure 4.5 A). Loss of non-crop land resulted in lower PPA on average (figure 4.5 B) but loss of ag_grass was part of more worst-case across the 8 templates, than was loss of non-crop land (figure 4.3 A).

Syrphid larvae per aphid (SLPA) was also predicted to increase when arable area was reduced in most landscapes (figure 4.5 A), but increased ag_grass proportional area was more commonly part of the scenario producing high SLPA than was greater non-crop area (figure 4.3 A and 4.5 C).

Aphid abundance decreases, arguably the most important measure from the perspective of the farmer, was not favoured by reduced arable area, unlike PPA and SLPA. Rather, replacement of ag_grass with arable and non-crop land was the scenario most commonly producing benefits (table 4.3). The opposite change was not the usual scenario producing the most consistent aphid increases however; aphid increases were more common when arable and ag_grass displaced non-crop land. When considering the average responses to all scenarios as opposed to the "best " or "worst" scenarios for aphids, the outcome of arable decrease or stasis is not consistently positive or negative, indicated by small absolute C-indices (table 4.3). In contrast, when arable increased, there were both consistent decreases (desirable) when only ag_grass was replaced and increases (not desirable) when non-crop land was a target.

The optimal scenarios for beneficial changes in all three groups combined show good agreement on growth of non-crop and ag_grass land, with shrinking arable area (figure 4.3 A). Unlike for individual responses, here the converse changes did produce the worst outcome.

Best and worst case scenarios were also differentiated well when configuration changes were assessed. The best outcomes were predicted in more cases when changes occurred in a random or dispersed manner, than in an aggregated one (figure 4.3 B). The difference was most marked for SLPA, enemies combined and all three responses combined.

There was no clear pattern in boundary changes across all responses however, although on its own, PPA increase and decrease were much more commonly favoured by shorter and longer field boundary lengths respectively (figure 4.3 C).

4.3.2 Interactions between proportional area, configuration and boundary changes

The effect of configuration and boundary length modified the predicted response of PPA, SLPA and aphid abundance to changes in proportional area in some cases, but not in others (table 4.3).

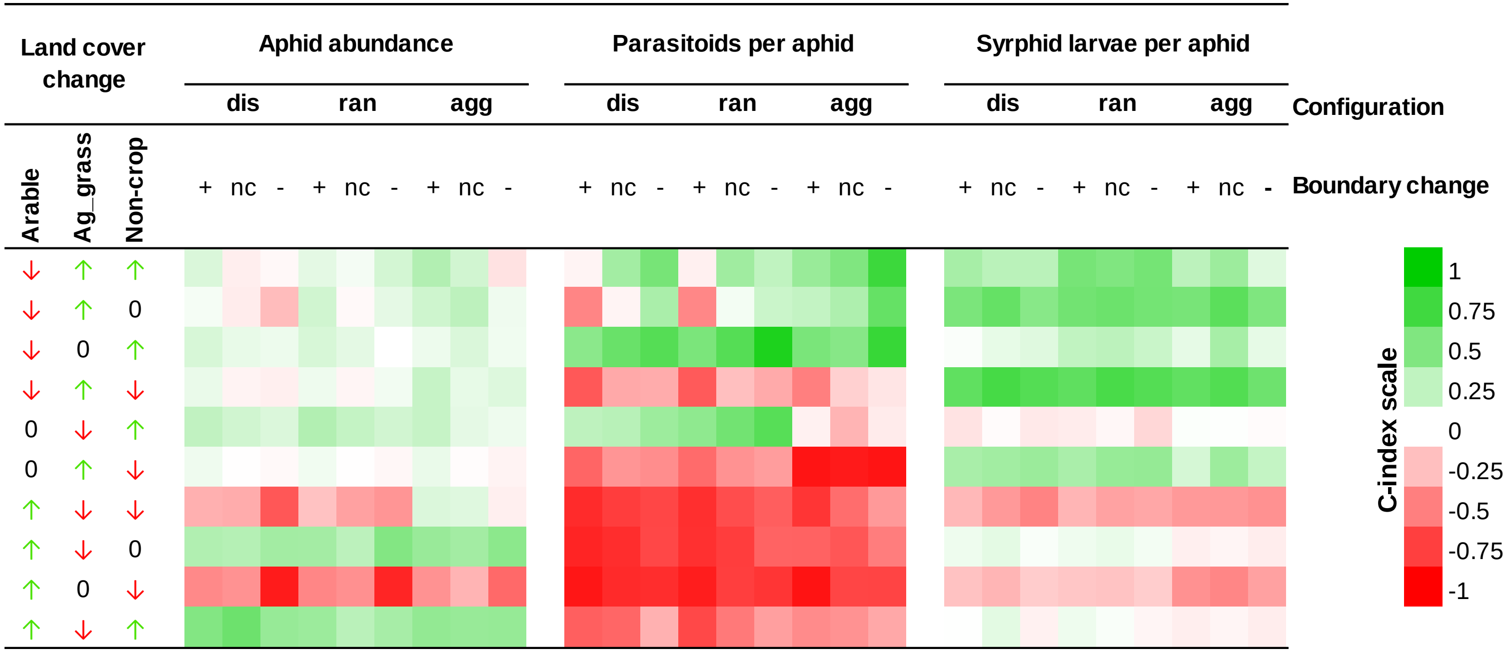
When the predictions are averaged across all templates (table 4.3), the clearest interaction is seen when non-crop land displaces ag_grass; PPA increased if this change occurred in a dispersed or random way, but decreased under aggregated change. Almost as noticeable is that aphid abundance increases when arable replaces non-crop and ag_grass land, but much more consistently so when it does so in a random or dispersed manner (table 4.3). In general, when configuration is relevant, aggregated changes tend to differ from dispersed or random ones.

Boundary changes also had an effect in some cases. There was a tendency for worse results (lower C-index) for PPA when field boundaries are added (figure 4.6 B), especially evident when arable land was replaced by ag_grass in dispersed or random manners (table 4.3). Also noticeable was greater consistency of rises in aphid abundance (lower C-indices) when field boundaries were removed, particularly when non-crop land was removed (table 4.3).

In contrast, other scenarios showed a lack of sensitivity to configurational or boundary changes; for example, SLPA consistently increased when ag_grass replaced arable and non-crop land. This resulted in small marginal effects of configurational and boundary changes when averaged over all scenarios (figure 4.6).

Table 4.3: Direction and consistency of predicted response to all scenarios, averaged across templates

Contingency table showing the occurrence and consistency (C-index) of desirable (green) or undesirable (red) predictions from all scenarios, averaged across all landscapes. "Desirable" means a decrease in aphid abundance, and an increase in the other two variables; "undesirable" is the opposite. Rows represent proportional area changes, defined by the red (200 ha decrease) and green (200ha increase) arrows on the left. If two classes go in same direction, 200 ha is shared between them. Columns show how the effect of area change depends on the configuration of the change ("Configuration") and the concomitant field boundary change, for Aphid abundance, parasitoids per aphid, and syrphid larvae per aphid separately. "+" refers to a 30km addition of boundary prior to area changes, "nc" to no change and "-" to a 30km removal. Where the colours are similar for corresponding cells this indicates scenarios producing win-win (all green) or lose-lose (all red) predictions; where different it implies a trade-off. Between-template differences in outcome to scenarios are explored below.



4.3.3 Trade-offs and synergies between predicted responses

In general, fewer scenarios resulted in trade-offs between SLPA and PPA, than did so between desired outcomes for natural enemies as a whole and aphid abundance. This is reflected by the relative proximity of points in figure 4.3 A.

When considering C-indices averaged across all template landscapes (table 4.3), replacement of ag_grass by arable land usually reduced aphid numbers (a desirable outcome), but provoked declines in natural enemies per aphid (undesirable). The most consistent trade-off between PPA and SLPA occurred when ag_grass displaced non-crop land, which favoured SLPA but was detrimental to PPA. For the converse proportional area change, PPA was favoured under dispersed and random changes but not aggregated ones; SLPA benefited from aggregated changes only.

4.3.4 Between-template variation in responses

The consistency and even the sign of responses to a given change scenario varied between template landscapes (figures 4.5 and 4.6, table 4.10, appendix 3).

There was some indication that the outcome of manipulations varied systematically with the character of the original landscape. For example, addition of arable area had a positive effect on SLPA when the initial percentage was low, but a negative effect at the highest original values (figure 4.5 A). The same pattern was observed for the effect of addition of ag_grass on PPA (figure 4.5 C). This effect was strong enough to cause a reversal of the relative benefit of an increase and decrease between landscape templates with low and high initial proportions. Another effect of this was that whether changes resulted in synergies or trade-offs was also context-dependent. At low arable percentage, PPA and SLPA benefit from opposite changes in arable area, but at higher original proportion they are both favoured by decreased arable area (figure 4.5 A). The opposite trend was seen for ag_grass proportion; at low initial proportions an increase in ag_grass benefited both PPA and SLPA, but at greater initial proportions there was disagreement (figure 4.5 C)

The original landscape context also altered the overall likelihood that responses would be positive or negative for particular groups, regardless of the change scenario applied. For example, the numbers of aphids and PPA were much more likely to decrease in any scenario, when the initial landscape had intermediate field boundary complexity, and aphid decreases were also favoured at intermediate ag_grass proportions.

The importance of configurational and boundary changes in modifying the effect of proportional area manipulations varied between template landscapes (figure 4.6, table

4.10 in appendix 3), though this variation was not obviously related to the initial value of configurational or boundary complexity.

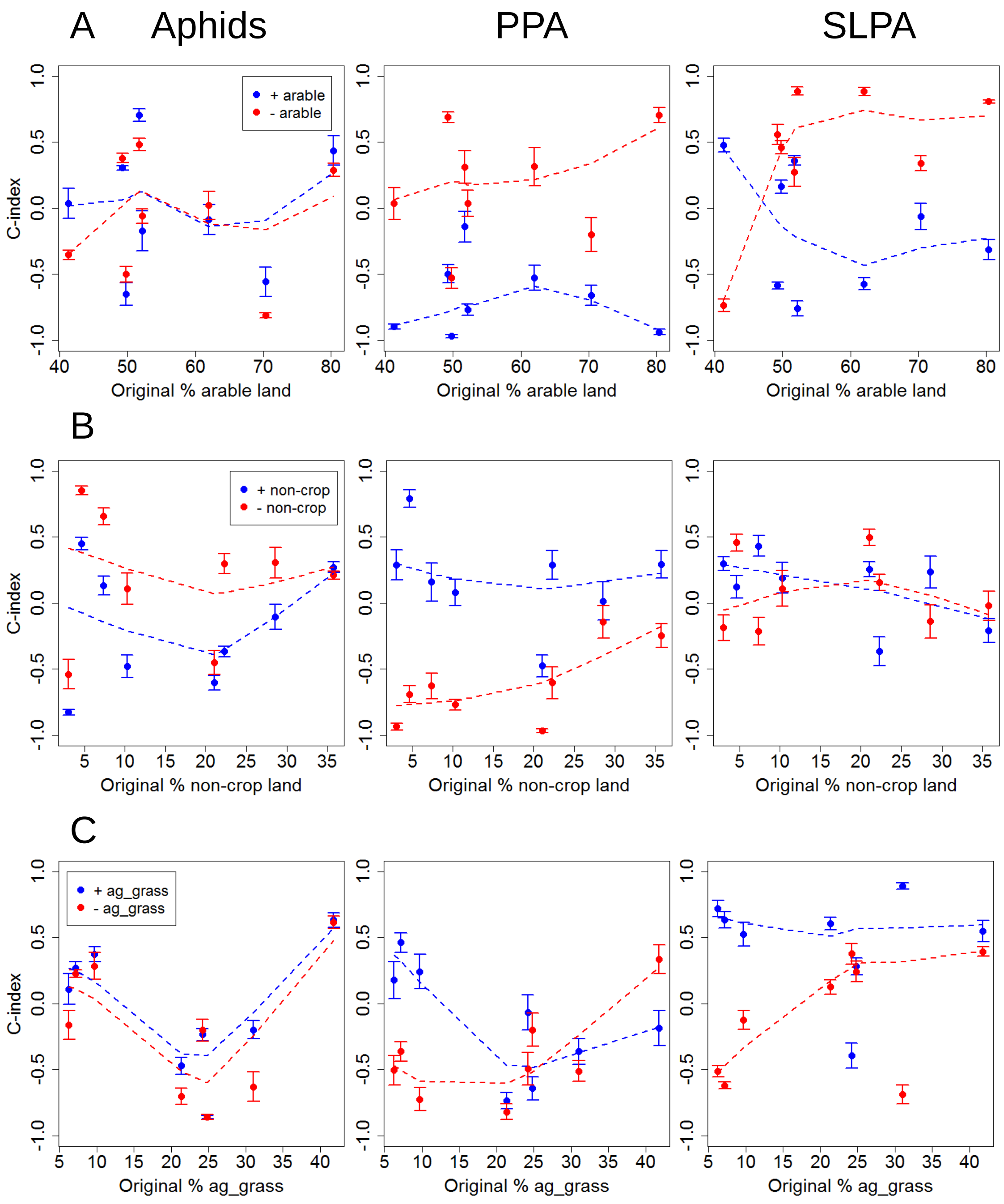


Figure 4.5: The influence of initial landscape context on responses to proportional area changes

Plots showing the direction and consistency (the C-index) of responses of aphid abundance, PPA and SLPA to 200 ha changes in the area of arable (A), non-crop (B) and ag_grass (C) land, plotted against the original area of that land cover type in each template map. In this case, the C-index for indicates an increase in aphid number (undesirable) if it is positive, unlike in table 4.3. Blue points, standard error bars and smooth lines correspond to the effect of increases in the area of the relevant land cover class, red ones a decrease. The responses are averaged across all scenarios where the particular change occurs. The net effect of changes, such as a general positive effect of decreased arable land on PPA, can be seen by comparing each pair of red and blue points. The influence of initial landscape is evident, for example in the lower negative effect of non-crop loss (B, red) on PPA when the initial percentage is high.

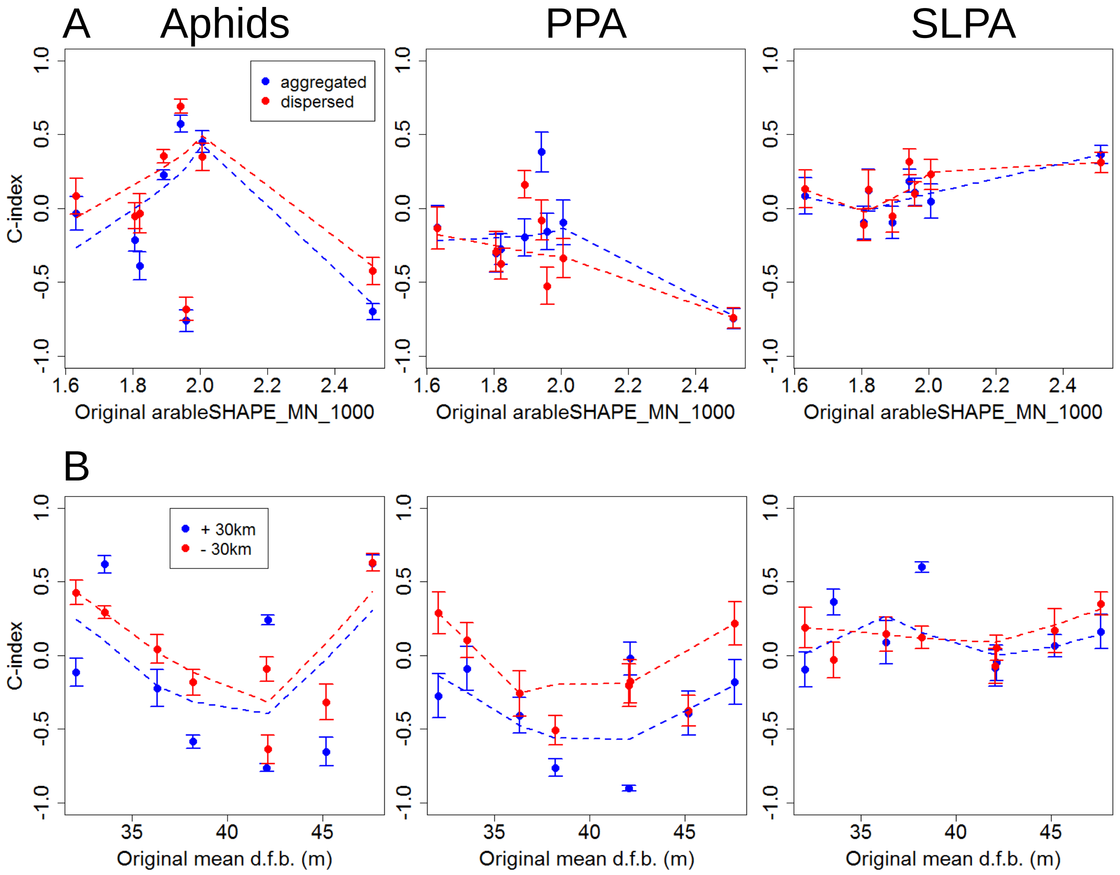


Figure 4.6: The influence of initial landscape context on responses to varying configuration and boundary length

Concept as for figure 4.5, but considering the influence of initial landscape context on responses when varying the configurational manner (A), and length of boundary (B). Original arable SHAPE_MN_1000 was used as a measure of configurational complexity. The mean **d**istance **f**rom a field **b**oundary (d. f. b.) is used to quantify the initial boundary complexity. Variation in the average response according to initial boundary length is evident, showing that in general decreases in aphids and PPA are more likely at intermediate levels of boundary complexity.

4.4 Discussion

This chapter demonstrated an efficient method to simulate changes in the vegetation composition and spatial configuration of land parcels, using digital maps and including stochasticity. By coupling the landscape patterns generated by the simulations to statistical models of the abundance of aphids and their natural enemies, scenarios of change resulting in synergies and trade-offs between different outcomes were identified. The results established the crucial influence of the initial landscape context on the outcome of a change, but also highlighted where general recommendations could be made. Below, the interpretation of results, the utility of the simulation method and the implications for decision making are discussed.

4.4.1 Overall predictions

Simulated increases in the proportion of non-crop vegetation in landscapes consistently resulted in lower aphid densities and larger numbers of parasitoids (PPA) and syrphid larvae per aphid (SLPA), especially if changes were made in a dispersed or random configuration. Scenarios where the proportion of arable land was reduced favoured high PPA and SLPA (figure 4.5 A), but in general reduction in agricultural grassland area rather than arable favoured decreased aphid abundance (figure 4.3 A; figure 4.5 A and C). There is thus more scope for win-win scenarios promoting abundance of the two natural enemy groups, than there is for ones causing beneficial changes in all three groups. This discrepancy is depicted graphically in figure 4.3 A, where the point showing the best scenarios for all three groups lies relatively close to those representing the best scenarios for the two natural enemy groups individually, but far from the point showing the best aphid abundance decreases, and also revealed by the relatively low C-indices of best scenarios for all three responses combined (table 4.8 in appendix 3). The balance of direct and indirect landscape influences on aphid abundance may be an important determinant of the extent of synergies between changes benefiting natural enemies and aphids. When aphid abundance is most strongly related to level of top-down control, as it may be in some regions or years (Thies et al., 2011), there will be large overlap in the best management for aphid reduction and natural enemy enhancement. However, if direct effects of landscape context on aphid colonisation (Loxdale et al., 1993, Vialatte et al., 2007) are strong then there will be lower potential for win-win-win management.

In contrast however, there was much better agreement between aphids and the two natural enemy groups in which scenarios produced the worst outcomes. Again referring to figure 4.3 A, the point showing the average changes in the scenarios leading to the worst outcome (increases) for aphid abundance is very close to that for both natural enemy groups combined. Moreover, when the scores of aphids, parasitoids and syrphid larvae are combined, reduction of non-crop area is a feature of the worst-case scenario for all eight templates, arable land increases in seven, and this occurs in an aggregated manner in 6 of them (figure 4.3 A; table 4.9). Replacement of non-crop vegetation by arable land in an aggregated manner, is therefore strongly supported as a general “lose-lose-lose” scenario, independent of the original landscape context.

The results presented above may not provide a consensus on which deliberate changes to landscape management would be beneficial, but they do suggest which situations should be avoided. The adverse outcomes result from changes corresponding roughly to the patterns of land use change driven by agricultural intensification in recent history (Bianchi et al., 2006), so these results further support arguments that continuation of the same trends will be damaging to the ability of agricultural landscapes to naturally regulate pest populations.

4.4.2 Relating predictions to the underlying statistical models

Comparison of the landscape metrics forming the basis of the statistical models created in chapter 3 (tables 3.1 – 3.3) with the types of land use change scenario producing consistent positive or negative responses in simulations, demonstrates the importance of dependence among landscape metrics in determining the outcomes.

Simulated changes in proportional area of arable land (arablePLAND) had consistent effects on all three responses, but only the model of syrphid larval abundance explicitly included an effect of arablePLAND at any scale. Instead, configurational metrics such as the shape complexity of arable land (arableSHAPE_MN) and the interspersion of patch types (landIJI) were strong predictors in models of aphid and parasitoid abundance instead. Therefore, proportional area changes produced responses in aphids and parasitoids through their indirect influence on configurational metrics. The relationship between proportional area change and configurational metrics is non-linear over certain ranges of values, and dependent on the configurational manner of the change (figure 4.7).

4.4.3 Interaction of proportional area changes with configurational style and boundary length

The marginal effects of configurational and boundary changes (i.e. the difference between treatments averaged across all scenarios) were not as marked as those of proportional area (figure 4.3 B and C; figure 4.6), but their interactions with proportional area changes were more obvious (table 4.3; table 4.10 in appendix 3). There is a clear translation between whether a proportional area change is made in an aggregated or dispersed way, and the resultant change in configurational landscape metrics, which then drives the responses from the statistical models. For example, the average change in arable shape complexity within 1000 m is positive when arable land replaces agricultural grass and non-crop land in a random way (figure 4.7 C), leading to increased aphid abundances (table 4.3), but negative when this occurs in an aggregated manner (figure 4.7 D), with a concomitant decline in aphid numbers. The interactions imply that in cases where the change in value of a key landscape metric is sensitive to the manner of land use change, the effects of potentially negative trends in large scale land use brought about by economic or political drivers (Mattison and

Norris, 2005) could be ameliorated, or the beneficial effects of planned landscape management enhanced, by controlling the spatial pattern of change.

It is more difficult however to synthesise a hypothesis for how addition or subtraction of field boundaries influenced landscape metrics, and thereby abundance responses. PPA tended to be favoured by removal of field boundaries, but it is unclear why. Field boundary density, or field size were not predictors selected in the statistical models used to predict responses. A proximate explanation is that this created larger fields, which when converted from or to arable, was more likely to result in an increase in arable shape complexity because it created larger dents or extensions to the perimeter of aggregated patches of the same land cover class. Equally, when field size is large the probability of it being a neighbour of more than one other land cover class may be increased, resulting in an increase in the patch interspersion and juxtaposition index (landIJI_2500), which was another important predictor in the model of parasitoid abundance (table 3.2 in chapter 3). Boundaries are associated with many other benefits in agricultural landscapes however (e.g. Cranmer et al., 2011, Concepción et al., 2012), so it would silly to advocate removing hedgerows on the basis of these simulations. The results merely display a tendency for proportional area changes to occur in a more beneficial way when fields are larger, but deliberate planning could emulate this effect without boundary removal.

4.4.4 Contingency of responses on the original landscape structure

The non-linear way in which the simulated changes were translated, via the underlying statistical models, into the responses of aphids, parasitoids and syrphid larvae was the most likely cause of two striking features of the results: the asymmetry of scenarios producing best and worse outcomes, and between-template variation in the consistency or direction of response.

In the absence of dependency between landscape metrics, it might be expected that the scenarios resulting in the best and worst outcomes would be roughly mirror images. However, asymmetry in several best/worst pairs was observed. For example, aphid abundance reduction was predicted to be favoured by replacing parcels of agricultural grassland with arable and non-crop vegetation in most scenarios, but growth of arable land also favoured aphid increases, if non-crop land was replaced instead of agricultural grass (table 4.3). Other asymmetries were more subtle; increased non-crop area was part of almost all of the best scenarios favouring high PPA (figure 4.3 A), but decreasing non-crop area from the original value did not have a consistent negative effect.

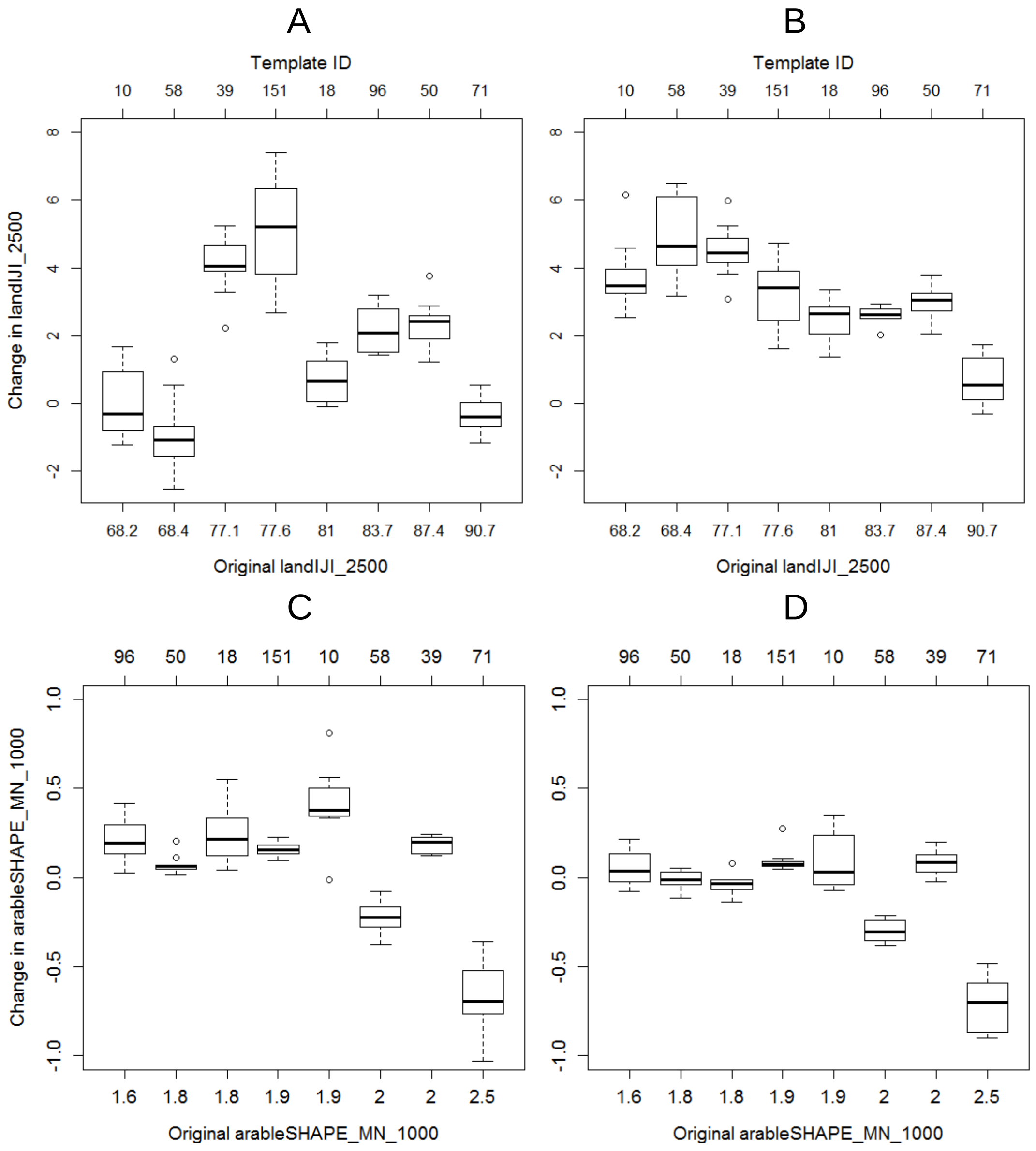


Figure 4.7: Between-template variation in changes of a configurational landscape metric resulting from the same simulation scenario

Box plots illustrating the dependence of the changes in the interspersion and juxtaposition index within 2500m (landIJI_2500; A and B) and the shape complexity of arable parcels (arableSHAPE_MN_1000; C and D) on template identity, from the same simulated scenario. The scenario depicted in A and B is replacement of arable land by both ag_grass and non-crop vegetation; that in C and D is the opposite. Changes in a random (A and C) and aggregated (B and D) style are contrasted, with no boundary changes. Each box plot shows the distribution of values from the 10 replicate simulations. Template Ids are ordered by their original landIJI_2500/ arable SHAPE_MN_1000 score. Panels A and B show how the aggregation modifies the relationship between the initial value and change in land IJI_2500. Panels C and D show how aggregation shifts the value of the change in arableSHAPE_MN_1000 downwards. ArableSHAPE_MN_1000 was included in both aphid and parasitoid abundance models, and landIJI_2500 predicted parasitoid abundance strongly (figure 3.4 and table 3.2 in chapter 3).

The between-template variation in the direction of response to a particular scenario was very striking, and emphasised the importance of considering the existing landscape patterns when predicting the outcome of land use change (figure 4.5 and 4.6). Intuitively, the effect of additional resources should depend on their original abundance, and this was reflected for example by a reduced negative effect of removing non-crop land when it is relatively plentiful (figure 4.5 B). However non-linearities were not explicitly included in the statistical models, so were not directly responsible for this dependence. The change in proportional area itself was manipulated directly and was therefore independent of starting conditions, but configurational metrics were only indirectly altered by the manipulations. Once again, it is the dependency between the proportional area of a land cover class and patch shape or configuration that is likely to be responsible for variation in outcomes between scenarios. There was good evidence that this mechanism was important here; the magnitude of change in landIJI_2500 and arableSHAPE_MN_1000 – important predictors in the model of parasitoid abundance (table 3.2 in chapter 3) - to a particular scenario varied widely between template landscapes, and could even be of opposite signs (figure 4.7).

The effect of initial landscape composition may intuitively be expected to change the direction of response to an increase or a decrease (such as for PPA in figure 4.5 C), but less intuitive is why the overall chance of increases or decreases, regardless of the scenario of change, should vary between template landscapes (figure 4.5 C and 4.6 B for aphids; figure 4.6 C for PPA). In this case, intermediate levels of agricultural grass percentage and boundary complexity are more likely to produce negative changes in both aphids and PPA. Increased arable shape complexity promotes high abundance of both of these groups, so this metric may have a local or even global peak at these intermediate values of boundary density and proportion of ag_grass (figure 4.8 A and B), indicating that initial conditions according to these two variables could not be improved upon from the perspective of aphids or parasitoids; any change is detrimental.

When proportional area was an explicit predictor in a statistical model, interactions with other variables could have been responsible for between-template variability of predicted responses to the same simulated changes. Here, an interaction between the proportion of arable land within 1500 m and rough grassland within 200 m may explain why the response of syrphid larvae (SL) to changes in arable area were varied (figure 4.5 A, table 4.10 in appendix 3). In the absence of rough grassland, increasing arable area was modelled as having a negative impact on SL numbers, but in its presence had a positive effect.

Acknowledgment that the outcome of change depends upon initial conditions is important, and suggests that management decisions should be planned with regard to the specific landscape in question. However, this naturally raises the question of whether what constitutes appropriate management is predictable from simple measures of initial landscape context, which could be generalised to other landscapes without the need for repeated simulations. There was some evidence of systematic patterns presented above (figured 4.5 and 4.6, table 4.10 in appendix 3), and the principal components technique used to select template landscapes here could be extended as a means of classification, to capture a greater number of variables. However in order to draw firmer conclusions considerably more than eight templates would be needed, and characterisation of templates would probably have to be carried out with metrics at several spatial scales. Accordingly, much of the between-template variation in response was difficult to attribute to specific characteristics of initial conditions explored here, arising instead from idiosyncratic landscape structure that may be challenging to quantify.

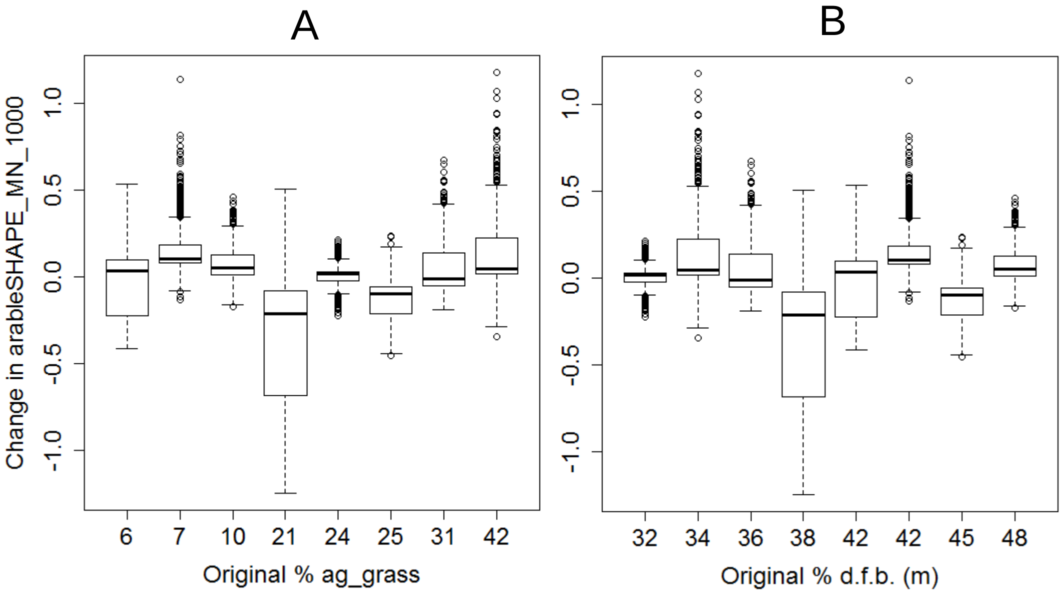


Figure 4.8: Variation in the mean change in arable shape complexity according to initial proportion of agricultural grassland and boundary complexity
Illustration of the tendency for any changes, regardless of their nature, to produce either positive or negative changes in a landscape metric (arableSHAPE_MN_1000) under particular starting values of percentage of agricultural grassland within 2500 m (A) and boundary complexity (approximated by the mean **d**istance **f**rom a field **b**oundary (d. f. b.)). This may indicate that intermediate values are local optima for arableSHAPE_MN_1000. The trend is not very clear with only 8 templates, and is dominated by one landscape with very negative responses of arableSHAPE_MN_1000.

4.4.5 Evaluation of the simulation method

The simulation method used in this chapter was a framework for evaluating the responses of several variables to a set of pre-defined, but stochastic, manipulations. Although many studies have quantified the effects of landscape context on pests and natural enemies, this is one of few that have predicted the outcome from changes to maps based on real agricultural landscapes.

The process is also the first, to the author’s knowledge, to apply changes to the boundaries delineating parcels in landscapes as part of simulations. Allowing field boundary patterns to become simpler or more complex both increased or decreased linear habitat available and altered the “grain” of the landscape, thereby enabling a greater range of changes in the aggregation of patch types to occur. In other patch-based simulations, such as “LUPOlib” (Holzkämper and Seppelt, 2007b), parcel boundaries are fixed, precluding this possibility. Changes in field size and shape through hedgerow removal, and the loss of linear habitats themselves have been key drivers of farmland biodiversity decline (Bianchi et al., 2006), so this is clearly an important aspect of change to consider.

It is important to understand the limitations of this map-based simulation approach, and there are aspects where improvement would be desirable.

Firstly, the use of statistical models to extrapolate the value of emergent patterns to new conditions is not recommended. Process based models defining the response of the constituent parts (individual organisms in ecology) of a system to their environment allow emergent properties under new conditions to be modelled indirectly, and are much more likely to give sensible quantitative answers (Evans et al., 2012). For extrapolatory purposes, the process-based InVEST or ARIES modelling tools would provide an excellent framework. However, these require more detailed knowledge of the system than was available here to parameterise, and when many individual processes are important in the dynamics of a system, creating an effective model may be difficult to achieve. As was argued in section 3.1.4 in chapter 3, modelling the emergent properties (the observed patterns) directly may be more effective when little information is available, and extrapolation is not extreme. Process-based models using InVEST can also require considerable computation time to run relative to statistical models (Richard Gunton, University of Leeds, personal communication), which may be a severe limitation if many, large landscape maps must be processed. A hybrid approach may be to use process-based models to predict the effects of land use change well outside of current conditions, then derive statistical relationships from this extrapolated dataset for faster prediction.

Here, the pitfalls of extrapolation from statistical models were avoided by quantifying the consistency in the sign of the response, rather than the absolute magnitude. Unfortunately this inevitably limited the information available from the simulations. The consistency of the sign of response is likely to be correlated with its magnitude, but only within a certain range of values. Truly quantitative predictions are important for cost-benefit analyses of particular scenarios; for example here, whether or not a management change really is worthwhile for a farmer will depend on the net effect on crop yield, which can only be calculated from quantitative estimates of aphid population and area farmed. Random forest models developed in chapter 3 would have made more “sensible” predictions, as they are not able to extrapolate; predictions are bounded to the range of the response to which the model was fitted. However, their inferior attributes for predicting test data (table 4.2), and their slowness in making many predictions were deemed too high a cost.

4.4.6 Land use scenarios

In this chapter a pre-determined set of land use changes were made to explore a range of situations producing “win-wins”, trade-offs, and importantly also “lose-loses” between changes in parasitoid, syrphid larva, and aphid abundance. However, the actual land use changes occurring in this approach could be viewed as somewhat arbitrary, because the range of changes evaluated is only a small subset of the set of possible changes, and there was no theoretical rationale underlying the changes implemented.

The most feasible way to introduce objectivity into land use change simulation, and simultaneously augment the topical relevance of the results, would be to use the human-driver storyline approach (political, economic and social drivers) discussed in the introduction to this chapter. It may be possible, with hindsight, to match some of the land use changes imposed in this chapter to historic trends or realistic future policy, but this is likely to be a weak linkage. On the other hand, using multi- actor models to translate human drivers into land use change through many small decisions creates a strong link between policy or economics and the provision of pest-control.

In Europe, there are currently debates surrounding the impacts of land use change driven by major EU policies for food production, energy generation and conservation, which would benefit from studies using this human actor driven approach. For example, the EU renewable energy directive (Directive 2009/28/EC) has set targets of producing 20% of EU energy requirements from renewable sources by 2020, and consequent increases in the area of biofuel crops such as short rotation coppice willow has potential benefits for natural enemies (Langer, 2001) and farmland bird populations (Sage et al., 2006). Likewise, proposed reforms to the common agricultural policy (EFRA, 2012) that will require an increase in crop diversity, retention of permanent pasture and designation of 7% of every farm as “ecological focus areas”, may have implications for natural enemy and pest populations. If many farms must increase the area of uncropped habitats to meet the 7% target, and crop diversification results in higher configurational complexity, the results of this chapter suggest this would be beneficial for natural enemies.

There is also currently an academic debate over whether the best solution for reconciling food production and wildlife conservation is through a “land-sparing” or “land-sharing” strategy (Green et al., 2005). This question can perhaps be better framed recently as the choice of the appropriate spatial grain for separating land dedicated to food production and conservation, with sparing and sharing being at opposite ends of a continuum (Phalan et al., 2011a). For tropical birds, Phalan et al. (2011b) showed that coarse scale division of farmland and high quality habitat is generally preferable to a fine-grained mosaic, but for natural enemies using crop pests as an important resource a finer grain may result in better pest control. Using this debate as a framework, a series of objective “spatial grain” scenarios could be developed to evaluate the best strategies for multiple species conservation, and multiple ecosystem service provision.

Storyline based approaches could perhaps also be complemented with optimisation procedures (section 4.1.4), allowing one to assess how far from optimal the land use patterns produced by proposed policies are, for a particular set of objectives. This might make a powerful combination for producing information of greater objectivity and applied relevance than was achieved in this chapter, but to achieve this, existing tools will require further development to be able to incorporate potential alterations to the parcel boundary structure of landscapes.

4.4.7 Conclusions and wider perspectives

The simulation method presented here was the first to be used to predict the effects of lands use change on a natural enemy system. The results suggest that replacing arable land with non-crop vegetation should produce win-wins for parasitoid and syrphid larval abundance, but that this may not favour the greatest decrease in aphid abundance. However, replacing non-crop habitat with arable land, and increasing the degree of aggregation produced adverse outcomes for all responses.

Nevertheless, these results leave further important questions unanswered. Firstly, should farmers prioritise landscape management optimally reducing pest densities, even if this does not benefit natural enemies? Alternatively, if the response of natural enemies to landscape structure is more consistent in the long term, is managing for them a safer strategy given the time investment in landscape management, even if in some years this management is not optimal for reducing pest populations? Incorporation of the long-term effects of interventions into mainstream pest management will be an exciting development, but few studies have addressed how this may be done effectively (see Zhang and Swinton, 2009).

Secondly, if taking arable land out of production results in a decrease in crop damage from aphids, would the yield saved on the remaining land outweigh that lost through the smaller crop area? This question emphasises the need for future studies to provide accurate quantitative predictions of how pest density would respond to a change in landscape context.

That alone however would still not be sufficient. There are many competing pressures feeding into a farmer's decisions, and like other business the costs and benefits must be valued financially to stand on an equal footing. Government subsidies provide short-term incentives to farmers to manage in ways beneficial to natural enemy communities, but agricultural policy can be capricious. In the current climate of subsidy cuts (Myers, 1998), it is important that managing for natural enemies or other ecosystem service providers be linked to the resulting increased crop yield, in order to reduce the perceived trade-off between farming for wildlife and for high yields. Quantifying the added value of greater natural enemy numbers for farmers will be the subject of the next chapter.

Finally, the importance of the degree of aggregation or dispersion with which changes in proportional area occur demonstrated by these results raises an interesting issue. Recommendations for absolute areas of a particular habitat on a large scale could be implemented by individual farmers easily, as is proposed for the upcoming "greening" of the CAP. In contrast, configurational properties are dependent on *where* changes take place, which would require more planning. Moreover, given that the scale at which spatial configuration matters here is larger than that of most individual farms, planning would be most effective if neighbouring farmers cooperated to implement joint strategies; an example of a scale mismatch between the traditional management unit, and that important for the process in question that has been noted by other studies (e.g. Gabriel et al., 2010, Sutherland et al., 2012). Exploring existing and potential incentives for landscape-scale management will be a key theme in chapter 6, the general discussion.

5. Estimating the economic benefit of aphid control by parasitoids and syrphid larvae during wheat grain ripening

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Abstract

Natural enemies of insect crop pests provide an economic subsidy to farmers by reducing crop yield loss, and limiting the need for insecticide applications. Managing to increase natural enemy abundance may provide a net economic return, and ease conflicts between production and biodiversity conservation on farms. However, valuation of the costs and benefits of such management is necessary for farmers to make decisions, and these may depend on the pest management strategy employed.

In this chapter, the economic benefit of natural enemy action between the flowering and milk-ripening growth stages was estimated for 64 winter wheat fields in Yorkshire, UK, for a series of hypothetical insecticide application thresholds. A statistical model of cereal aphid population growth was created for this 14 day period. The effect of predation by hoverfly larvae and parasitoid wasps on aphid growth rate was estimated, and the extra yield loss and spraying cost in the absence of this effect predicted for each field.

Averaged across fields, natural enemy action saved an estimated £29 ha^{-1} of yield loss when no insecticide was applied. Controlling for initial aphid abundance and crop phenology, avoided yield loss varied by £40 ha^{-1} among fields, implying a significant benefit of increased natural enemy abundance. At low initial aphid abundances, a hypothetical spraying threshold of 15 aphids per tiller resulted in greater potential benefit from natural enemy action than a no-spray policy, due to saved application costs. At thresholds above 30 aphids per tiller, average economic benefit across all fields was greater than for a no-spray policy. Under some conditions, conventional farmers may thus gain as much as organic farmers from managing for natural enemies.

Hoverfly larval abundance was less tightly correlated with aphid abundance than was parasitism rate, implying that hoverfly oviposition is more limited by other factors, and so possibly more responsive to beneficial habitat amendment. However, the economic and intrinsic value of other biodiversity and ecosystem services should also be taken into account, when making management decisions.

5.1 Introduction

Predatory and parasitic insects ("natural enemies") are among the most important agents of mortality regulating insect herbivore populations in natural systems (Polis, 1999). In agricultural systems also, farmers are the beneficiaries of a pest-control subsidy from natural enemies, reducing the level of economic damage to crops from herbivory by an estimated $4.5 billion per year in the USA (Losey and Vaughan, 2006).

There is widespread acknowledgement that aspects of modern conventional farming are detrimental to the ability of natural enemies to control herbivore populations (e.g. Bianchi et al., 2006, Tilman, 2001), in particular the application of synthetic insecticides. Insecticides reduce natural enemy populations in addition to those of pests, in some cases increasing the frequency of pest outbreaks (Pimentel et al., 1992). Insecticide use itself is also costly to farmers in terms of expenditure for labour, fuel and chemicals, and reduced market value of goods if premium prices are paid by consumers for goods produced with pesticide-free management (e.g. organic) (Cullen et al., 2008). There is thus a twofold cost to reliance on chemical insecticides, and consequently integrated pest management (IPM) strategies now form a central part of advice and legislation concerning pesticide use (Chandler et al., 2011).

Management to enhance the abundance of natural enemies – "conservation biological control" - forms a key part of both pesticide-free control and IPM strategies. Often, this comprises creating linear habitat features providing shelter from disturbance (e.g. "beetle banks"), alternative prey, and non-prey resources such as floral nectar (Poehling et al., 2007). Recent studies, including previous chapters in this thesis, have also emphasised the importance of large scale vegetation patterns in influencing pest and natural enemy abundance, suggesting the possibility of landscape-scale management for biological control potential (e.g. Bianchi et al., 2006, Tscharntke et al., 2008, Kremen et al., 2007, Tscharntke et al., 2012).

However, habitat management for conservation biological control has economic costs: the time and materials necessary for implementation; the reduction in the area of land being farmed if it involves setting aside uncropped areas, and perhaps also reduced efficiency of farming operations - hedgerow removal was often undertaken to make fields more amenable to operating large machinery. In order for spontaneous uptake of conservation biological control measures by farmers to occur, rather than via subsidised agri-environment schemes, the impact of these measures in reducing yield losses from crop pests or decreasing the necessity to apply insecticides must also be valued economically. In other words, the costs and benefits of management can only be properly compared when expressed in the same currency. This is especially relevant for decisions involving quantitative changes in management (as opposed to an all-or-nothing intervention); if for example there is a saturating population response of natural enemies to increased management for conservation biological control, there will be an optimum level above which the costs incurred outweigh the benefits. Limited adoption of conservation biological control management to date has been attributed mainly to the lack of such economic assessments (Cullen et al., 2008, Griffiths et al., 2008), though social dynamics also play a part (see van der Horst, 2011).

Furthermore, insect natural enemy assemblages are made up of diverse groups of predators and parasitoids, and any management for conservation biological control will likely favour some over others. In chapters 3 and 4, parasitoid and syrphid larval abundance in winter wheat fields were related to the surrounding landscape context, and predictions made regarding what landscape-scale changes might favour each group. When there are trade-offs in management for parasitoids and syrphids (see section 4.3.3 in chapter 4), the decision over which group receives priority may be influenced by their relative capacity to control aphid populations. Of course, targeting management of field margins solely to enhance control of cereal aphids would be very narrow minded. Considering only biological control, the relative capacity of natural enemy groups to control different economically important pest species on a farm may vary widely. Moreover the total value of natural enemies to farmers and society is greater than merely their ability to control pests, including both other economic aspects and intrinsic value that is difficult to quantify. Syrphids, for example, are also efficient pollinators of crops such as oilseed rape (*Brassica napus*) (Jauker and Wolters, 2008), aesthetically pleasing charismatic insects, and interesting examples of imperfect Batesian mimicry for scientific study (Gilbert, 2005). More importantly, every species of natural enemy has intrinsic existence value as a part of biodiversity.

Nevertheless, it would seem sensible to encourage management targeting particularly effective natural enemy species or functional groups, as long as the cost to other species is not too high.

5.1.1 Cereal aphid control by natural enemies

Aphids are among the most serious insect pests of cereal crops worldwide (Poehling et al., 2007). Previous studies have demonstrated the regulatory impact of generalist or aphid specialist predators and parasitoids on cereal aphid populations, through selective exclusion experiments or correlative field observations (e.g. Chambers and Adams, 1986, Schmidt et al., 2003, Tenhumberg and Poehling, 1995, Thies et al., 2011), though the identity of which species or functional group is found to most important has varied between studies and between years. For instance, Schmidt et al. (2003) showed that exclusion of parasitoids caused the largest increase in aphid population growth, whereas Chambers and Adams (1986) found that aphid-specific predators were most likely to be responsible for keeping *Sitobion avenae* densities below the economic threshold for insecticide application. The importance of particular natural enemy groups may also vary within a season, with generalist predators likely to have more effect early in the season when other prey is scarce (Harwood et al., 2009, Ekbom et al., 1992). In the field observations contributing to earlier chapters of this thesis, it was noted that syrphid larvae were present in far lower abundance than parasitoids (section 3.3 in chapter 3). However, given that individual syrphid larvae can consume many aphids during development (Ankersmit et al., 1986), which group contributed most to aphid suppression overall is therefore an open question.

Despite the relative wealth of studies demonstrating reductions in aphid populations due to natural enemies, few of these have attempted to place an economic value on their effect. Östman et al. (2003) estimated the value of aphid predation by ground dwelling arthropods by measuring the yield of barley in control and exclusion cages, finding that it reduced yield losses by 303 kg/ha on average. This could then easily be converted to the direct monetary value of the yield saved. However, the authors also point out that the benefit farmers receive from natural enemies will depend on the pest management strategy they adopt. Direct reduction in yield loss ("avoided damage") is an accurate valuation for farmers not using insecticides (e.g. organic farmers), but conventional farmers use insecticides aphid density exceeds an economic threshold (above which the benefits of spraying outweigh the direct costs). Valuation for conventional farmers is thus more complex; they can benefit from higher yields, but also save money from a reduced need for insecticide use (i.e. save the "replacement cost" of natural enemy control). When aphid numbers surpass the threshold however, if conventional farmers apply insecticides they temporarily forfeit the potential yield savings attributable to natural enemies. Consequently, the relative economic benefits of natural enemies accruing to farmers operating insecticide-free and spraying threshold pest management strategies will be dependent on pest abundance in the field and the value spraying threshold used. Although thresholds are recommended by agricultural advisory services which remain constant from year to year (e.g. DEFRA, 2011b), in reality the changing cost of spraying and price of wheat makes dynamic thresholds more realistic (Larsson, 2005). This issue has received little attention, but is an important consideration when analysing the costs and benefits of any conservation biological control intervention for a particular landowner.

5.1.2 Objectives

This chapter aims to use observations of cereal aphid and natural enemy abundance in winter wheat fields to model the effect of parasitoids and syrphid larvae on aphid population change between two sampling occasions, when wheat is vulnerable to aphid damage. Although inferring the impact of natural enemies on herbivores through correlative methods is less reliable than experimental manipulation (Kidd and Jervis, 1996), provided that results are interpreted with care using such methods with observational data has the advantages of greater realism and replication. Other generalist predators such as coccinellids or entomopathic fungi occurred infrequently in the year and region in which field observations were made, permitting more reliable estimation of the impact parasitoids and syrphid larvae from a statistical model than might otherwise be possible.

Using the model of aphid population change, the objective is to predict the aphid abundance in the absence of the natural enemies. Combining these predictions with published assessments of the impact of aphids on wheat yield will then provide estimates of the economic value of pest suppression by parasitoids and syrphid larvae during the period in question.

The analysis does not claim to provide a comprehensive estimate of the economic value of aphid control by parasitoids and syrphids over the course of a whole year, and still less an estimate of the “total value” of these natural enemies, as mentioned above for the example of syrphids. One of the main mechanisms of potential winter wheat yield loss from aphids is through the transmission of barley yellow dwarf virus (BYDV) to seedlings in autumn. Yield losses to BYDV are potentially greater than those through direct feeding (Kennedy and Connery, 2005), so the economic importance of natural enemies might be expected to be greatest during this period, and this is likely to be true for organically managed wheat. However for conventional farmers, seed treatments using systemic insecticides such as neonicotinoids (e.g. imidacloprid) are a common means of protecting wheat seedlings against aphid attack, which are applied before drilling rather than in response to aphid densities during the vulnerable seedling period. Seed treatments therefore replace any potential economic benefit from natural enemy action during the seedling stage. If an insecticide spray is the preferred BYDV control method, application may be in response to regional risk forecasts, or a presence/absence threshold rather than one based on abundance (HGCA, 2000). Thus, unless natural enemies reduce aphid numbers sufficiently for none to be found in a typical pest survey, their potential local economic impact will likewise be largely replaced by the insecticide. It could be argued therefore that although the potential yield loss to aphids in spring and summer is relatively small, the use of abundance based spraying thresholds in summer allows conventional farmers to benefit more economically from natural enemy control at this time than in autumn. Nevertheless, even if the omission of autumnal aphid control by natural enemies has a small impact for this analysis, the effect of natural enemy action on aphid population trajectory in the spring and summer before the period studied in this chapter is also not accounted for. If control of aphids is more sensitive to variation in natural enemy action early in the season than later on (Ekbom et al., 1992), then what is estimated below is likely to be a fraction of the full economic benefit conventional farmers receive from aphid control by parasitoids and syrphids.

In this chapter, emphasis is placed on comparative economic benefit received during a short but important interval between wheat flowering and grain ripening in summer. In particular it will focus on the following questions:

1. Do syrphid larvae or parasitoids contribute more, *en masse*, to pest suppression?

2. How does the value of natural enemy action vary with initial pest abundance?

3. What is the difference in the value of natural enemies between where they are common and where they are scarce? This will provide a useful approximation of the potential benefits of management for conservation biological control.

4. Are natural enemies expected to be more valuable under an insecticide-free or threshold-spraying regime? And how do the relative values change with varying aphid abundance and spraying threshold?

5.2 Methods

5.2.1 Sampling design

Live aphids, parasitised (mummified) aphids, and syrphid larvae were counted in 94 winter wheat fields on four occasions between ear emergence and harvest in June and July 2011. In each field 60 tillers were inspected in six groups of 10; 3 along one edge and 3 parallel to these ~35 m into the field. Fields were selected to provide variation in the composition of the surrounding landscape, which influences the abundance of aphids and natural enemies in the crop. For full details of site selection the sampling design, see sections 2.2.1 and 2.2.2 in chapter 2.

5.2.2 Fitting the aphid population growth model

The basis of all economic value estimations was a statistical model, using data from two consecutive sampling occasions to quantify the lagged effects of parasitoid and syrphid larval abundance on the change in aphid populations over the intervening 14 day period. The data was collected from sixty-two of the sampled fields known to have not received any insecticide applications during this time, ensuring that insecticide mortality was not a confounding factor when modelling the impact of natural enemies.

The time period of particular interest was that between the second and third round of visits to fields (round 2: 20th June – 3rd July, round 3: 4th – 16th July), corresponding approximately to the end of flowering and milk-ripening stages respectively, during which the risk of yield loss to aphid feeding is high. Rounds of sampling proceeded in a South to North direction to try to minimise phenological differences between crops in the same sampling round. All aphid species were pooled into a single functional group for modelling, because although *Sitobion avenae* has the potential to cause more damage to wheat than *Metopolophium dirhodum* (Poehling et al., 2007), numbers of the former were very low over the period of interest so could not be modelled separately, and *Rhopalosiphum padi* occurred only in negligible numbers. The abundance of mummified aphids (discounting those where the parasitoid had already emerged) was used to quantify the numerical impact of parasitoids on aphids, which although likely to yield an underestimate of true parasitism is nonetheless correlated strongly with this value. The magnitude of parasitism and syrphid larval predation over the period of interest was estimated by linear interpolation of the number of parasitised aphids and syrphid larvae counted at the second and third sampling occasions. For parasitoids this incorporates the effect of undetected parasitism at the first observation and additional parasitism before the second one; for syrphid larvae it accounts for predation by those hatching from unseen or newly laid eggs between the two observations, and parasitism occurring between the two sets of observations. Ideally, much more frequent visits would have been made, allowing the daily impact of the natural enemies to be quantified (as Chambers and Adams, 1986), but in the collection of the data used here a greater number of fields was a priority over sampling frequency. Interpolation therefore provides a pragmatic compromise. All count data were aggregated to field-level totals, to average over unwanted variation in local aphid abundance resulting from small-scale aphid movement, and to aid model fitting. A generalised non-linear least squares model was fitted of the following form:

Equation 5.1:

$$\boldsymbol{A_{3_i} = aA_{v2_i} - a\left(\frac{P_{2_i} + P_{3_i}}{2}\right) - ab\left(\frac{S_{2_i} + S_{3_i}}{2}\right) - cJ(A_{2_i}) - d\left({A_{2_i}}^{2}\right) + \varepsilon_i}$$

Aphid abundance at visit 3 ($\boldsymbol{A_3}$) in field $\boldsymbol{i}$ was modelled as a function of aphid abundance at visit 2 ($\boldsymbol{A_2}$) multiplied by a growth parameter $\boldsymbol{a}$. Losses to parasitoids ($\boldsymbol{P}$) and syrphid larvae ($\boldsymbol{S}$) interpolated between visits 2 and 3 comprised the absence of offspring from parasitised and predated aphids (assumed to equal the number of aphids killed multiplied by ***a***), with an additional parameter ***b*** estimated to model the consumption rate of syrphid larvae. The effect of differences in plant phenology due to the spread of sampling dates (Julian days; ***J***) on growth, and the negative density-dependence of aphid growth were also included in the model (***c*** and ***d***). Residual variation, ε was assumed to be normally distributed. Significant spatial autocorrelation was present initially in the residuals of the model, observed by fitting a correlogram and comparing the value of Moran's I to a null distribution (Moran's I = 0.139, p = 0.0459). To correct for the bias autocorrelation can introduce into parameter estimates (Beale et al., 2010), the model was re-fitted with an exponential error correlation structure (range estimated at 565 metres; a similar scale to the most important landscape predictors of aphid abundance). Numbers of aphids, parasitised aphids, and syrphid larvae were square-root transformed before fitting the model, to meet the assumptions of normality and homoscedasticity of residuals.

Uncertainty in the coefficients of ***a, b, c*** and ***d*** was quantified by fitting the model to 999 bootstrap samples of the data, and using the quantiles of the coefficient estimates to calculate confidence intervals (table 5.1). This was deemed more reliable than using the parametric standard errors, because the coefficient distributions were skewed in some cases.

The model was fitted with the `gnls` function in the R package "nlme" (Pinheiro et al., 2011), and Moran's I calculated using the `moran.mc` function in the package "spdep" (Bivand et al., 2012).

Table 5.1: Parameter estimates for the aphid population change model
Coefficients and confidence intervals for the four parameters estimated in the discrete aphid population growth model (equation 5.1). Upper and lower confidence interval values are the 2.5th and 97.5th percentiles of parameter distributions, obtained from fitting the model to 999 bootstrap samples (i.e. with replacement) of the data.

Parameter	Coefficient estimate	95 % Confidence intervals	
		Lower	Upper
a	3.08	2.71	3.51
b	1.53	0.413	2.74
c	0.101	0.0702	0.128
d	0.0136	0.00574	0.0208

5.2.3 Estimating the impact of natural enemies on aphid abundance

The fitted aphid population growth model was used to estimate the effect that natural enemies have on the number of aphids observed at the end of the period of interest. Predictions were made of the expected aphid abundance from the full model, and three different reduced models where the terms describing the effect of parasitoids alone, syrphid larvae alone and of both natural enemies combined were excluded (figure 5.3 A). The result was therefore four different predictions for every field.

5.2.4 Translating aphid abundance into yield loss

The impact of aphid abundance on yield during the period in question was approximated by the number of aphid-days per tiller. This is a cumulative measure of feeding injury shown to correlate strongly with yield loss in winter wheat tillers (Kieckhefer et al., 1995).

The number of aphid-days per tiller ($\boldsymbol{D}$) in field $\boldsymbol{i}$ for prediction $\boldsymbol{j}$ (where j corresponds to one of the four fitted models) was calculated by first taking the mean of the square-root transformed field-level aphid abundance (the sum of all 60 tillers examined) observed at the beginning ($\boldsymbol{A_2}$) and predicted at the end ($\boldsymbol{A_3}$) of the period. This result was then multiplied by fourteen to give total aphid-days for the field, and divided by the sixty tillers to give an estimate of aphid-days per tiller (equation 5.2; illustrated graphically in figure 5.2 A).

Equation 5.2:

$$\boldsymbol{D_{ij}} = \frac{\mathbf{14}}{\mathbf{60}} \left(\frac{\sqrt{\boldsymbol{A_{2_i}}} + \sqrt{\boldsymbol{A_{3_{ij}}}}}{\mathbf{2}} \right)^{\mathbf{2}}$$

Next, the number of aphid-days per tiller was converted into estimates of yield loss in the presence and absence of natural enemies. It is important to consider several factors when deriving yield loss estimates from aphid-days: i) the damage per aphid-day increases approximately linearly with the potential maximum yield (influenced by cultivar and the abiotic environment); ii) yield loss varies with growth stage, being greatest in mid-flowering (Kieckhefer et al., 1995, Rossing, 1991); iii) impact varies between aphid species, with *S.avenae* having approximately twice the direct effect of *M.dirhodum* or *R.padi* due to their different feeding styles (Poehling et al., 2007), and iv) each additional aphid-day causes a smaller marginal yield loss as the total number of aphid-days increases owing to physiological responses of the plants (Moewes et al., 1997).

Unfortunately, literature searches failed to reveal any studies having established the functional form of the relationship between yield loss and aphid-days over a wide range of values, so instead published values were used to derive a function displaying desirable properties within the limits of aphid-days observed in the field.

The yield loss (L) in field i for prediction j was calculated as a power-law function of aphid-days (D) per tiller (after Ostman et al., 2003) which resulted in a decreasing rate of expected yield loss as the number aphid-days increased (equation 5.3). The function was fitted so that the average yield loss per aphid-day up to 300 aphid-days was 2 kg/ha (figure 5.1). The value of 2 kg/ha per aphid-day was chosen to correspond with a yield loss estimate for the post-anthesis period at a potential yield of 9000 kg/ha and a low number of aphid-days from Rossing (1991), which is appropriate for the crops in this analysis. This is actually slightly lower than suggested by Rossing's figures as these were based on feeding by *S.avenae*, whereas *M.dirhodum* was the dominant aphid observed in this study. Three hundred aphid-days was taken as the calibration point for the function, because Hansen (2000) found that above 300 aphid days the damage per aphid day in barley fell from 2.68 to 1.25 kg/ha, providing an estimate for the upper boundary of "low" numbers of aphid-days.

Finally, the predicted yield loss was adjusted to the density of tillers (T) in each field, relative to the mean density in all fields.

Equation 5.3

$$\boldsymbol{L_{ij}} = \frac{\boldsymbol{T_i}}{\frac{\mathbf{1}}{\boldsymbol{n}}(\sum_i^n \boldsymbol{T_i})}\left(\mathbf{13.91} \times (\boldsymbol{D_{ij}})^{\mathbf{0.66}}\right)$$

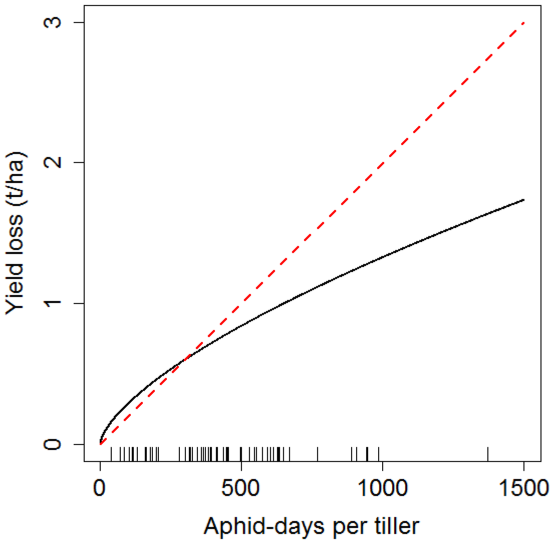


Figure 5.1: The relationship between the number of aphid days and yield loss

Yield loss per ha modelled as a power-law function of aphid days per stem, assuming a potential yield of 9000 kg/ha at average tiller densities. The black line indicates the yield loss function. The red dashed line shows a slope of 2 kg/ha loss per aphid day, to which the curve was calibrated at 300 aphid-days. The power of 0.66 was used by Östman et al. (2003) to model yield loss in barley, and gives a diminishing yield loss rate at higher numbers of aphid-days. The barcode-like "rug" of black ticks at the bottom of the plot shows the distribution of aphid-day values from predictions in the absence of natural enemy action.

5.2.5 Deriving predictions of economic value

The calculations described above resulted in estimates of the yield loss caused by the observed aphid abundance, and from predictions of their abundance in the absence of control by parasitoids, syrphid larvae or both natural enemy groups together. The next step was to transform yield losses into monetary terms.

As discussed in section 5.1.1 above, the economic value of a reduction in aphid abundance is likely to depend on the pest management strategy used. Accordingly, here a valuation framework was used which differentiated between the benefits that would accrue under insecticide-free management, and when insecticides are applied only if aphid numbers exceed an economic threshold (figure 5.2). In all cases, the economic value of natural enemy action was considered to be equal to the increase in costs incurred by the farmer in the simulated absence of aphid control.

For insecticide-free management, valuation merely consisted of multiplying the estimated yield loss during the 14 day period of interest by the market price of wheat. For the purposes of this analysis, the price was taken to be £180 per metric tonne (£0.18 per kg) based on 2011 values for milling wheat (HGCA, 2012).

For threshold-spraying management valuation was more complex, and depended on the decisions made in response to aphid abundance observed at the two time points at either end of the period of interest (figure 5.2 B). As the data used to parameterise the aphid population growth model (equation 5.1) came exclusively from fields receiving no insecticide applications, the framework represented purely hypothetical spraying decisions. The hypothetical farmer was able to make decisions of whether or not to spray at either the first or second observation, but not in the intervening 14 days.

If aphid density was above the economic threshold at the first observation, the farmer was assumed to apply insecticide immediately, reducing both aphid and natural enemy populations. In this case the farmer would not suffer any extra costs by simulated natural enemy absence, so their value was zero (figure 5.2 B, bottom right). If instead initial aphid density was below the threshold, three outcomes were possible. If the abundance at the second observation surpassed the threshold, the farmer sprayed, and the value of natural enemy action over the period was equal to the yield loss saved before that point, as for insecticide-free management. Likewise, if aphid abundance remained below the threshold and would have done so even in the absence of natural enemy action (figure 5.2 B, top left), again the farmer benefits only from the yield loss saved. In the fourth case however, where the observed aphid abundance remains below the threshold but would have exceeded it without natural enemy action, natural enemy action has both reduced yield loss and averted the need to spray, thus providing greater economic value than under insecticide-free management.

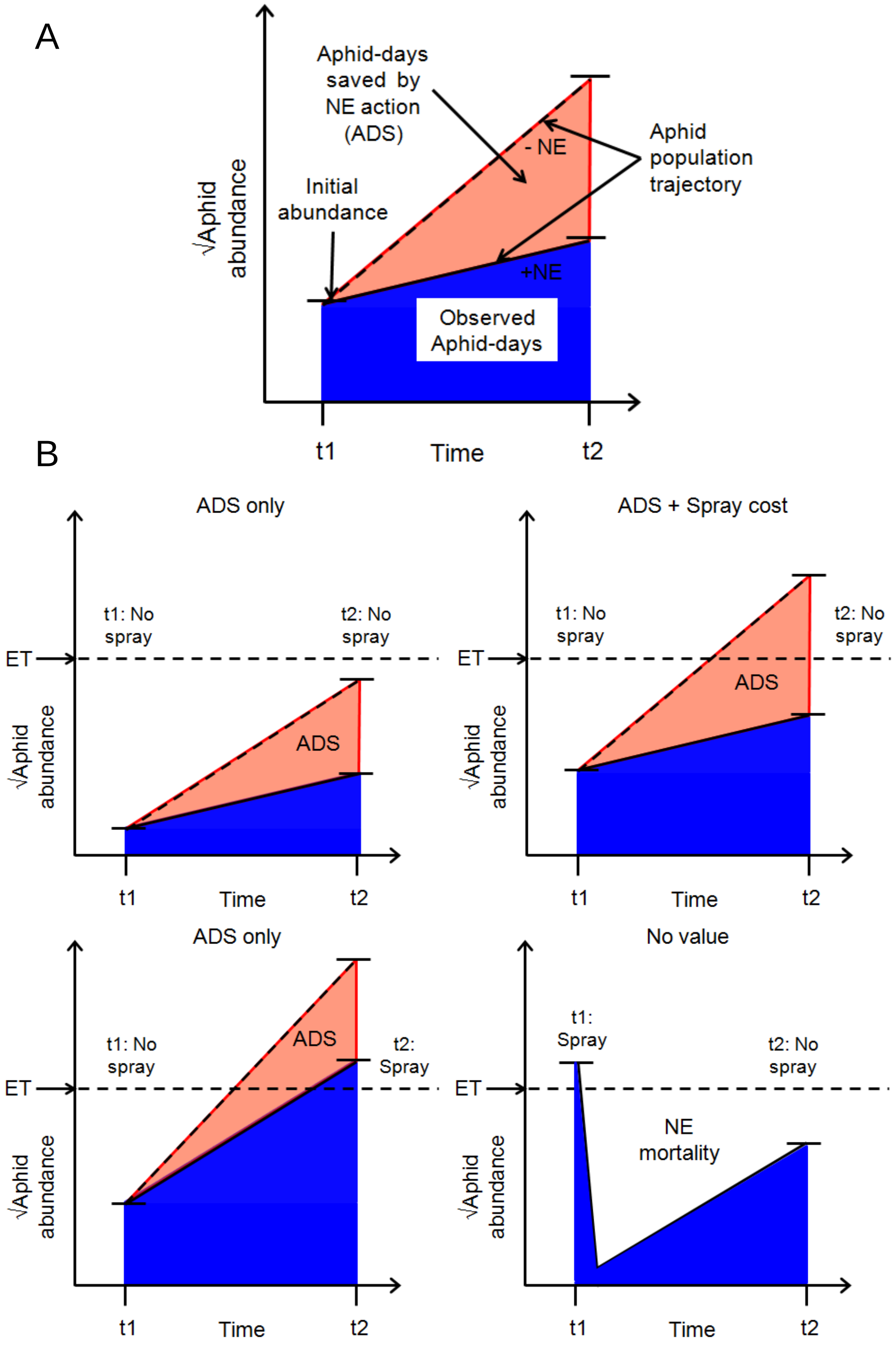


Figure 5.2: Conceptual valuation framework

Decision making under different aphid population change scenarios between two observations (t1 and t2), used to derive expected economic savings for farmers. (A) Depiction of aphid days (blue area) from observed population change (solid black line), and predicted additional aphid days (pink area) with the aphid population trajectory in the absence of natural enemies (NE) (dashed line). (B) Hypothetical decision making when observing an economic threshold (ET) for insecticide application, under four possible scenarios. The decision to spray or not is made at t1 and t2. When aphid density is below ET at t1, the benefit of aphid-days saved (ADS) is accrued (top row and bottom left), but no benefit occurs (during this time period) if aphids exceed ET at t1. If spraying is necessary at t2 (bottom left), ADS is the only benefit. If it is not, but would have been in the absence of NE, then the cost of spraying is also saved (top right). If ET would not have been exceeded in the absence of NE (top left), then ADS is again the only benefit.

The cost of spraying was approximated as the price of the insecticide used plus contractor rates (which summarise the cost of machinery, labour and fuel) per hectare (ha). The insecticide cost was set at £4 per ha, assuming use of lambda-cyhalothrin applied at 50 ml per ha, at £80 per litre (source: www.farmingforum.co.uk, thread title: “chemical price checker”). Contractor rates were taken as £13.10 per ha (NAAC, 2011), giving a total spray cost of £17.10 per ha.

The effect of varying the level of the economic threshold used by farmers was explored by performing a separate valuation at each of ten different levels from 5 to 50 aphids per tiller, in increments of 5. This covered a wide range of reluctance or inclination to spray on the part of farmers, at the higher end approaching insecticide-free management.

All procedures described above were carried out using R version 2.14.0 (R Development Core Team, 2011).

5.3 Results

5.3.1 Effects of natural enemy action on aphid growth

The model fitted to estimate the effect natural enemies on aphid population change over the period of interest (equation 5.1) showed negative impacts of both parasitoids and syrphid larvae on aphid population growth (table 5.1). In the absence of both natural enemy groups, aphid abundance would have been on average 109% higher than was observed at the end of the period of interest (figure 5.3 B).

Parasitoids were modelled as having a larger impact *en masse* on aphid abundance, with on average 58% more aphids being present when the absence of parasitoids was simulated, compared to a 40% increase without syrphid larvae (figure 5.3 B). Per individual however, syrphid larvae had a greater negative impact on aphid population (shallower contour lines in figure 5.3 D than in C). Their lower overall impact resulted from their being far less numerous than parasitised aphids, particularly in fields with high initial aphid densities.

The average proportional impact of natural enemies on aphid population increased at higher aphid abundances, with the increase in parasitism impact being slightly greater than that of syrphid larvae (figure 5.3 B). There was also evidence that density dependence influenced aphid population growth over the period, with growth rate declining at higher initial abundance, even in the absence of natural enemy action (figure 5.3 A).

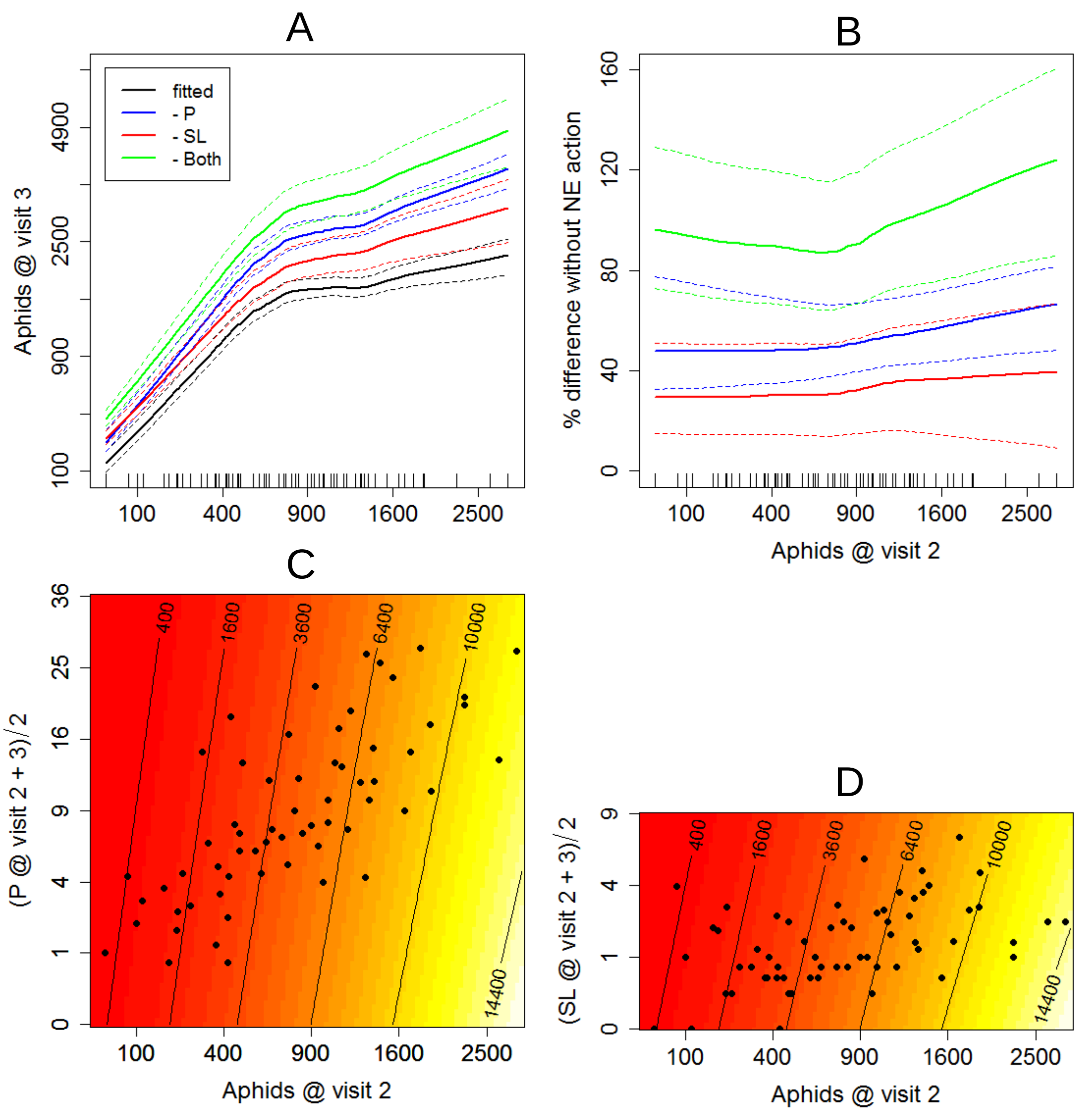


Figure 5.3: Predictions and partial responses from the model of aphid population change

Panels A and B: predictions ± bootstrapped standard error of aphid abundance at visit 3 (A) versus visit 2, showing the observed value (black line), and the effect of excluding the natural enemy groups individually and together (other colours – see legend). B shows the proportional increase in aphid abundance ± standard error relative to the observed value at visit 3, with the same colour coding as A. Lines are lowess smooths through the mean of predictions for the 62 fields. The rug shows the distribution of aphid abundance at visit 2. Panels C and D: contour plots of the partial prediction of aphid abundance at visit 3 as a function of abundance at visit 2 and the parasitism pressure (“P”; C) or syrphid larval predation (“SL”; D). Predicted aphid abundance increases from red to white colours, with scale shown on contour labels. Black points depict observed values of predictors, and thus the region where the prediction is most reliable. D is reduced in height to make the scales of C and D equal. Syrphid larvae were much less numerous, particularly at high aphid abundance, but had a greater impact per individual.

5.3.2 Estimates of economic value

Using the valuation framework, parasitoids were predicted to be more valuable to farmers than syrphid larvae, reflecting their greater effect on aphid abundance *en masse.* Under insecticide-free management, the mean cost of simulated parasitoid absence was £18.07 per ha from lost yield, compared to £11.14 per ha without syrphid larvae. The mean cost of removing both enemy groups was £29.68 per ha (figure 5.4 A).

At a realistic economic threshold of 15 aphids per tiller, the mean value of natural enemy action under threshold-spraying management was lower, at £9.36, £6.00, and £15.00 per hectare for parasitoids, syrphid larvae and both groups respectively (figure 5.4 B).

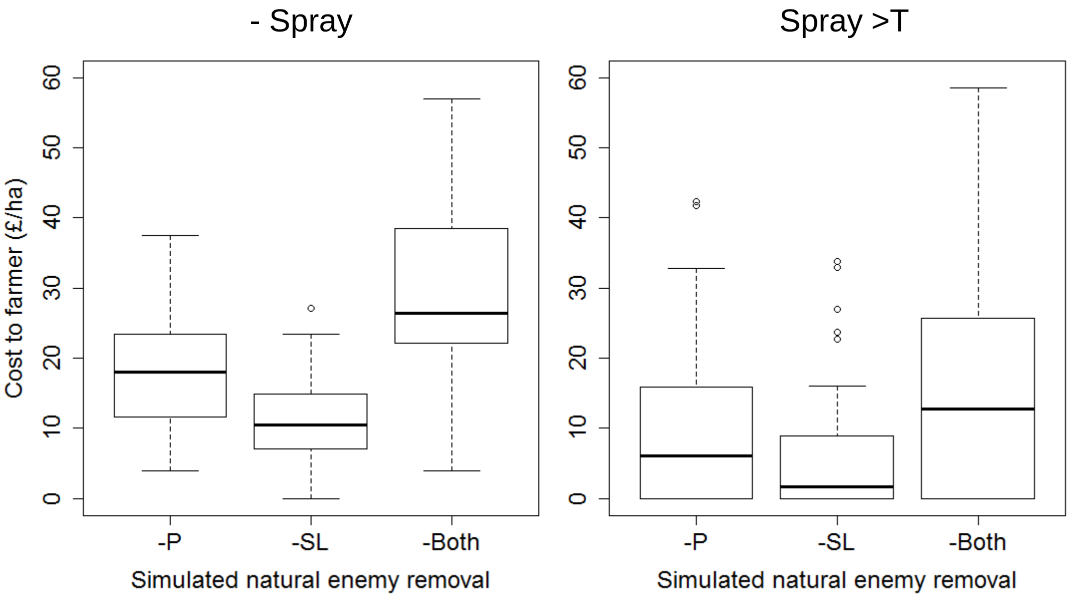


Figure 5.4: The economic value of natural enemies under insecticide-free and threshold-spraying management

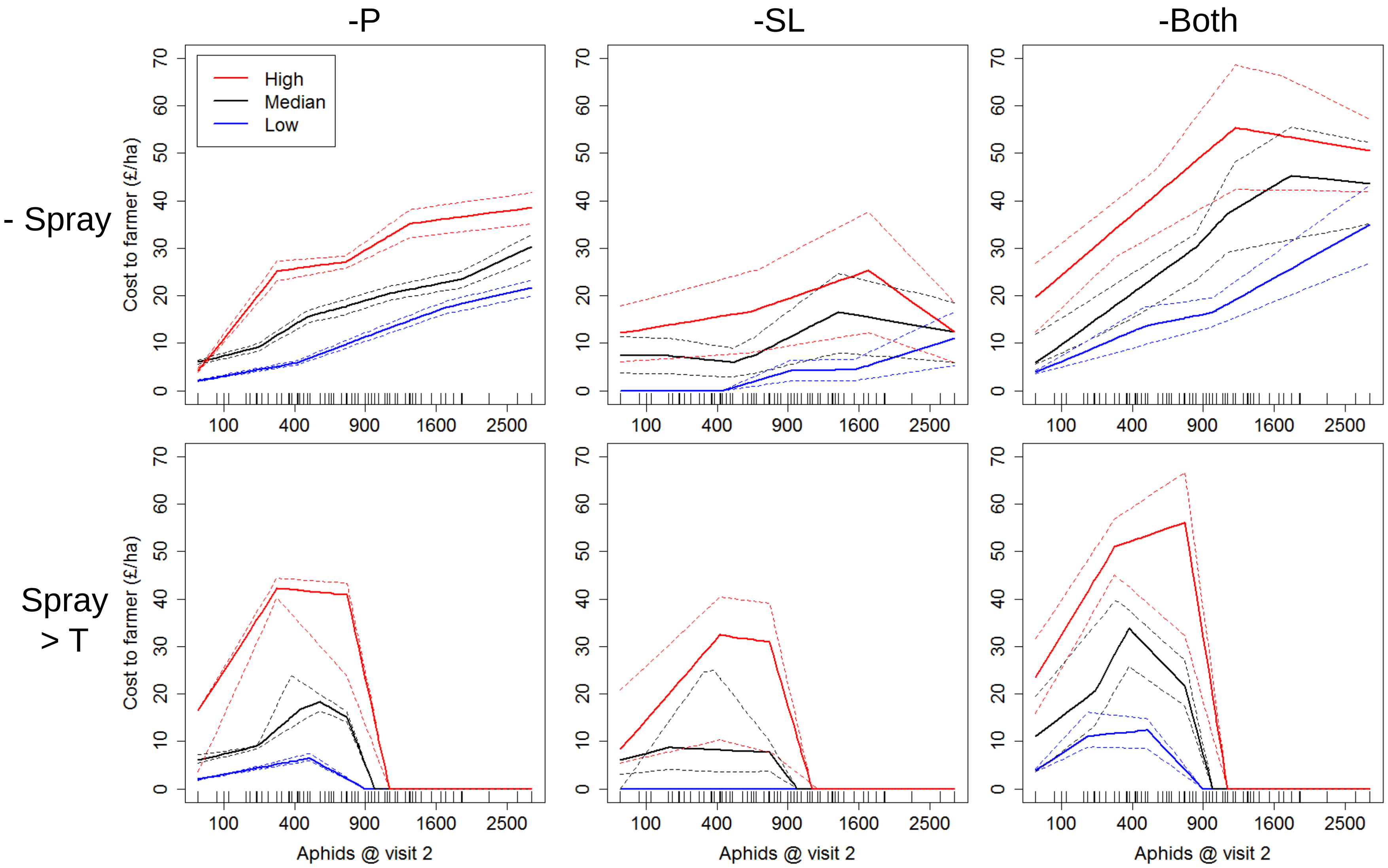
Box plots showing the costs to farmers resulting from simulating removal of the impact of parasitoids (-P), syrphid larvae (-SL) and both groups (-Both), for insecticide-free management (-Spray) and threshold-spraying management (Spray >T). The values shown apply to an economic threshold of15 aphids per tiller. Considerable variation between fields is noticeable, which is discussed below.

When the level of the spraying threshold was raised above 30 aphids per tiller however, the mean value of both natural enemy groups combined under threshold-spraying management exceeded that of an insecticide-free strategy, peaking at £34.86 per ha (figure 5.6 A).

There was considerable variation in natural enemy value between fields depending on aphid density at the beginning of the period (figure 5.5). In the absence of spraying, the median value of natural enemy action increased with initial aphid abundance from around £5 per ha to over £40 per ha, reflecting their greater impact on absolute aphid abundance over the period when they were many aphids to begin with (figure 5.5 top row; black lines). This trend was much more marked for parasitism than for syrphid larvae, such that at low aphid abundance syrphid larvae were more valuable whereas at high aphid numbers the opposite was true. Applying a spraying threshold of 15 aphids per tiller, median natural enemy value showed a hump-backed relationship, rising more steeply initially and attaining higher value at low aphid abundance than for an insecticide-free regime, peaking at £33 per ha when there were about 7 aphids per tiller initially, then falling to zero when initial aphid abundance surpassed the threshold (figure 5.5 bottom row; black lines). Varying the level of the economic threshold altered both the magnitude and the position of the peak in mean natural enemy value. As the threshold level was increased, the peak value became steadily greater, and was located at higher initial aphid abundance (figure 5.6 B).

Between-field differences in natural enemy value resulting from variation in their abundance were equally important. The peak difference between the 2.5th ("low") and 97.5th (high) percentiles of natural enemy value was generally larger under threshold-spraying management (red and blue lines in figure 5.5, dashed confidence intervals in figure 5.6 A). Peak values were £42, £32 and £55 per ha for fields with many parasitoids, syrphid larvae and both combined respectively, compared to £5, £0, and £11 with few. In the absence of insecticides, these differences were smaller; peak values were £39, £25 and £55 per ha for fields with high abundance versus £22, £11 and £35 for those with low numbers. This result demonstrates a greater economic benefit of high natural enemy numbers to farmers who could also save on spraying costs, provided that initial aphid densities were below the economic threshold. The opposite was also true however; in fields with low natural enemy abundance, the benefit was usually greater for an insecticide-free manager. In summary, differences in natural enemy abundance thus result in more variation in their economic value under threshold-spraying than insecticide-free management.

Figure 5.5 (next page): Economic value of natural enemies in relation to initial aphid abundance, under insecticide-free and threshold-spraying management
Plots showing the cost to farmers of simulated removal of the impact of natural enemies, and how this varies with initial aphid abundance (abbreviations as in figure 5.4). The spraying threshold used for this plot was 15 aphids per tiller. In each plot a quantile smoothing spline is fitted to the 2.5th (blue line; "Low field"), 50th (black line; "Median") and 97.5th (red line; "High field") percentile of the distribution of costs, ± the bootstrapped standard error. This illustrates the variation in the cost of simulated enemy removal between fields, due to differing natural enemy abundance, thus demonstrating the potential value of enhancing their abundance. Quantile smoothing was performed using the `rqss` function in the R package "quantreg" (Koenker, 2012).


-P
-SL
-Both
- Spray
Spray > T
High
Median
Low
Cost to farmer (£/ha)
0
10
20
30
40
50
60
70
100
400
900
1600
2500
Aphids @ visit 2

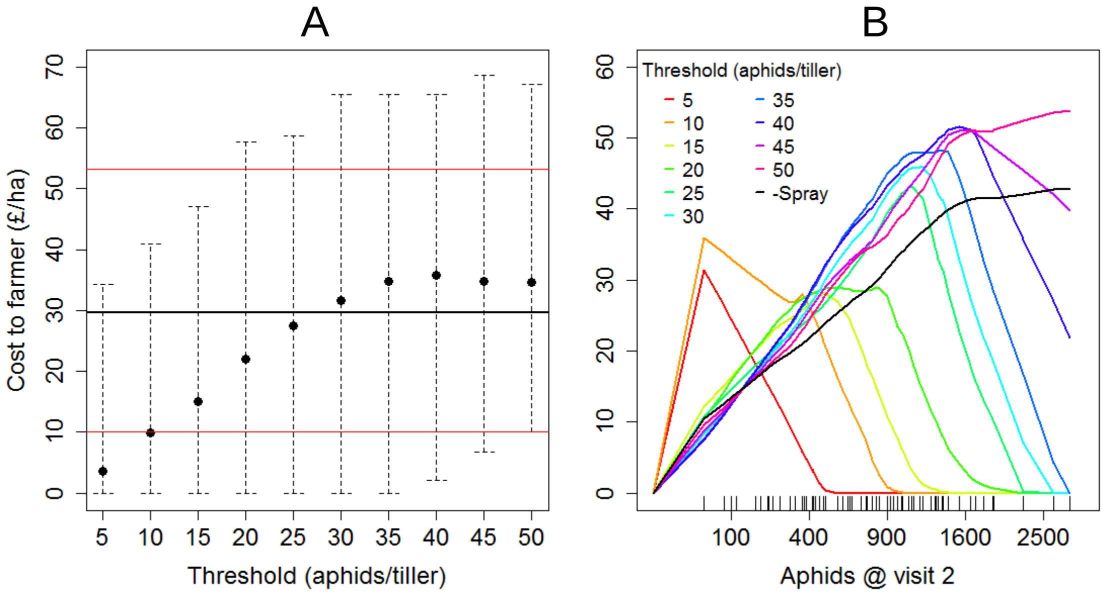


Figure 5.6: The effect of varying the spraying threshold on the economic value of natural enemies under threshold-spraying management
Panel A: The mean cost to the farmer of simulated removal of both parasitoids and syrphid larvae together (black dots) ± 95% confidence intervals (dashed bars), when using different spraying thresholds. The horizontal thick black and red lines are the mean cost ± 95% confidence intervals of absence under insecticide-free management, shown for comparison. Natural enemies combined are more valuable on average to threshold-spraying farmers, when the threshold is greater than 30 aphids per tiller. Variation in value is also larger than for insecticide-free management above 15 aphids per tiller. At a sufficiently high threshold, the value under the two management systems will converge. Panel B: as panel A, but showing relationship between initial aphid abundance and the cost of simulated natural enemy absence as the spraying threshold is varied. Lines are lowess smooths through the mean value at each point on the x axis (rather than the low and high estimates shown in figure 5.5)

5.4 Discussion

5.4.1 The overall value of natural enemies

Valuation of the ecosystem services supporting agricultural production must play an increasingly central role, if intensification of agriculture to meet growing demand is to be sustainable (Power, 2010). This chapter demonstrated the use of a valuation framework to estimate the economic benefit of aphid control by two important predators during a vulnerable period in wheat growth. It also explored for the first time how the economic benefit of natural enemy action can vary with pest management strategies.

The results of this study established that the short-term economic subsidy from natural enemies received by farmers is likely to be considerable. In the absence of insecticide use, the estimated value of parasitoids and syrphid larvae combined from the end of flowering to the milky ripe stage was on average £29.68 per hectare (figure 5.6 A), equating to over £59 million for the ~2 million ha of winter wheat grown annually in the UK. Given that this estimate only applies to a two week period, the total annual value of aphid control by natural enemies is likely to be substantially greater. As discussed in section 5.1.2, natural enemies also impact autumn aphid populations on wheat, when the risk of barley yellow dwarf virus (BYDV) transmission by *S.avenae* is high (Poehling et al., 2007), representing another source of value not accounted for by this study. Moreover, although the valuation period corresponded with the peak occurrence of insecticide application against aphids and the highest aphid abundances recorded in this study, it probably did not coincide with the period where natural enemies can have the greatest impact on aphid populations, which is likely to be earlier in the season during aphid establishment (Ekbom et al., 1992, Ostman et al., 2003). In 2011 however, the aphid and natural enemy numbers found by the sampling intensity employed in this study were very low at the first visit (~ear emergence), which precluded the possibility of performing a similar analysis to this earlier period.

5.4.2 Variation in natural enemy value

The results also emphasise that the economic benefit of natural enemies to farmers is not fixed, but depend on market prices, the severity of aphid infestation, abundance of natural enemies in fields and the propensity of the farmer to use insecticides. Furthermore, there are likely to be interactions between these factors influencing economic benefit. On average it was predicted that farmers opting not to spray insecticides would benefit from greater saved costs due to natural enemies than those who apply them above a threshold aphid density (figure 5.4). However, if the spraying threshold was increased above 30 aphids per tiller, the relative benefit was reversed (figure 5.6 A). The economic threshold level itself logically depends on the cost of spraying – chemical, fuel and labour costs – versus the costs in yield loss of choosing not to. Accordingly, under high wheat prices but low spraying costs the threshold level used by conventional farmers should be very low, and so natural enemies would be far more valuable for organic farmers, for example. When spraying costs are high relative to wheat prices, the economic threshold would be greater, and so conventional farmers would benefit more, due to the action of natural enemies saving spraying costs. Varying aphid density is of course a major influence on how likely conventional farmers are to have to spray. When aphid pressure is low and the necessity of spraying is averted, the results here suggest that conventional farmers will derive greater value from natural enemies, whereas non-spraying farmers will do so at high aphid abundance (figure 5.5, right). Faced with such uncertainty in market prices and aphid populations operating over short time-scales, reactive management to temporary economic circumstances may be infeasible. Both non-spraying and threshold-spraying farmers would benefit in the long term from maintaining a high “constitutive” potential for biological control in their crops, to allow them to capitalise on natural enemy services when they are at their most valuable.

The comparison above of natural enemy value between spraying and non-spraying management has several caveats however. Firstly, all the fields sampled in this study were conventionally farmed, so the upper ranges of natural enemy numbers found may still be lower than those found in organic fields (Bengtsson et al., 2005, Gabriel et al., 2010, Krauss et al., 2011, Ostman et al., 2001, Thies et al., 2011). Secondly, goods from pesticide-free operations demand a premium price, possibly increasing the potential savings of reduced yield loss. These factors combined would suggest that the value of natural enemies to non-spraying farmers was underestimated, and may be greater than for threshold-spraying farmers in a much larger range of circumstances than was presented above. On the other hand, non-use of pesticides often forms part of a broader certification scheme such as organic management, where the use of synthetic fertilisers and growth regulators is also forbidden. This may result in lower potential yields of wheat (Gabriel et al., 2010), which would in turn reduce the amount of yield lost per aphid-day (Rossing, 1991). These additional factors were not included in this analysis, and therefore the comparisons made above may not be generalisable to organic and conventional farms overall. Finally, when considering the economic benefit of natural enemy action over the whole year, spraying farmers are more likely to apply insecticide to protect their crop from BYDV infection in autumn than to apply summer sprays (personal communication), and so this factor would also tend to increase the relative benefit of natural enemy action for non-spraying farmers.

Between-field variation in aphid control due to differences in natural enemy abundance (per aphid) may provide a useful approximation of the added value that might be attainable through management for conservation biological control. Here the economic benefit of aphid control by natural enemies was estimated by removing their effect entirely, but even in the most hostile of fields there may be a small number, so the value of this minimal number may be a more realistic baseline in the absence of any beneficial management. Although non-spraying farmers may receive greater average benefit from natural enemies, this analysis showed that at low aphid abundances, variation in natural enemy numbers made a larger difference in value for threshold-spraying farmers, peaking at ~£55 per hectare versus ~£40 per hectare for non-sprayers. This is due to the added avoided cost of spraying from which the latter may benefit, when aphid numbers are kept below the threshold by greater natural enemy abundance (figure 5.5). Moreover, there are positive feedback mechanisms which may amplify the value of habitat management for threshold-spraying farmers over time; if providing additional non-crop resources (e.g. Landis et al., 2003) boosts natural enemy abundance sufficiently to reduce the necessary spraying frequency, the decrease in disturbance will augment numbers further, and possibly to a larger degree (Jonsson et al., 2012). Better knowledge of this temporal feedback will help the impact of insecticides on natural enemies to be incorporated more centrally into spraying decisions (Zhang and Swinton, 2009). A second value arising from a reduced need to spray would be an increase in the abundance of other arthropods in crops, providing alternative prey for generalist predators (Harwood et al., 2009) or food for farmland birds using cereal fields during summer (e.g. yellow wagtail *Motacilla flava*). Quantifying these feedbacks and communicating their value to farmers would provide an added impetus for adoption of conservation biological control management (Cullen et al., 2008).

In the context of sustainable intensification of production, a key question is whether the yield benefits of implementing habitat management for conservation biological control outweigh the yield costs, rather than financial value *per se*. In this study, the predicted per hectare yield benefit of natural enemy impact over the two week period ranged from 0.2% to 4%, meaning that where natural enemies are most common, only 96.3% of the area would need to be cropped to attain the same yield as where they are most rare. If local and landscape management solutions to increase the under-yielding fields to the same level could be found that required less than 3.7% of the arable land to be taken out of production, then this would be worthwhile, as has been demonstrated for “beetle banks” in the UK (Sotherton, 1995). While perhaps not a very rigorous example, it serves to reiterate the need to establish quantitative links between land use change and the provision of ecosystem services such as pest control. This is especially important when habitat management may result in synergies or trade-offs for more than one service (Polasky et al., 2008, Power, 2010), as if in this example habitat management also boosted pollination services to another crop, it might take up more than 3.7% of land and still be worthwhile.

5.4.3 Should management be prioritised for parasitoids or syrphids?

A key theme of this chapter was the comparison of the value of parasitoids and syrphid larvae as aphid predators. Syrphids were modelled as having a larger effect per individual than the number of parasitised aphids, but the far greater abundance of parasitised aphids, especially when aphids were also abundant, resulted in parasitism being valued more highly on aggregate. The close relationship between aphid and parasitoid abundance on average suggests that parasitoids were a more consistent source of aphid mortality across fields. The relationship is linear across most of the range of aphid abundance (figure 3.4 E in chapter 3, figure 5.3 C), and the proportional impact of parasitoids rose more steeply than for syrphid larvae (figure 5.3 B), so parasitoids remain a significant force even at high aphid densities.

However, the greater range in syrphid value between fields, particularly for threshold-spraying farmers, implies that there may be greater scope for attracting and rewarding syrphids through targeted habitat management (e.g. Haenke et al., 2009) than there is for parasitoids. This is also evident in the greater scatter around the relationship between syrphids and aphids, than that between parasitoids and aphids (compare figure 3.4 E with 3.5 C in chapter 3), hinting that non-aphid resources are more limiting (and therefore more effectively manipulated) for syrphids than for parasitoids. Measures of landscape context did not explain syrphid abundance very effectively in the modelling procedure of chapter 3 (section 3.3.3; Nagelkerke’s R^2 for fixed effects was 0.18), but this may have been through lack of availability of data for important variables such as floral abundance, as other studies have found strong positive effects of increased proportion of natural vegetation (e.g. Chaplin-Kramer, 2010). Management for syrphids, such as providing wild flower strips, has the added advantage that it can also boost crop pollination, both by the adult syrphids themselves and other pollinators capitalising on the same resources (Haenke et al., 2009); an excellent example of synergy between two supporting services. Perhaps the close interspersion of cereal and oilseed rape (*Brassica napus*) fields might be an effective strategy.

Moreover, the model fitted in this chapter may have underestimated the impact of syrphid larvae on aphid abundance. The finding that parasitoids were more valuable was slightly surprising, given the number of studies finding that polyphagous predators have a greater capacity to control aphid populations than do parasitoids (e.g. Chambers and Adams, 1986, Poehling et al., 2007, Tenhumberg and Poehling, 1995, Gosselke et al., 2001, but see Schmidt et al., 2003). Indeed, the modelled voracity of syrphid larvae was unexpectedly low at only 2.34 (consumption = $b^2 = 1.53^2$; table 5.1) aphids per syrphid larva considering that 5 day old larvae are capable of consuming 42 aphids per night in good conditions (Ankersmit et al., 1986). Perhaps the localised scale at which syrphid larvae deplete aphid populations (Bargen et al., 1998) resulted in a misleadingly weak negative relationship between syrphid larva and aphid abundance.

5.4.4 Aphid population growth models

The likely underestimate of the importance of syrphid larval predation by the aphid population growth model is an example of the limitations of correlative models of population dynamics. Positive or negative associations between abundances can occur for a variety of reasons and there is a lack of experimental control of confounding conditions. Empirical studies such as those using exclusion cages (e.g. Schmidt et al., 2003, Thies et al., 2011), or laboratory assessment of consumption rates (e.g.

Chambers and Adams, 1986, Ankersmit et al., 1986) isolate the impact of natural enemies more reliably, but often also create conditions unlike those encountered in the field which can influence pest movement and vital rates (Kidd and Jervis, 1996). Correlative studies on the other hand use data from natural conditions, and permit greater replication of treatments due to the lower input of time and expense.

A solution to reconcile these competing features of pest-natural enemy models is to create simulations based on laboratory estimates of vital parameters such as consumption rates and development time of predators, then to validate and calibrate the models with real field observations to provide estimates of more elusive parameters such as immigration rates. Such a model – "GETLAUS" (Gosselke et al., 2001) - has been used to assess the impact of predators on yield loss in wheat in a similar manner to that shown here, by removing predator agents from the simulation. The large amount of information required to build such a model however, meant that it was beyond the scope of this thesis. Nevertheless, as discussed in chapter 4, process based simulation models are likely to be superior to correlative models in predicting the response of a system to change (Evans et al., 2012). If non-spatial population dynamic simulations such as GETLAUS could be combined with spatially-specific models of the movements of insects, this would increase the utility of both models simultaneously, providing a process-based (and therefore perhaps more robust) quantitative link between land use change and ecosystem service provision.

5.4.5 Potential pitfalls of valuation approaches for informing management

There are caveats that must be borne in mind when considering possible recommendations stemming from valuation of conservation biocontrol, or of management aimed at enhancing this.

Firstly, models based upon data from a single year, and from a relatively small region, may give a distorted impression of the economic benefit from different natural enemy species or conservation biocontrol management over the long term, or in other regions. The relative abundance of different species or functional groups of natural enemies varies between regions and between years (Thies et al., 2011), due to factors such as weather or pathogen outbreaks, which are outside the influence of beneficial management. Specific management to attract a single effective aphid predator or boost its population would thus be ineffective if limited by other factors. It is not known how much of the economic benefit of conservation biocontrol management might in the long term result from the insurance effect of increased diversity of the natural enemy community, rather than targeting specific species, but it may be significant (Macfadyen et al., 2012). Studies running over decadal timescales and large spatial scales are required to answer this question fully.

The second major caveat is that although valuation has the potential to reduce the trade-off between biodiversity conservation and food production on farmland, it does this only for species that obviously help to improve the quantity or quality of food produced. In the absence of conservation subsidies, this would result in a bias against species of lower (or less obvious) economic importance to farmers, if their resource requirements are dissimilar to the targeted species. But, as mentioned in the introduction to this chapter, the intrinsic non-economic value of biodiversity is nonetheless important to society. Economic valuation of the benefit of farmland biodiversity for food production should not be used as grounds to remove conservation payments for biodiversity, through agri-environment schemes for example. Rather, it should be viewed as a lever to help change the attitudes of farmers who currently view wildlife on their farm as an unnecessary luxury, and perhaps to encourage uptake of agri-environment schemes that also have potential benefits for conservation biocontrol.

5.4.6 Conclusions

This chapter has demonstrated the considerable pest control value that parasitoids and syrphid larvae provide in winter wheat crops in the UK, and has explored the biological and social factors causing this value to vary temporally and spatially. Prioritising management for syrphid larvae may be most effective for controlling aphid numbers, but parasitoids have a stronger positive relationship with aphid abundance, so probably have more effect on aphid abundance in the absence of specific management. Despite the perception of the larger reliance of organic farmers on natural enemies, conventional farmers may in some circumstances derive more economic value from high natural enemy numbers. This emphasises that the availability of insecticidal chemicals does not reduce the value of managing to maintain biological control potential, and doing so may have synergistic benefits for biodiversity and other ecosystem services. Recommendations of management for conservation biological control should however be drawn preferentially from long term studies, and balanced with the need for conservation on less economically important species.

6. General Discussion

Predicting how the ecosystem service of pest control is impacted by the local and landscape-scale environment, and what sort of management to enhance this service is worthwhile, is a key challenge for the sustainable intensification of agriculture. This thesis aimed to contribute to tackling this challenge, by focusing on the following questions and objectives:

> 1. Although landscape “complexity” has been widely found to influence pest and natural enemy populations, several correlated aspects of landscape composition and structure are often confounded. Which aspects of complexity - measures of vegetation composition, field boundary density, shape complexity of land parcels, or interspersion of land cover types - are the strongest predictors of the abundance of aphids and their natural enemies in winter wheat fields, and at what spatial scale?
>
> 2. How does the importance of the predictors of aphid and parasitoid abundance vary temporally?
>
> 3. To predict the effect of simulated land use change on aphids and their natural enemies, so that synergies and trade-offs between desired outcomes from potential landscape-scale management strategies can be assessed.
>
> 4. To link landscape-scale management to the economic benefit arising from pest control services, by modelling how variation in natural enemy abundance translates into decreased yield loss and expenditure on insecticides.

This discussion will evaluate how well the thesis managed to address the issues above, then will explore the implications of the findings and possible future research directions.

6.1 Overview of the thesis

6.1.1 Disentangling landscape complexity

Past agricultural intensification has symptomatically involved concurrent shifts in suites of variables describing the management and spatial structure of farmed landscapes (Tscharntke et al., 2005). Many studies have tried to examine the impact of intensification as a whole, along a single gradient summarised by a representative variable. In contrast, here study fields were selected along three separate axes of landscape context – proportion of arable land, field boundary density, and the aggregation of arable land – to deliberately provide variation in, and reduce the correlation between, different aspects of landscape “complexity” affected by intensification. This represents a step forwards in methodology to better understand how intensification impacts biological control, and other studies are beginning to recognise the importance of this (e.g. Jonsson et al., 2012).

Aphids and their primary parasitoids were found to be more strongly dependent on aspects of landscape configuration, than on the proportion of arable land or semi-natural habitats. The shape complexity of arable parcels within 1000 metres of the focal field had a positive effect on overall abundance of aphids and of parasitised aphids, even when the close relation of the latter to aphid number was accounted for (chapter 3). The interspersion of land cover types within 2500 metres was also positively associated with the number of parasitised aphids. There was no lack of variation in compositional metrics such as the percentage of arable land across study sites (range 41 – 80% within 2500 m). Therefore, given that proportional area is often correlated with other aspects of landscape context (e.g. Gagic et al., 2011, Steffan-Dewenter et al., 2002), other studies finding relationships between the proportion of natural vegetation and parasitoid abundance (e.g. Roschewitz et al., 2005, Thies et al., 2005) may too have found configurational measures of complexity to be more relevant had they included them explicitly in analyses. However, the strong but non-linear relationship between changes in proportional area and the value of configurational landscape metrics (such as arable shape complexity) identified in chapter 4 suggests an alternative interpretation. Configurational metrics could appear important not for their true effect, but because they represent the most parsimonious way to model non-linear responses to proportional area. This ambiguity exposes the limitations of correlative models for causal inference, and illustrates why studies of the mechanisms contributing to insect abundance in a focal field are valuable.

The abundance of syrphid larvae on the other hand was most strongly related to the percentage of arable land within 1500 metres of the focal field (in addition to their aggregation to higher aphid densities), but this interacted strongly with the percentage of rough grassland - which may have provided floral resources to adult syrphids - within 200 metres. By demonstrating the difference in landscape-scale variables influencing syrphid larval and parasitoid abundance, chapter 3 provided a good example of the variety of ways in which landscape context can interact with the biology of an organism. The most common syrphid species laying eggs in wheat fields is *Episyrphus balteatus,* which travel to Northern Europe through active long-distance migration each summer, because overwintering can only occur in very mild winters (Aubert et al., 1976, Hart and Bale, 1997). The adult flies’ behaviour and longevity is then influenced by the availability of oviposition sites, mating territories, and floral nectar sources (Meyer et al., 2009). Due to their excellent directed flight ability, spatial configuration may have little influence on syrphid behaviour. It is the first generation of larvae that provides the main source of predation during early aphid population build-up (Tenhumberg and Poehling, 1995), so the ability of the *E. balteatus* to persist permanently in a particular landscape is not relevant (though if winters become warm enough to permit regular overwintering, this may become important). In contrast, parasitoids and aphids can overwinter in non-disturbed vegetation, and generations colonising wheat in spring often issue from relatively local alternative plant and aphid hosts (Loxdale et al., 1993, Vialatte et al., 2007, Vorley and Wratten, 1987). Thus, landscape context probably plays a more temporally continuous role in determining the in-field abundance of aphids and parasitoids; influencing multi-annual population build-up and the ease of dispersal from alternative hosts, in addition to the immediate effects on behaviour and longevity in common with syrphids.

6.1.2 Temporal variation in the role of landscape context

The second chapter constituted another step forward in the way the effects of landscape context on pest and natural enemy populations are examined. Although studies of the temporal flow of insects between different vegetation types in agricultural landscapes are present in the literature (e.g. Pons and Starý, 2003, Vorley and Wratten, 1987), no previous work (to the authors knowledge) on the influence of landscape context on pest and natural enemy abundance has considered how this changes over time; either within a season or between years. Contrary to expectations, landscape context continued to impact aphid and parasitoid abundance in fields throughout the period of sampling, rather than its effects being restricted to initial colonisation. Considerable seasonal and inter-annual differences were apparent in which aspects of the landscape were most important. This suggests that models of landscape effects on organisms should either average effects over longer periods of time, or be temporally explicit. Factors influencing the abundance of different species of aphid and parasitoid became more similar as the season progressed in both years of the study, implying increasing synchronisation of resources. There was some evidence that drivers of parasitoid abundance tended to shift from non-crop related measures to those describing the shape complexity of arable land as the season progressed, implying that earlier maturing arable crops may replace non-crop vegetation as the main source of immigrating parasitoids for later-maturing crops, as the former senesce. The role of within-field intercropping for biological control has received considerable attention (e.g. Al-Doghairi and Cranshaw, 2004, Xie et al., 2012), whereas the possibility of manipulating cropping patterns at a larger spatial scale to encourage the flow of natural enemies between them has been less studied (but see Van Driesche et al., 1996). The ability of natural enemies to move between crops may differ between different pairs of crop species or cultivars, according to the similarity of the herbivore community (for specialist natural enemies), or the olfactory attractiveness of new herbivore-plant associations, where natural enemies have learned preferences (see section 1.7.4 of the general introduction). The potential variety of crop-crop interactions will therefore have implications for how spatial patterns of crops affect herbivore and natural enemy dispersal between crops. In general, mapping of landscapes should perhaps move away from anthropocentric descriptions of vegetation, and towards a more functional definition of suitability of patches and mosaics for different species. In the context discussed here, this might constitute assigning a value to other land parcels as sources of natural enemies colonising a focal land parcel, according to their relative attractiveness to the natural enemies in question, relative plant phenologies and spatial separation. This should form an important part of future research into conservation biological control management, because optimising cropping patterns in space and time may represent a more cost-effective option for farmers than management of non-crop habitats. This topic is further discussed below with reference to the potential to manipulate olfactory cues to enhance crop-crop spillover.

6.1.3 Analytical approaches with large numbers of explanatory variables

This thesis also contributed methodological advances which have the potential to be applied to a wide range of questions. The embracing of multiple aspects of landscape context, at several spatial scales, produced a very large set of potentially important explanatory variables, displaying a high degree of colinearity. Traditional parametric statistical models perform poorly under these conditions (Carrascal et al., 2009, Graham, 2003), and model selection procedures based upon them are either unstable (in the case of backwards selection) or computationally infeasible (all-subsets selection) (Burnham and Anderson, 2002). To tackle this issue, novel use was made of the random forests algorithm – a machine-learning procedure – in two different ways. Random forests are collections of tree models, which can implicitly model non-linear responses and interactions without the need to explicitly specify model structure. Averaging predictions over trees gives greater overall accuracy, and importantly allows a variable importance score to be extracted (Breiman, 2001, Cutler et al., 2007).

In chapter 2, emphasis was placed on comparing the importance of a constant set of predictor variables among several different response variables (i.e. different species, sampling occasions, and years). The variable importance scores from the random forest models were used to represent the response variables in a “variable importance space", allowing multivariate methods to be applied to determine the main sources of variation among response variables. This represented a qualitatively different way of dealing with complexity, by avoiding the necessity of model selection procedures.

Chapter 3 also made use of random forests, this time to reduce the number and colinearity of variables prior to carrying out parametric statistical analyses, using a similar philosophy to Bradter (2010) . In other studies this has been carried out in subjective, biased, or simplistic ways which only consider the marginal effects of variables in a linear relationship (i.e. regressed individually against the response). Backwards stepwise deletion of variables from random forest models provides a means of objectively reducing the number of predictors in models, whilst retaining those which might be important only in non-linear or interactive ways. If further studies show this method to be robust, it removes a significant analytical barrier to better understanding of the complex ways in which species respond to landscape context.

6.1.4 Predicting the effects of land use change

A central objective of this thesis was to translate observed associations between patterns of landscape context and aphid/natural enemy abundance into predictions of the outcome of changes in land use. Using a valuation framework, the results of changes could then be quantitatively linked to yield loss or expenditure on insecticides. This thesis fell short of achieving such a complete quantitative link, but established a qualitative relationship between land use and value in two separate parts: the effect of changes in land use was predicted for the aphid-natural enemy system, and the effect of variation in this system on the value of natural enemies to farmers.

Through simulating land use change scenarios, it appears that replacement of arable land with non-crop vegetation should produce synergistic benefits for parasitoid and syrphid larval abundance, especially if this is implemented in a dispersed rather than an aggregated manner. Interestingly, as direct effects of landscape context on aphids were part of the predictive model, the greatest decreases in aphid abundance resulted from different changes, underlining the need to establish the priority of management. On the other hand, simulated conversion of non-crop habitat to arable land, alongside increased aggregation, produced consistently undesirable outcomes in all respects. Chapter 4 thus provided a clear answer on the sorts of land use change that would be best avoided; sustainable intensification in the coming decades must occur in a very different manner to the Green revolution of the 20th century. In the discussion of chapter 4 it is proposed that in order to assess what changes would be most beneficial to aphid control, a set of land use changes resulting from realistic future political, economic and social drivers should be developed. This would allow comparison of a set of agronomically realistic alternatives, rather than the somewhat arbitrary array of land use changes used in the analysis in chapter 4, or “optimal” landscapes for aphid control that are completely unrealistic for any other purpose.

Another key message to emerge from the simulations was that the outcome of the same land use change scenario often varied according to the character of the original landscape. Although in some cases this contingency was predictable - for instance the addition of arable land had a positive effect on syrphid larval abundance when the percentage of arable land was originally low, and vice-versa – in other cases it was not, and implies that planning of appropriate land use strategies to improve biological control should be carried out on a case-by-case basis.

The valuation of natural enemy services to farmers also produced striking results, showing that savings of up to £55 per hectare could be made in reduced yield loss and avoided spraying costs (during only a two-week period) by increasing natural enemy abundance in the field. The effects of syrphid larval predation may have been underestimated however, suggesting both that this figure could in reality be much higher, and that the correlative model of aphid population growth used to estimate value may not have been the optimal methodology.

Unfortunately, these two parts of the jigsaw could not be linked quantitatively using the data presented in this thesis, due to two incompatibilities: i) the statistical models used to predict the response of aphids and natural enemies to simulated land use change were constrained (for statistical reasons) to estimate the summed abundance over all four visits, whereas the model quantifying the impact of natural enemies on aphid growth focused on the period between two time points only (though there is probably good correlation between these), and ii) as the models underlying the simulation were linear, the predictions were framed in terms of the consistency in response direction rather than a quantitative numerical change to prevent unrealistic answers from extrapolation. This consistency measure was incompatible with the abundance-based models of natural enemy value.

This thesis cannot therefore provide results concerning the cost-effectiveness of implementing landscape-scale management for natural enemies, but has produced useful and novel findings for the two halves of the problem and demonstrates where improvements need to be made in order to achieve this goal.

6.2 Future directions and wider perspectives

6.2.1 Conservation biological control research

The research approach taken in this thesis was to study the emergent properties of the effect of landscape context on aphids, parasitoids and syrphids, by measuring their abundances in focal fields. This style of research, coupled with novel analysis techniques, uncovered interesting patterns that shed new light on the findings of previous work in the field. An equally useful output from this thesis however is the synthesis of the ideas and potential for future research that it stimulates.

The knowledge obtainable from studying at this level of organisation is bounded on both sides: the patterns of aphid and natural enemy abundance in individual years may be too noisy to reliably determine the long-term average effect of landscape context on yield loss or insecticide expenditure for farmers; at the other end of the scale it is difficult to infer causal mechanisms from correlative patterns, and without this knowledge of underlying processes, predictions of how the emergent properties (i.e. yield loss to farmers) will respond to new conditions are unreliable (Evans et al., 2012). Future research should address both ends of this continuum from reductionism to holism.

Firstly I echo calls made by others (Chaplin-Kramer et al., 2011) for the effects of landscape on long-term occurrence of pest outbreaks to be studied, rather than instantaneous differences in abundance (for an example see Lu et al., 2012). This should if possible include crop type-specific data, to reveal consistent positive or negative associations between crops. Analysing correlative patterns on the scale of decades would not only allow the long-term average effects of landscape context on pests and natural enemies to be studied, but also the long-term time evolution of natural enemies and pests after a change in management practice, such as implementing a conservation biological control measure, or reducing spraying frequency. These long-term effects have been little studied, but may be the only way in which the full value of management changes can be estimated, particularly the value arising from maintenance of natural enemy diversity. Relating spraying frequencies to landscape structure or conservation biological control management might be interesting from a theoretical perspective too – if there are positive feedbacks between beneficial management for natural enemies and reduced need to spray (as postulated in chapter 5), then one might expect alternative stable states to exist at either end of the scale. The long-term datasets necessary to answer these questions may be too difficult or expensive for scientists to collect directly, but making use of “citizen science” could be an alternative solution, through collaboration with farmers and agronomists over a period of years.

Secondly, a priority for predicting the response of pest-natural enemy systems to change is to develop quantitative, spatially explicit and mechanistic models of how landscape context influences the dispersal patterns of herbivores and their natural enemies. In the general introduction and in the discussion of chapter 4, two spatial evaluation frameworks – InVEST and ARIES – are described that could be developed further to include such mechanistic models. These frameworks have the added advantage that other ecosystem services such as pollination or carbon storage could be simultaneously evaluated using built-in models, to explore interactions or correlations with these. These dispersal and colonisation models can then be linked to non-spatial population dynamic models (such as GETLAUS (Gosselke et al., 2001)) to project pest population change in response to specific management at particular locations. If this is implemented as a simulation over time, it would predict the movement and abundance of all relevant groups over the course of a whole year, and through connection to a population dynamic model predict the cumulative value of a management change, rather than during a short period as in chapter 5. Making such a spatial model would be far from easy, as it is difficult to empirically quantify the movement of small insects (Turchin, 1998). One possible method would be to use correlative models, such as those derived in chapter 3, based on very detailed maps of crop and field boundary vegetation over a large area, then use these to parameterise an *a priori* mechanistic model using an approximate bayesian computation approach (Beaumont, 2010). Another possibility is to develop new techniques to monitor the movements of individual small insects, in order to parameterise mechanistic models directly. For parasitoids with strong learned preferences of their natal environment, choice assays might be used to infer the provenance of a field caught parasitoid, and by reference to vegetation maps, the minimum dispersal distance required to get to their capture location. This reductionist approach would not be a replacement for long term studies - error propagation in any complex system would make long-term forecasts unreliable (as for weather forecasting) - but rather would complement them by allowing exploration of the short term effects of a large number of different management scenarios on a few target species.

Finally, there is great scope for applying both kinds of landscape ecological research described above to enhance the efficacy of crop breeding and plant protection technology. Herbivore induced plant volatiles (HIPVs) are released ordinarily by plants in response to herbivore attack, and are used by natural enemies as olfactory stimuli for prey location (Kaplan, 2012). Trials involving application of synthetic HIPVs (Simpson et al., 2011), induction of HIPV production in crops through intercropping (Khan et al., 2008) and genetic modification of crops to produce herbivore alarm pheromones (Yu et al., 2012) have shown promising results for increasing the attractiveness of fields to natural enemies. Potentially, these technologies could shorten the crucial lag time between herbivore and predator population build-up (Ehler and Miller, 1978), and thus produce more effective control. Despite the mismatch between the cues provided by synthetic lures and by the herbivores and plants themselves, increased attraction into fields has frequently been translated into enhanced herbivore predation and parasitism (e.g. Titayavan and Altieri, 1990, Williams et al., 2008).

Crucially, predator attraction is an explicitly spatial process and therefore dependent on the landscape context of application (Kaplan, 2012). For example, if a treated field is surrounded by other fields where semiochemical attractants are also being applied or produced, then there will be no spatial variation in attractiveness for predators at this scale, and therefore no net movement. When considering aphid parasitoids, the ability of HIPVs to attract them into a field is also likely to be influenced by learned preferences for olfactory cues. Given the strong preference females aphidiid parasitoids have for their natal aphid-plant complex discussed in the general introduction (Powell et al., 2003, Powell and Wright, 1988, van Emden et al., 1996, Wickremasinghe and Emden, 1992), it would be interesting to know whether genetic augmentation of HIPV production in wheat would attract them more effectively from closely related neighbouring crops such as other wheat cultivars or barley, than it would from more dissimilar crops, harbouring different aphid species, such as oilseed rape. Another intriguing experiment would be to investigate whether synthetic HIPV lures with profiles matching that of the dominant neighbouring crop attract more parasitoids than either a non-specific HIPV mixture, or augmented production of the HIPVs produced by the focal crop.

In order to create desirable gradients of attractiveness for predators and enhance spill-over effects, optimisation of the temporal and spatial configuration of insect-resistant crops and of synthetic HIPV application will be vital. This may be a key route by which spatial ecologists can collaborate with other disciplines of crop science, to further a common cause.

6.2.2 The implementation of landscape-scale management

A common recommendation emerging from recent literature, and indeed chapters in this thesis, is that management for provision of ecosystem services in agricultural landscapes would be best implemented at spatial scales often larger than that of individual farms (e.g. Concepción et al., 2012, Gabriel et al., 2010, Sutherland et al., 2012, Turchin, 1998). However, the mechanisms by which farmers could be incentivised to coordinate their management with neighbours are not yet clear. Cooperation is most crucial for producing desirable outcomes in configurational aspects of landscape structure, as this could not be achieved through existing schemes targeting individual farms.

The problem can be separated into two separate issues: i) if farmers can perceive direct benefits from the services provided by landscape management (such as better pollination or pest control), what social structures could lead to successful cooperation? And ii) where the main benefits of a service accrue to wider society (such as unpolluted water or biodiversity), what incentives can be provided to encourage cooperative action between neighbours?

Central to the first issue is the question of trust between landowners (Reed, 2008). If farmers suspect that neighbours will free-ride and jeopardise their own efforts, collaboration will be less likely (Sutherland et al., 2012). An example of free-riding could easily occur from the use of predator attractant HIPVs, if a farmer who can afford to use the technology “steals” natural enemies from a neighbour who cannot. Cooperation would be encouraged by local examples of landscape-scale management obviously benefiting groups of farms (such as tenanted estates or conglomerates), as neighbour networks have been shown to be important in farmer’s decision making (Sutherland et al., 2012, Schmit and Rounsevell, 2006).

Incentive schemes for supply of ecosystem services not perceived to be of direct economic benefit to farmers (PES) already exist, but cannot currently encourage particular spatial configuration of management (Goldman et al., 2007). For example, the higher level stewardship scheme in the UK is targeted to farms in key areas for the conservation of important species or habitats, but focuses on the management of individual farms rather than groups. Possible mechanisms for administering payments for coordinated management across multiple farms include encouraging landowner-driven entrepreneurial collectives, centrally planned “ecosystem service districts” with legislation to enforce compliance (Goldman et al., 2007), or a spatially varying PES structure whereby a farmer might receive a bonus payment for managing habitat adjacent to another area under similar management (an “agglomeration bonus”) (Parkhurst and Shogren, 2007). Given the understandable misgivings farmers might have about further centralised regulation of their businesses, perhaps a bottom-up entrepreneurial approach where groups of farmers freely propose an ecosystem service delivery plan, for which they are then reimbursed provided it meets the required standards, is a more promising strategy than creating legislative districts. These same groups of farmers, assembled to supply services to wider society, could then form the necessary social structure to enable management for directly self-interested supporting services.

What is less straightforward is how groups of farmers might actually go about planning an optimal spatial configuration of land use, particularly when planning must keep pace with the rapid economic fluctuations which continually alter the value of different land uses. As seen in chapter 4 of this thesis, contingency on initial landscape structure probably precludes issuing of general guidelines for changes that could be made. One option would be enlisting the help of skilled local advisors (Reed, 2008). In the UK advisors from Natural England already liaise with farmers individually to plan environmental stewardship options, so perhaps this role could be extended to include advice for farmer cooperatives on ecosystem service provision. As a more hi-tech solution, one could imagine open-source software available to farmers which can predict optimal landscape patterns tailored to their specific location, incorporating spatially explicit models of ecosystem processes such as those described above.

Considering the potential importance of planning for coordinated management for ecosystem service provision, addressing the issues outlined above should form a major focus of research into sustainable agriculture. One opportunity for research is that the efforts of groups of farmers need not only represent the application of knowledge, but would also themselves constitute long-term experiments on the effects of landscape management. Taking full advantage of this for scientific gain would obviate the need for vast research grants to fund landscape-scale manipulation, and would enable the testing of simulation predictions with the real-life outcomes of change.

6.3 Concluding thoughts

There is great optimism in the scientific community that by coordinated application of current technology and reduction in waste we can weather the storm of peak food demand from 9 billion people sustainably. If this optimism is justified, when population begins to fall at the end of this century the state of our ecosystems may be no worse, or even perhaps better, than it is now (Godfray et al., 2010).

However, UN population projections include several scenarios containing different assumptions about future trends in demographic parameters. Their “high” projection expects 15.8 billion people to live on the planet by 2100 (UNDESA, 2011). Can the volume of agricultural production needed to feed this number still lie within the limits of sustainability? In all likelihood, short-term need for increased production food will trump the supply of other vital ecosystem services if they cannot be satisfied simultaneously, with potentially disastrous consequences for humans in the long-term. Perhaps the huge scientific effort being expended on sustainable intensification of agriculture will only be worthwhile if parallel efforts are made to accelerate reduction in fertility rates, and thereby prevent the UN’s “high” population projection from becoming a reality.

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Appendix 1. Efficacy of site selection

Maximising variation in variables of interest (VOI)

Eighty percent of the initial variation across all metrics used in the statistical analysis was retained in the landscapes surrounding the study fields.

Minimising the colinearity between VOI

By selecting equal numbers of sectors in each of the 8 treatment categories, the mean correlation between the VOI was reduced from 0.32 in the initial set of sectors, to 0.08 for the chosen study fields.

Minimising correlation of VOI with confounding spatial environmental variables

The correlation between the multivariate distance between 1km sectors in confounding environmental variables (comprising the 12 variables used for environmental matching) and the multivariate distance in VOI decreased from 0.14 before selection, to 0.09 after selection (see figure A1.1).

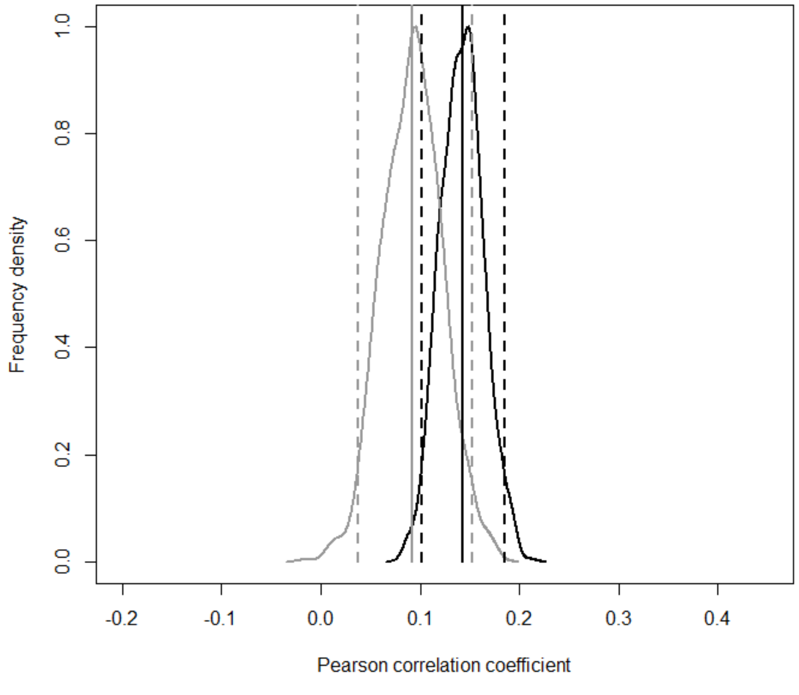

Figure A1.1: Correlation between distance in variables of interest and confounding environmental variables before and after site selection.
Distribution (dome shaped solid lines) of correlation coefficients before (black) and after (grey) site selection, between the multivariate distances among sites in variable of interest space and a space made up of confounding environmental variables. Observed correlations (solid vertical lines) and their confidence intervals (vertical dashed lines) are also shown.

Relationship between VOI and other environmental gradients

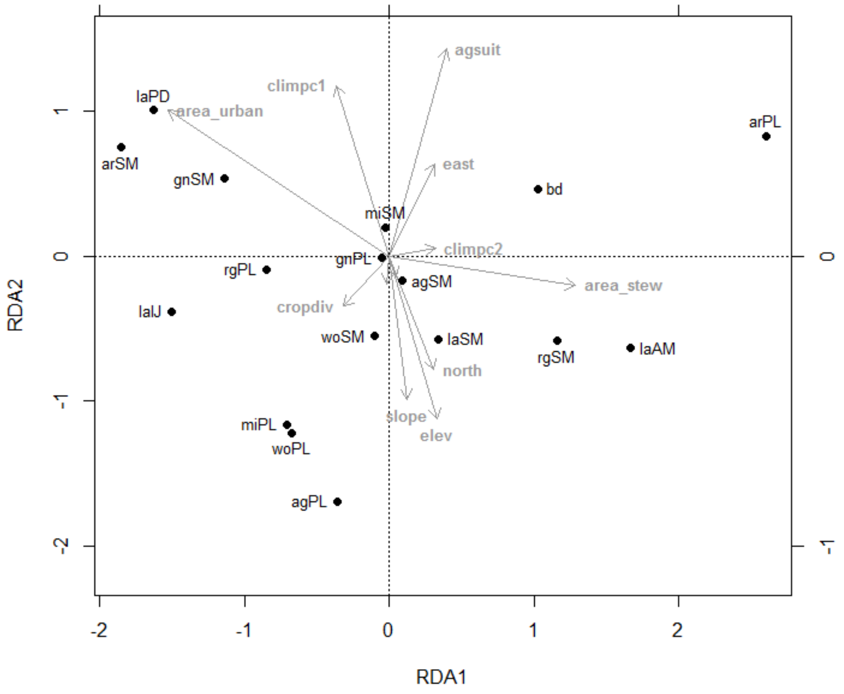

Figure A1.2: Redundancy analysis biplot showing how variation in variables of interest (VOI) between 1km sectors is related to confounding environmental factors.

The positions of VOI are shown as black points and text, those of environmental factors as grey arrows and text. VOI: ar = arable, ag = ag_grass, wo = woodland, mi = mixed, gn = "garden, rg = rough_grass, la = land, bd = boundary density, PD = patch richness density, SM = mean shape index, PL = percentage cover, AM = mean patch area, IJ = land cover interspersion . Environmental factors: "cropdiv" = Shannon crop diversity, elev = mean altitude, climpc1 = temperature related composite climatic axis, climpc2 = rainfall related composite climatic axis, area_stew = area under environmental stewardship, agsuit = arable suitability, north = latitude, east = longitude.

Using redundancy analysis, the linear combinations of confounding environmental variables best explaining variation in variables of interest were found for the candidate 1km circular sectors (i.e. before site selection). Across Yorkshire, topography climate/northerliness and arable suitability of the soil influence the balance between grassland (agPL in figure A1.2) and arable land (arPL). In more urbanised areas, the shape complexity of arable parcels (arSM) and the patch richness and interspersion (laPD and laIJ respectively) are higher. Proportion of arable land is also related strongly to the area under environmental stewardship schemes. Site selection aimed to remove these relationships as much as possible

Appendix 2. R code for iterative landscape change functions

```
library(compiler)
library(maptools)
library(rgeos)
library(sp)
library(raster)
library(shapefiles)
```

```
##All text after “#” is annotation, not code.
```

Changing polygon class:

```
#provide the named shapefile ("layer")
#Define a (list of) target class(es) to be subject to change - this is called "target".
#Define a (list of) class(es) who's area is going to be increased - this is called "grower"
#(For example, a reduction in arable area would make arable the "target", and all other
#classes "growers", whereas an increase in arable area would make all other classes
#"targets" and arable the "grower")
#Define area to change ("area").
#Choose between aggregated, random, or dispersed changes by argument "style" (options: "agg", "ran", "dis").
#Choose randomly from list of target polygons.
#Determine the neighbouring polygons from the list of "grower" polygons.
#If aggregated, change the class with probability as proportion of perimeter next to grower.
#If dispersed, ditto, but probability as 1 - proportion.
#If random, prob 0.5 for all, with identity of change for multiple grower being determined by proportional area.
#If the grower is >1 class, change to a class with probability based on the individual proportion of perimeter
#for each class (e.g. if an arable patch shared 0.3 of its perimeter with ag_grass, and 0.4 with woodland,
#the probability of changing to ag_grass and woodland would be 0.3 and 0.4 respectively.)

#Also optional, is to supply user defined probability vectors of which of the growing classes will be likely to fill
#a polygon, and which of the target classes are more vulnerable to being changed ("gprobs" and "tprobs" respectively)
#If "adj" == TRUE, the gprobs weights are multiplied by the proportion of perimeter/area, so a class will not be chosen
#(no matter how highly weighted in gprobs) if it doesn't border the polygon/is not present in landscape
#, if false, then gprobs weights alone are used as sample weights for deciding which class to choose, so non-bordering
# or non-present in landscape classes can still be chosen.
#Another parameter "padd", is the amount to extend the range of the random number generator, in order to ensure the
#algorithm doesn't get stuck when the proportion of a polygon's perimeter shared with a growing class is 0 in the "agg" style,
#or 1 in the "dis" style. If "padd" is 0.025, this means there is still a 1/41 chance of the change occurring.

#Repeat the above until area/proportion threshold is reached. If i want a proportion, then just work this out as an area before running the function.
#Output the new shapefile

##Importantly, the polygon which represents the field in which I actually sampled should not be able to change in any
##of the functions.
##This is identified as the polygon which contains the field centroid.

-----------
```

```
change_class<-function(layer, target, tprobs = NULL, grower, gprobs = NULL, adj = FALSE, area, style, npass = 1,padd = 0.025,exempt){
          samp_field<- layer[row.names(layer) == exempt,]
          layer<- layer[-which(row.names(layer) == exempt),]
          cumarea<-0
          if(style == "ran"){                                                                                                                          ###RANDOM STYLE
                    while(cumarea <= area){
                              targ<-row.names(layer)[layer@data$combin_pat %in% target]                                                     #get ids of polygons of target class(es)
                              if(length(targ)== 0){
                                        print("No remaining target polygons")
                                        break
                              }
                              grow<-row.names(layer)[layer@data$combin_pat %in% grower]                                                     #get ids of polygons in the growing class(es)
                              print(length(grow))
                              if(!is.null(tprobs)){                                                                              #if a user defined vector of target probabilities is supplied
                                        probvec<-tprobs[match(layer@data[targ,]$combin_pat,target)]                                         #sample from targets weighted by these probs.
                                        choice<-sample(targ,1, prob = probvec)
                              }else{
                                        choice<-sample(targ,1)
                              }
                              thispol<-layer[choice,]
                              areas<-rep(0,length(grower))                                                                                                      # Calculate relative areas of grower classes
                              for(i in 1:length(grower)){
                                        if(any(layer@data$combin_pat == grower[i])){
                                                  areas[i]<-gArea(layer[which(layer@data$combin_pat == grower[i]),])
                                        }
                              }
                              if(!is.null(gprobs) && adj == TRUE){
                                        probs<-gprobs*(areas/sum(areas))                                                                                        #If user supplied probabilities, multiply by relative
                              }else if(!is.null(gprobs)){                                                                                                       #areas to get final probabilities
                                        probs<-gprobs
                              }else{
                                        probs<-areas/sum(areas)                                                                                       #Use these to define probabilities of changing to the class
                              }
                              pick<-runif(1)
                              if(pick <= 0.5 && sum(probs)>0){                                                                            #If random number 0>x<1 is >0.5, move to next polygon without changing
                                        cumarea<-cumarea+ gArea(thispol)                                                                          #If <0.5, assign new class according to probabilities calculated above
                                        new<-sample(grower,1,prob = probs)
                                        layer@data[row.names(thispol),"combin_pat"] <- new
                              }
                    }
          }
          if(style == "agg"){                                                                                                                          ##AGGREGATED STYLE
                    strikes<-0
                    while(cumarea <= area && strikes < 500){
                              targ<-row.names(layer)[layer@data$combin_pat %in% target]                                                     #get ids of polygons of target class(es)
                              if(length(targ)== 0){
                                        print("No remaining target polygons")
                                        break
                              }
                              grow<-row.names(layer)[layer@data$combin_pat %in% grower]                                                     #get ids of polygons in the growing class(es)
                              print(length(grow))
                              if(!is.null(tprobs)){                                                                                       #if a user defined vector of target probabilities
                                        probvec<-tprobs[match(layer@data[targ,]$combin_pat,target)]                                         #sample from targets according to these probs.
                                        choice<-sample(targ,1, prob = probvec)
                              }else{
                                        choice<-sample(targ,1)
                              }
                              thispol<-layer[choice,]
                              print(choice)
                              neigh<-gTouches(layer[grow,],thispol,byid = TRUE)                                                             #Are there any neighbours of the grower class(es)?
```

```
        if(any(neigh)){                                                                       # If not, move to next polygon. If there are, do the following.
            neigh_pols<-layer[(dimnames(neigh)[[2]][neigh == TRUE]),]                         #Find neighbouring polygons
            perims<-rep(0,length(grower))
            for(i in 1:length(grower)){                                                       #Calculate proportion of perimeter each class shares with target polygon
                if(any(neigh_pols@data$combin_pat == grower[i])){
                    thisclass<-try(gIntersection(neigh_pols[neigh_pols@data$combin_pat == grower[i],],thispol,byid = FALSE))
                    if(class(thisclass) == "try-error"){
                        thisclass<-gIntersection(neigh_pols[neigh_pols@data$combin_pat == grower[i],],thispol,byid = TRUE)
                    }
                    perims[i]<-gLength(thisclass)
                }
            }
            prop<-perims/gLength(thispol)
            pick<-runif(1,min = 0 - padd)
            if(pick <= sum(prop)){                                                    #If random number < the total fraction of focal polygon's perimeter
                cumarea<-cumarea+ gArea(thispol)                                      #shared with growing classes change class according to probabilities.
                if(!is.null(gprobs)&& adj == TRUE){
                    newprobs<-gprobs*(prop/sum(prop))                                 #If user defined probs, then proportional perimeter is multiplied by them
                }else if(!is.null(gprobs)){                                           #to avoid having 0 probability of changing when prop == 0,
                    newprobs<-gprobs                                                  #let random number range go slightly below 0.
                }else{                                                                # If >, move to next polygon without changing.
                    newprobs<-prop/sum(prop)
                }
                layer@data[row.names(thispol),"combin_pat"]<-sample(grower,1,prob = newprobs)
                strikes<-0
            }
        }
    strikes<-strikes+1
    }
}
if(style == "dis"){                                                                               #DISPERSED STYLE
    strikes<-0
    while(cumarea <= area && strikes < 500){
        targ<-row.names(layer)[layer@data$combin_pat %in% target]                             #get ids of polygons of target class(es)
        if(length(targ)== 0){
            print("No remaining target polygons")
            break
        }
        grow<-row.names(layer)[layer@data$combin_pat %in% grower]                             #get ids of polygons in the growing class(es)
        print(length(grow))
        if(!is.null(tprobs)){                                                                 #if a user defined vector of target probabilities
            probvec<-tprobs[match(layer@data[targ,]$combin_pat,target)]
            choice<-sample(targ,1, prob = probvec)                                            #is supplied, re-order polygons putting most likely first.
        }else{
            choice<-sample(targ,1)
        }
        thispol<-layer[choice,]
        print(choice)
        neigh<-gTouches(layer[grow,],thispol,byid = TRUE)
        if(any(neigh)){                                                                       #If any neighbours of growing class, do the following.
            neigh_pols<-layer[(dimnames(neigh)[[2]][neigh == TRUE]),]                         #Same as for "agg" but for one thing (see below)
            perims<-rep(0,length(grower))
            for(i in 1:length(grower)){                                                       #Calculate proportion of perimeter each class shares with target polygon
                if(any(neigh_pols@data$combin_pat == grower[i])){
                    thisclass<-gIntersection(neigh_pols[neigh_pols@data$combin_pat == grower[i],],thispol,byid = FALSE)
                    if(class(thisclass) == "try-error"){
                        thisclass<-gIntersection(neigh_pols[neigh_pols@data$combin_pat == grower[i],],thispol,byid = TRUE)
                    }
                    perims[i]<-gLength(thisclass)
                }
```

```
                                }
                                prop<-perims/gLength(thispol)
                                pick<-runif(1, max = 1 + padd)
                                if(pick > sum(prop)){                                                   #This time, probability of changing decreases, as more of
                                        cumarea<-cumarea+ gArea(thispol)                                #the focal polygon's border is shared with grower classes.
                                        if(!is.null(gprobs)&& adj == TRUE){                             #If user defined probs, then proportional perimeter is
                                                newprobs<-gprobs*(prop/sum(prop))                       #multiplied by them to give the final weightings.
                                        }else if(!is.null(gprobs)){
                                                newprobs<-gprobs
                                        }else{
                                                newprobs<-prop/sum(prop)
                                        }
                                        layer@data[row.names(thispol),"combin_pat"]<-sample(grower,1,prob = newprobs)
                                        strikes<-0
                                }
                        }else{                                                                  #If no neighbours of grower classes, change.
                                areas<-rep(0,length(grower))                                            #Identity of new class is calculated from relative areas
                                for(i in 1:length(grower)){                                             #in the entire map, as for the "ran" selection.
                                        if(any(layer@data$combin_pat == grower[i])){
                                                areas[i]<-gArea(layer[which(layer@data$combin_pat == grower[i]),])
                                        }
                                }
                                if(!is.null(gprobs)&& adj == TRUE){
                                        probs<-gprobs*(areas/sum(areas))                                #If user supplied probabilities, multiply by relative
                                }else if(!is.null(gprobs)){
                                        probs<-gprobs
                                }else{
                                        probs<-areas/sum(areas)
                                }
                                if(sum(probs)>0){
                                layer@data[row.names(thispol),"combin_pat"]<-sample(grower,1,prob = probs)
                                strikes<-0
                                cumarea<-cumarea+ gArea(thispol)
                                }
                        }
                        strikes<-strikes+1                                                      #"strikes" is a counter, so that function exits if no viable
                }                                                                               #changes are made for 500 iterations in a row.
        }
        print(cumarea)
        final_layer<- rbind(layer,samp_field)
        return(final_layer)                                                                     #return the modified shapefile
}

cchange<-cmpfun(change_class)
#-----------------------------------------------------------------------------------
nohole<-function(polys){                                                                        #Function to get ids of polygons without holes.
        lens<-rep(0,length(polys))
        for(i in 1:length(polys)){
                lens[i]<-length(polys[i,]@polygons[[1]]@Polygons)
        }
        ids<-row.names(polys)[lens == 1]
        return(ids)
}

chole<-cmpfun(nohole)
near<-function(cent,boundary){                                                                  #Function to find the nearest point of the polygon
        sqdist<-(boundary[,1] - cent[1])^2 +(boundary[,2] - cent[2])^2                          #boundary to the polygon centroid.
        nearest<-boundary[which(sqdist == min(sqdist))[1],]
        return(nearest)
}
```

```
cnear<-cmpfun(near)

predecimalplaces <- function(x) {                                                    #Two functions involved in finding the line to split
    if ((x %% 1) != 0) {                                                             #polygons. "predecimalplaces" finds the number of predecimal digits in a number.
        nchar(strsplit(sub('0+$', '', as.character(x)), ".", fixed=TRUE)[[1]][[1]])
    } else {
        return(0)
    }
}

conversion<-function(min, sigfig){                                                   #"conversion" uses the number of digits to round up the number

          pdp<-predecimalplaces(min)                                                 #  at a decimal place in proportion to its size.
          multi<-(10^(sigfig-1))/(10^(pdp-1))
          new<-ceiling(min*multi)/multi
          return(new)
}
```

Splitting polygons

```
#input the polygon ("polys") and line ("lines") data
#consider only  polygons in the target class(es) , without holes.
#Sample from these randomly, but optionally weighting by area or inverse area.
#split polygons in this order until the threshold length of line ("len")
#has been added.
#Add new lines onto the end of the full lines file and give them ids paste("new",try)
#Remove old larger and add new smaller polygons onto the full polygon file,
 #and call the new ones paste("new",try)
 #Re-id both the line and polygon files at the end.
 #only allow fields to be split or merged from specified classes - "targets"

--------------------

split_poly<-function(polys,lines,length,targets, incdec = "ran"){
          print(date())
          cumlen<-0
          nohole<-polys[chole(polys),]                                               #find polygons without holes
          holed<-polys[!(row.names(polys)%in% chole(polys)),]
          rel<-nohole[nohole@data$combin_pat %in% targets,]                          #create initial list of target polygons
          try<-1
          addlines<- lines[1,]
          while(cumlen <= length){
                    if(incdec == "dec"){                                             #Is random sample be weighted by area, inverse area, or unweighted?
                              probs<-as.numeric(gArea(rel,byid = TRUE))/sum(as.numeric(gArea(rel,byid = TRUE)))
                    }else if(incdec == "inc"){
                              probs<-1/(as.numeric(gArea(rel,byid = TRUE))/sum(as.numeric(gArea(rel,byid = TRUE))))
                    }else{
                              probs<-NULL
                    }
                    choice<-sample(row.names(rel),1,prob = probs, replace=FALSE)
                    thispol<-rel[choice,]
                    print(row.names(thispol))
                    cent<-try(gPointOnSurface(thispol))                              #Find centroid (or central point inside if true centroid is outside)   and boundary coordinates
                    if(class(cent) == "try-error"){                                  #move on if mis-specified polygon
                    print("Geometry Exception
                    try<-try+1
                    next}
```

```
boundary<-gBoundary(thispol)
mindist<-gDistance(cent,boundary)                                                                                          #Find min distance from boundary to centroid
buffrad<-conversion(mindist,4)
circ<-gBoundary(gBuffer(cent,width = buffrad,quadseg = 4000))                              #Draw a buffer around the centroid to intersect the boundary at its nearest point
nearest<-coordinates(gIntersection(circ,boundary))[1,]
cent<-coordinates(cent)
xdiff<-cent[1]-nearest[1]
ydiff<-cent[2]-nearest[2]
newx1<-cent[1]+100*xdiff
newy1<-cent[2]+100*ydiff
newp1<-c(newx1,newy1)                                                                         #Make new point on the extrapolation of the line, well outside the polygon.
newx2<-cent[1]-100*xdiff                                                                                #this will force an intersection when finding polygon parts.
newy2<-cent[2]-100*ydiff
newp2<-c(newx2,newy2)
ps<-rbind(newp2,nearest,cent,newp1)
prov_line<-Line(ps)
pline<-Lines(list(prov_line),ID= "a")
plines<-SpatialLines(list(pline))                                                                       #Join up the three points into a line
bound<-Line(coordinates(boundary))
bline<-Lines(list(bound),ID = "b")
blines<-SpatialLines(list(bline))
intersects<-coordinates(gIntersection(blines,plines))                                                    #Find intersection of line with the boundary.
opp<-intersects[!(abs(intersects[,1] - nearest[1])<0.1 & abs(intersects[,2] - nearest[2])<0.1),]
if(!(is.null(nrow(opp)))){opp<-cnear(cent,opp)}                                                         #in case of >2 intersections, take the one closest to the centroid
newps<-rbind(nearest,cent,opp)                                                                          #make new point from the relevant intersection
new_line<-Line(newps)                                                                                   #make new line from the three points
nline<-Lines(new_line,ID = paste("new",try,sep=""))
nline2<-SpatialLines(list(nline))
len<-gLength(nline2)
cumlen<-cumlen + len                                                                                    #add length to cumulative counter
ang<-atan2(ydiff,xdif
xadd<-0.1*(cos(ang))
yadd<-0.1*(sin(ang))
s_oppx<-opp[1] + xadd                                                                         #Make line slightly longer, in order to split the polygon.
s_oppy<-opp[2] + yadd
s_nearx<-nearest[1] - xadd
s_neary<-nearest[2] - yadd
s_opp<-c(s_oppx,s_oppy)
s_near<-c(s_nearx,s_neary)
s_ps<-rbind(s_near,cent,s_opp)
slin<-Line(s_ps)
sline<-Lines(slin, ID = "splitter")
sline2<-SpatialLines(list(sline))
parts<-gDifference(blines,sline2)                                                                                          #Split the polygon
if(length(parts@lines[[1]]@Lines)== 3){                                                                                    #If the new line splits the boundary into 3 bits (most likely)
          pt1<-parts@lines[[1]]@Lines[[1]]@coords
          pt2<-parts@lines[[1]]@Lines[[2]]@coords
          pt3<-parts@lines[[1]]@Lines[[3]]@coords
          n1<-Polygon(rbind(pt1,pt3))
          n2<-Polygon(rbind(pt2,pt2[1,]))
          if(nrow(n1@coords)==3 || nrow(n2@coords)==3){
                    try<-try+1
                    next
          }
}else if(length(parts@lines[[1]]@Lines)== 2){                                                                              #If 2 bits
          pt1<-parts@lines[[1]]@Lines[[1]]@coords
          pt2<-parts@lines[[1]]@Lines[[2]]@coords
          n1<-Polygon(rbind(pt1,pt1[1,]))
          n2<-Polygon(rbind(pt2,pt2[1,]))
          if(nrow(n1@coords)== 3 || nrow(n2@coords)== 3){
```

```
                                        try<-try+1
                                        next
                              }
                    }else{                                                                                                                              #otherwise, it hasn't worked so move to next
                              try<-try+1
                                        next
                    }
                    np1<-Polygons(list(n1),ID = paste("new",try,"a",sep=""))
                    np2<-Polygons(list(n2),ID = paste("new",try,"b",sep=""))
                    newpolys<-SpatialPolygons(list(np1,np2))
                    newpolys_xml<-rep("xml_area",2)                                                                                                     #Make data for polygons.
                    newpolys_class<-rep(as.character(thispol@data[,"combin_pat"]),2)                      #the class of the original polygon goes to both offspring after splitting.
                    newpolys_data<-data.frame("xml_type" = newpolys_xml,"combin_pat" = newpolys_class)
                    row.names(newpolys_data)<-c(paste("new",try,"a",sep=""),paste("new",try,"b",sep=""))
                    newpolys_spdf<-SpatialPolygonsDataFrame(newpolys, newpolys_data)
                    nohole<-rbind(nohole[!(row.names(nohole)==row.names(thispol)),],newpolys_spdf)         #Add new polygons onto the map, and remove old one.
                    type<-"xml_line"
                    nlin_dat<-data.frame("xml_type" = type,"length" = len)
                    row.names(nlin_dat)<-paste("new",try,sep="")
                    nlin_sldf<-SpatialLinesDataFrame(nline2,nlin_dat)
                    addlines<-rbind(addlines,nlin_sldf)
                    rel<-nohole[nohole@data$combin_pat %in% targets,]
                    try<-try+1
                    print(cumlen)                                                                                         #move onto next polygon.
          }
          new_polys<-rbind(holed,nohole)
          new_lines<-rbind(lines,addlines[-1,])
          row.names(new_polys)<-as.character(seq(0,length(new_polys)-1,1))                                  #Re-id polygons and lines
          row.names(new_lines)<-as.character(seq(0,length(new_lines)-1,1))
          print(date())
          return(list("Polygons" = new_polys,"Lines" = new_lines))                                          #Out put changed polygons and lines as a list
}
csplit<-cmpfun(split_poly)

#-------------------------------------------------------------------------------------
```

Merging polygons:

```
#as above, input polygon and line data, and extract polygons in target class(es), with no holes
#Randomly pick polygons from the list, but optionally favouring biggest or smallest first.
#find neighbouring polygons of the same class, and choose randomly the one to merge with.
#Remove the old two smaller polygons and add the new larger one to list
#Remove line segment from the list
#Go through relevant polygons until the threshold of line length as been exceeded
#Re-add data to line file
#re-id both files

#-----------------------------

merge_poly<-function(polys,lines,length,targets,incdec = "ran"){
          print(date())
          cumlen<-0
          nohole<-polys[chole(polys),]
          holed<-polys[!(row.names(polys)%in% chole(polys)),]
          try<-1
          rel<-nohole[nohole@data$combin_pat %in% targets,]
          strikes<-0
          remlines<- as.SpatialLines.SLDF(lines[1,])
```

```
        while(cumlen <= length & strikes < 200){
                if(incdec == "dec"){                                                                                        #Is random sample to be unweighted, weighted by area, or by inverse area?
                        probs<- as.numeric(gArea(rel,byid = TRUE))/sum(as.numeric(gArea(rel,byid = TRUE)))
                }else if(incdec == "inc"){
                        probs<-1/(as.numeric(gArea(rel,byid = TRUE))/sum(as.numeric(gArea(rel,byid = TRUE))))
                }else{
                        probs<-NULL
                }
                choice<-sample(row.names(rel),1,replace=FALSE,prob = probs)

                thispol<-rel[choice,]

                print(row.names(thispol))

                thisclass<-row.names(rel[rel@data$combin_pat == thispol@data$combin_pat,])
                neigh<-gTouches(rel[thisclass,],thispol,byid=TRUE)
                if(any(neigh)){                                                                                             #Are there any neighbours of the same class?
                        strikes<-0
                        neighs<-dimnames(neigh)[[2]][neigh == TRUE]                                                         #If not, move onto next polygon.If yes, do the following.
                        partner<-rel[sample(neighs,1),]                                                                     #Randomly pick one of the neighbours
                        new<-gUnion(thispol,partner)                                                                        #create a union polygon of the focal and partner polygons
                        new@polygons[[1]]@ID<-paste("new",try,sep="")                                                       #create data for new polygons
                        new_id<-paste("new",try,sep="")
                        new_xml<-"xml_area"
                        new_class<-as.character(thispol@data$combin_pat)
                        new_data<-data.frame("xml_type" = new_xml,"combin_pat" = new_class)
                        row.names(new_data)<-new_id
                        new_spdf<-SpatialPolygonsDataFrame(new, data = new_data)
                        nohole<-rbind(nohole[!(row.names(nohole)==row.names(thispol) | row.names(nohole)==row.names(partner)),],new_spdf)        #take old polygons off and add new.
                        line<-gIntersection(thispol,partner)
                        if(class(line) == "SpatialPoints"){
                                try<-try+1
                                next
                        }
                        row.names(line)<- "new"                                                                                     #Now deal with lines
                        len<-gLength(line)
                        cumlen<-cumlen + len                                                                                        #add length of line to total
                        remlines<-rbind(remlines,line)
                        row.names(remlines)<- as.character(seq(1,length(remlines),1))                                               #remove line segment

                }
                try<-try+1
                strikes<-strikes+1
                rm(rel)
                gc()
                rel<-nohole[nohole@data$combin_pat %in% targets,]
                print(cumlen)
        }
        lines<- gDifference(lines,remlines[-1,])
        new_polys<-rbind(holed,nohole)
        type<-rep("xml_line",length(lines))
        len<-gLength(lines, byid=TRUE)                                                                                      #add length of removed line to the length counter
        lin_dat<-data.frame("xml_type" = type, "length" = len)                                                              # make data for line map so a SpatialLinesDataFrame
        lin_sldf<-SpatialLinesDataFrame(lines, data = lin_dat)                                                              #can be made. (necessary to export it as a shapefile).
        row.names(new_polys)<-as.character(seq(0,length(new_polys)-1,1))
        row.names(lin_sldf)<-as.character(seq(0,length(lin_sldf)-1,1))
        print(date())
        return(list("Polygons" = new_polys,"Lines" = lin_sldf))                                                             #Export polygons and lines as list
}
```

Appendix 3. Supplementary tables for chapter 4

Table 4.4: Scenarios predicting the most consistent reduction in aphid abundance

Each row of the table describes the scenario resulting in the most consistent decrease in aphid abundance for a single template landscape. The ID and position on the two landscape principal components of the template are shown at the left. Red and green arrows have the same meaning for proportional area change as for table 4.3. Ticks in the configuration and boundary change columns identify the other conditions of the scenario. The C-index of the response is also given, to show the strength. While not capturing the magnitude of the response, it gives a measure of the reliability of the response to the change. On the bottom row, the totals of the columns defining the scenarios are shown (with red arrows contributing -1 and green arrows 1), to provide a summary of the weight of “votes” for different sorts of change, when summed across templates. These numbers were used in figure 4.3. The best scenario is fairly consistent among templates for proportional area changes, but less so for configuration and boundary changes.

PC1 score	PC2 score	Template ID	Land cover change			Configuration			Boundary change			C-index
			Arable	Ag. Grass	Non-crop	Dis	Ran	Agg	↑30km	None	↓30km	
Low	Low	39	↑	↓	0		√				√	-0.97
Low	Mid	58	0	↓	↑			√		√		-0.93
Mid	Low	96	↑	↓	↑		√		√			-0.92
Mid	Mid	18	↑	↓	↑	√			√			-0.97
Mid	High	10	↑	↓	↑	√				√		-0.09
High	Low	151	0	↓	↑	√					√	-0.03
High	Mid	71	↓	0	↑			√		√		-0.97
High	High	50	↑	↓	0			√		√		-0.92
Overall			4	-7	6	3	2	3	2	4	2	

Table 4.5: Scenarios predicting the most consistent increase in aphid abundance

As table 4.4, but showing scenarios resulting in the most consistent aphid increase – the worst outcome. Most templates show the worst outcome when arable land increases at the expense of non-crop land, but for templates 10 and 151 an increase in ag_grass would be most detrimental.

PC1 score	PC2 score	Template ID	Land cover change			Configuration			Boundary change			C-index
			Arable	Ag. Grass	Non-crop	Dis	Ran	Agg	↑30km	None	↓30km	
Low	Low	39	↑	0	↓			√		√		0.97
Low	Mid	58	↑	0	↓		√				√	0.93
Mid	Low	96	↑	0	↓	√				√		0.92
Mid	Mid	18	↑	0	↓		√			√		0.98
Mid	High	10	0	↑	↓			√		√		0.98
High	Low	151	↓	↑	↑			√			√	0.86
High	Mid	71	↑	0	↓	√					√	0.97
High	High	50	↑	0	↓		√			√		0.92
Overall			5	2	-7	2	3	3	0	5	3	

Table 4.6: Best scenarios for parasitoid and syrphid abundance per aphid combined

Format is the same as previous tables. The desirability of a change in both parasitoids and syrphid larvae per aphid is judged by adding their individual C-indices, hence they can vary between -2 and 2, rather than -1 and 1. The proportional area changes are less consistent between templates for the combination than for either individually (figure 4.3 A in chapter 4).

PC1 score	PC2 score	Template ID	Land cover change			Configuration			Boundary change			C-Index
			Arable	Ag. Grass	Non-crop	Dis	Ran	Agg	↑30km	None	↓30km	
Low	Low	39	↓	↑	0			√		√		1.83
Low	Mid	58	0	↓	↑	√					√	1.74
Mid	Low	96	↓	↑	↓	√					√	1.99
Mid	Mid	18	↓	0	↑		√				√	1.86
Mid	High	10	0	↓	↑		√			√		1.64
High	Low	151	↓	↑	↑		√		√			1.86
High	Mid	71	↓	0	↑		√		√			0.87
High	High	50	0	↑	↓		√			√		1.59
Overall			-5	2	3	2	5	1	2	3	3	

Table 4.7: Worst scenarios for parasitoid and syrphid abundance per aphid combined

As table 4.6, but with negative C-indices to indicate the worst scenario.

PC1 score	PC2 score	Template ID	Land cover change			Configuration			Boundary change			C-index
			Arable	Ag. Grass	Non-crop	Dis	Ran	Agg	↑30km	None	↓30km	
Low	Low	39	↑	0	↓			√	√			-1.83
Low	Mid	58	↑	0	↓			√			√	-1.87
Mid	Low	96	↑	0	↓	√			√			-1.87
Mid	Mid	18	↑	↓	0		√		√			-1.99
Mid	High	10	0	↑	↓			√			√	-1.20
High	Low	151	↑	0	↓			√		√		-1.85
High	Mid	71	↑	↓	0	√					√	-1.34
High	High	50	↓	↑	0	√			√			-1.79
Overall			5	0	-5	3	1	4	4	1	3	

Table 4.8: Best scenarios for all three responses combined

Format as for previous tables. In this case, the scenarios shown are those resulting in the best compromise for the combination of all three responses. Thus, C-indices can vary between -3 and 3. Note that C-indices are fairly low, indicating limited scope for win-wins involving all three responses in some landscapes.

PC1 score	PC2 score	Template ID	Land cover change			Configuration			Boundary change			C-index
			Arable	Ag. Grass	Non-crop	Dis	Ran	Agg	↑30km	None	↓30km	
Low	Low	39	↓	↑	↑	√					√	2.09
Low	Mid	58	0	↓	↑	√					√	2.59
Mid	Low	96	↓	↑	0			√		√		2.06
Mid	Mid	18	↓	0	↑		√				√	2.04
Mid	High	10	↓	↑	0			√	√			1.56
High	Low	151	↓	↑	0			√			√	1.50
High	Mid	71	0	↓	↑		√		√			1.43
High	High	50	0	↑	↓		√			√		1.47
Overall			-5	3	3	2	3	3	2	2	4	

Table 4.9: Worst scenarios for all three responses combined

Format as for 4.8, but showing scenarios producing the worst results. C-indices for lose- loses involving all three are much larger (in absolute terms) than for win-wins, indicating better evidence for which land use changes would be undesirable from this point of view. Aggregated increase of arable land is consistently detrimental.

PC1 score	PC2 score	Template ID	Land cover change			Configuration			Boundary change			C-index
			Arable	Ag. Grass	Non-crop	Dis	Ran	Agg	↑30km	None	↓30km	
Low	Low	39	↑	0	↓			✓			✓	-2.81
Low	Mid	58	↑	0	↓			✓	✓			-2.66
Mid	Low	96	↑	↓	↓	✓				✓		-2.48
Mid	Mid	18	↑	0	↓			✓			✓	-2.68
Mid	High	10	0	↑	↓			✓			✓	-2.18
High	Low	151	↑	0	↓			✓		✓		-1.98
High	Mid	71	↑	↓	↓	✓					✓	-2.10
High	High	50	↑	0	↓			✓	✓			-2.12
Overall			7	-1	-8	2	0	6	2	2	4	

Table 4.10: Between-template variability in predicted responses to the same proportional area change

The format of the table is similar to table 4.3, but in this case each row represents the consistency of predicted responses to one scenario for a different template. The ID and position on the landscape gradients of templates is shown at the left (as for tables 4.4-4.9). The proportional area change depicted is the replacement of 200 ha of arable land by non-crop vegetation. There is considerable between-template variation in the consistency and even direction of response. The effect of field boundary changes on the outcome is also evident for some templates but not others.