University of Reading

Spatial modelling of insect-delivered ecosystem services

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Declaration

I confirm that this thesis is my own work and the use of all material from other sources has been properly and fully acknowledged.

John W. Redhead

This thesis includes three chapters which have been published as co-authored manuscripts. Publication details and author contributions are given below:

Chapter 3: Redhead, J.W., Oliver, T.H., Woodcock, B.A & Pywell R.F. (2020) The influence of landscape composition and configuration on crop yield resilience. *Journal of Applied Ecology*, Published online

JWR undertook data handling, conducted spatial and statistical analyses and wrote the manuscript (~95% of the work). RFP coordinated the project under which this work was performed. THO and BAW advised on appropriate analyses and interpretation of results. All authors contributed to revising the manuscript.

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JWR performed data handling, spatial and statistical analyses, and wrote the manuscript (~95% of the work). THO and AJV coordinated the project under which this work was performed. BAW and MJOP supported ecological network analyses. RFP conceived the compilation of plant-pollinator interaction records. All authors contributed to revising the manuscript.

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JWR designed and built scenarios, constructed species distribution models (SDMs) and predictions and wrote the manuscript (~95% of the work). GDP advised on SDMs and use of biological records. BAW advised on functional diversity metrics. RFP coordinated the project under which this work was performed and co-conceived (with JWR) the scenario exploration approach. All authors contributed to revising the manuscript.

Approved by:

Tom Oliver Richard Pywell

Abstract

Insects are integral to many ecosystem services, including pollination of crops by insect pollinators and control of pests by natural enemies (i.e. predators and parasites). These beneficial insects are suffering widespread declines, partly due to agricultural expansion and intensification. We must therefore change the management of agricultural landscapes to preserve these ecosystem services and the resilience of the systems that depend on them. To make such changes, we first need to understand the relationships between landscapes, beneficial insect communities and the delivery of the services they provide. This thesis focuses on analysing novel combinations of large-scale spatial datasets to explore these relationships.

Firstly, a ten-year time-series of wheat yield data was analysed in conjunction with satellite-derived land cover data to explore national-scale relationships between crop yield resilience and landscape structure. Whilst relative yield was highest in landscapes dominated by arable land, stability and resistance were promoted by semi-natural habitats. Secondly, data from biological recording schemes were used to construct potential plant-pollinator networks across Great Britain and explore relationships between network structure and land cover. Networks were most robust to simulated extinctions in highly agricultural landscapes, because they supported distinctive, generalist pollinator communities. Finally, data on land cover and cropping patterns were used to develop a range of scenarios of agricultural change. These were linked to beneficial insect richness and functional diversity using species distribution models based on biological records. Scenarios involving restoration of semi-natural grasslands increased the richness and functional diversity of beneficial insects, even if cropped land remained intensive.

The findings presented in this thesis demonstrate the value of combining and modelling spatial data in exploring insect-delivered ecosystem services. Whilst there is much scope for further work, including integration with experimental data, spatial modelling remains key to providing the large-scale evidence required by policy makers and agricultural land managers.

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Chapter 1: Introduction

This thesis describes the novel analysis of existing datasets to explore spatial and temporal patterns in insect-delivered ecosystem services and the natural capital that underpins them. This introductory chapter outlines the importance of insect-delivered ecosystem services to global food production systems, explores the need for an understanding of spatial and temporal patterns in attempting to ensure the present and future delivery of these services, and summarises the value which integrating existing spatial datasets using new modelling approaches can bring to addressing key knowledge gaps. The chapter concludes with an overview of the thesis aims and a brief outline of the subsequent chapters.

1.1 The importance of insect-delivered ecosystem services

Ecosystem services are the benefits that humans derive from ecosystems (Mace et al. 2012). These are wide ranging, from the production of goods such as timber, to the provision of drinking water and the capture of nutrients from aquatic (e.g. sediment runoff) or atmospheric (e.g. CO_2) systems, to the pollination of crops and natural regulation of pests and pathogens. Use of the ecosystem service concept in science and policy has developed over the last 50 years (Bouwma et al. 2018), with a particular focus arising in the early 21st century from the Millennium Ecosystem Assessment (MA 2005). Ecosystem services are now widely used as a framework within which to assess likely impacts of environmental change in socioeconomic terms and to provide a rationale for conservation (Tallis et al. 2008, Braat and de Groot 2012, Bouwma et al. 2018). If ecosystem services are to be useful as a concept then it is vital to be able to map and model their current delivery and responses to potential environmental change (Malinga et al. 2015). Recent environmental policy has in many cases included aspirations to accurately quantify and map ecosystem services in order to improve environmental management, at both international (European Commission 2011, Maes et al. 2012) and national scales (Defra 2018a).

Whilst some ecosystem services are largely driven by hydrological or geological factors, many are very much linked to groups of species with a specific ecological function. As insects are the most speciose, diverse and abundant group of animal life on land (Grimaldi et al. 2005) it is unsurprising that they are integral to many of these services (Losey and Vaughan 2006).

Whilst there are many other ecosystem services mediated, or at least affected by, insects - decomposition of waste (Yang and Gratton 2014), predation of human disease vectors (Shaalan and Canyon 2009), contribution to human diets (Van Huis 2013), etc - the focus of this thesis is on two of the most widely studied and relevant to agricultural systems: pollination of crops by insect pollinators and natural control of agricultural pests by insect predators and parasitoids (collectively termed 'natural enemies'). The stocks of natural assets which provide ecosystem services are often termed 'natural capital' (Costanza et al. 1997, Perrings et al. 2006, Helm 2015) and are often used as a proxy for ecosystem services themselves where these are difficult to quantify. In the case of this thesis, the natural capital in question is the biodiversity of insect pollinators and pest-controllers (collectively 'beneficial insects' from hereon). It should be noted that exactly which aspects of beneficial insect biodiversity are most strongly related to actual ecosystem service delivery is complex and context dependent (Mace et al. 2012), an issue which will be revisited in subsequent chapters throughout this thesis.

In recent decades, a wide variety of studies have highlighted the importance of insect pollinators to crop production (Free 1993, Allen-Wardell et al. 1998, Klein et al. 2007, Winfree 2008, Eilers et al. 2011, Garratt et al. 2014) and wild plant communities (Ollerton et al. 2011). Animal-mediated pollination services (dominated by insects) have been valued at US$235-577 billion (Lautenbach et al. 2012). They are estimated to affect yield or quality for 75% of globally important crop types (Klein et al. 2007, Gallai et al. 2009) and are vital to crops providing key micronutrients (Eilers et al. 2011). Natural control of crop pests has similar global significance (Losey and Vaughan 2006) valued at US$400 billion (Costanza et al. 1997), with particular importance in specific cropping systems (e.g. Schroth and Harvey 2007, Colloff et al. 2013, Classen et al. 2014, Wotton et al. 2019).

At the same time, it has become widely recognised that both of these services are under threat. Widespread declines are evident in many insect groups (Kluser and Peduzzi 2007, Potts et al. 2010, Oliver et al. 2015b, Sánchez-Bayo and Wyckhuys 2019). While debate continues over the global extent and severity of these declines (Cardoso and Leather 2019, Montgomery et al. 2019, Saunders et al. 2019), there are indications that deficits in the services provided by insects in specific systems are either already occurring (Garibaldi et al. 2011, Gill et al. 2016) or imminent (Aizen et al. 2008), and that action is required to prevent these from worsening (Forister et al. 2019, Saunders 2019). Given the benefits that the services of crop pollination and crop pest-control confer on agricultural crops, it is ironic that the expansion and intensification of agricultural land that has dominated global patterns of land use change over the past 100 years (Goldewijk 2001, Lambin et al. 2001, Foley et al. 2005, Green et al. 2005, Lambin and Meyfroidt 2011) has historically been associated with largely negative effects on biodiversity, including insects (Allen-Wardell et al. 1998, Foley et al. 2005, Kluser and Peduzzi 2007, Potts et al. 2010, Ollerton et al. 2014), and on the services they provide (Allen-Wardell et al. 1998, Kremen et al. 2002, Vanbergen et al. 2013, Oliver et al. 2015b). With human populations projected to continue to rise over the next few decades, concerns over food security mean that agricultural production must increase (Godfray et al. 2010) but without continued negative impact on beneficial insects. The understanding that agricultural production is underpinned by ecosystem services which are suboptimal in many current, intensive agricultural systems, coupled with observations that the ability of technological advances to enhance crop yields appears to have plateaued in many systems (Grassini et al. 2013), has led to the proposal of so-called "ecological" or "sustainable" intensification. This involves using farming practices that promote natural capital and/or optimise ecosystem service delivery to enhance our ability to both provide food and reduce the environmental footprint of agriculture (Cassman 1999, Bommarco et al. 2013, Landis 2017, Kleijn et al. 2019). Although there is a growing evidence base that it is possible to both identify and successfully implement such practices (e.g. Pywell et al. 2015, Fusser et al. 2016, Tschumi et al. 2016b, Woodcock et al. 2016a, and other examples in Kleijn et al. 2019), there are several gaps in our understanding of the interaction between agricultural practices and landscapes, insect populations and ecosystem service delivery which are currently preventing widespread uptake of these practices in mainstream agriculture (Kleijn et al. 2019).

1.2 Knowledge gaps in protecting insect-delivered ecosystem services

Insect-delivered ecosystem services are hard to quantify and model because of the inherent complexity of ecological systems (Hortal et al. 2015) and the multiple trophic or mutualistic interactions on which service delivery depends. Provision of pollination and pest-control services are influenced by processes operating over a wide range of spatial scales and levels of ecological organisation, from behaviours of individual organisms, to traits of species, interactions within communities and large-scale trends in populations. Recent reviews (Vanbergen et al. 2013, Gill et al. 2016, Potts et al. 2016) have sought to identify key knowledge gaps which need to be addressed if we are to continue to derive our current level of service from beneficial insects under future environmental change or increase the uptake of sustainable intensification approaches (Kleijn et al. 2019). Such knowledge gaps can be broadly divided into three groups: i) the fundamental ecology of beneficial insects (e.g. how beneficial insect communities are structured in terms of the interactions between plants and pollinators and crop pests and their natural enemies, and how the ecological networks formed by these interactions respond to environmental context and change); ii) linking the natural capital of beneficial insect biodiversity to provision of ecosystem services (e.g. how insect species richness, abundance and diversity relate to spatial and temporal variation in service delivery and agricultural outputs); iii) the impacts of environmental change on beneficial insects and thus service delivery (e.g. pressures such as climate or land use change or benefits of proposed management and conservation actions). Many of these knowledge gaps are symptomatic of wider knowledge shortfalls in ecology as identified by Hortal et al. (2015), reflecting deficiencies in ecological data, understanding and theory, or mismatches between the spatial and temporal scales at which we can undertake experimental analyses and those at which service delivery occurs, management practices are implemented and policies are formulated (Hortal et al. 2015).

1.3 Data integration and spatial modelling

Some of these knowledge gaps can only be fully addressed with additional data at spatial, temporal or taxonomic resolutions which are as yet unavailable. Whilst there are ongoing advances in novel approaches to obtaining these data, such as large-scale analysis of organismal or environmental DNA (Kress et al. 2015) and/or automated analysis from sensor networks (Zaks and Kucharik 2011, Bush et al. 2017), there is also a key role for maximising the value of existing data. Indeed, we may be unable to target new data collection campaigns effectively and fully realise their value if we have not first understood the patterns in our current datasets and the issues which constrain our interpretation of them. There are a wide range of existing datasets which can be used to contribute to our knowledge on insect-delivered ecosystem services, if combined and analysed in novel ways. These datasets include data from citizen science programmes (Powney and Isaac 2015), earth observation platforms such as satellites (Rocchini et al. 2016, Pettorelli et al. 2018), large-scale surveys, precision agricultural data (Zhang et al. 2002, Gebbers and Adamchuk 2010, Field et al. 2016, Lindblom et al. 2017) and the collation of stakeholder knowledge and opinion (Raum 2018). Such datasets frequently have the advantage of having large spatial and temporal coverages which are virtually impossible to duplicate via traditional ecological survey methods and are thus invaluable for exploring patterns over time and space. Many of the traditional challenges of integrating datasets which may have originally been collected for quite different purposes (e.g. volume of data, processing time and differing formats) are now surmountable given advances in information technology and the development of a plethora of statistical and analytical methods and software. These ‘big data’ approaches (Hampton et al. 2013, Soranno and

Schimel 2014) are potentially particularly valuable in exploring insect delivered ecosystem services, as agricultural policy and practice are formulated and implemented over a range of spatial scales, from individual fields to farms, farmland landscapes and national patterns (Bullock et al. 2017). Agricultural systems are also highly variable and dynamic over space and time (exemplified in the wide range of variation in crop rotation, timing and type of agricultural management and landscape context found within a single, small country such as the UK). This has led to many experimental findings at a field- or farm-scale being non-representative of national-scale impacts or not transferable between contexts (e.g. Tscharntke et al. 2016). By encompassing larger spatial and temporal extents, ‘big data’ approaches have a greater capacity to generate transferable and robust results or to at least to explore how patterns vary over space and time and thus quantify the uncertainty associated with making predictions on ecosystem components and processes underpinning service delivery. Of course, there is an inherent trade-off in such approaches between the generality of their findings (e.g. spatial and temporal extent of analyses) and the uncertainty associated with them (e.g. ability to predict ecological processes and mechanisms at a given location) (Hortal et al. 2015). However, they have a valuable role alongside experimental data in contributing to the evidence syntheses underpinning policy and management decisions (Shackelford et al. 2019) and our ability to design sustainable agricultural landscapes (Landis 2017).

1.4 Thesis aims and outline

The work described in this thesis has the overarching objective of exploring spatial and temporal patterns of insect-delivered ecosystem services and their relationships with landscape structure. The approach is to use existing spatial datasets from a wide range of sources and combine these through novel analyses. I use the island of Great Britain (GB, i.e. the UK excluding Northern Ireland) as an example system, partly because of the wealth of spatial datasets on GB land cover, land use and biodiversity but also because it is a useful case study in several ways: 1) GB has a broad range of agricultural practices and landscapes. It thus forms a good test case for seeking to explore how such variation affects insect-delivered ecosystem services; 2) Most of GB is (and has long been) under some form of agricultural management, be that the intensive arable farming of lowland England or the grazing of semi-natural grasslands in the uplands of Wales; 3) GB is known to have undergone (and is probably still undergoing) declines in insect populations, with subsequent concerns over the sustainability of ecosystem service delivery (Ollerton et al. 2014, Oliver et al. 2015b, Powney et al. 2019); 4) GB is at a pivotal time for agriculture and its environmental impacts, with ongoing reforms of agricultural policy which explicitly acknowledge the role of natural capital (Defra

2018a). I here outline the structure of the subsequent chapters, with one review and three analytical chapters, each focussing on a particular knowledge gap where combining existing spatial datasets had the potential to shed light on aspects of insect-delivered ecosystem services.

Chapter 2 reviews some of the complexities surrounding the concept of 'resilience' in the context of insect-delivered ecosystem services and their relationships with agricultural production. Throughout much recent literature there is a particular emphasis placed on the role of ecosystem services in ensuring the resilience of agriculture (GFS 2015, Bullock et al. 2017), and a similar emphasis placed on the role of biodiversity (i.e. abundant, speciose or taxonomically or functionally diverse insect communities) in maintaining resilient ecosystem services (Oliver et al. 2015a, Oliver et al. 2015b). This chapter explores the use of resilience as a term in research and policy, and the considerable debate over its definition, usefulness, and quantifiability. I conclude with a working definition and potential ways in which to quantify resilience, which are then used in the subsequent analytical chapters.

Chapter 3 explores the extent to which spatial and temporal variation in crop yields are mediated by the distribution of beneficial insects and the habitats which support them (Potts et al. 2016, Woodcock et al. 2016a). Whilst beneficial insect populations and communities have been demonstrated to show relationships with landscape composition and configuration (Chaplin-Kramer et al. 2011, Blitzer et al. 2012, Potts et al. 2016, Woodcock et al. 2016a), the links between landscape and actual service delivery and the resultant changes in crop yield are harder to observe. Where this has been achieved, results have been more variable (Holland et al. 2016, Holland et al. 2017, Karp et al. 2018) and tend to focus on overall yield rather than exploring temporal variability (Martin et al. 2016, Martin et al. 2019). I used a ten-year time series of spatially-explicit data from a national survey of crop yields in England (Defra 2012), in combination with information on landscape composition and configuration derived from remotely sensed habitat maps, to explore the influence that the landscape has on crop yield resilience (as determined by three metrics) at larger spatial scales (10 km × 10km, i.e. 'hectad', resolution). The results showed that the influence of landscape context varies based on the precise metric of resilience chosen, with a general trend of increasing importance of semi-natural habitat (generally associated with increased abundance and richness of beneficial insects) and decreasing importance of arable land as resilience metrics were derived from shorter portions of the time series.

Chapter 4 explores national scale patterns in the structure and stability of plant-pollinator networks under potential environmental change (Gill et al. 2016). Whilst analysis of plant–pollinator networks has provided many valuable insights into how the ecosystem service of pollination is mediated by the structure of the plant and pollinator communities and their interactions, studies traditionally rely on obtaining well-characterised networks from field surveys, which are time consuming and costly to construct (Vázquez et al. 2009, Burkle and Alarcón 2011). There is thus a lack of information on ecological interactions across larger spatial, temporal and taxonomic scales (Hortal et al. 2015). I used citizen science data to construct a plant-pollinator interactions database and modelled plant and pollinator communities at hectad scale across GB. This enabled the construction of a potential plant–pollinator network for each hectad, followed by calculation of a series of metrics of network structure and robustness to simulated plant extinctions. The results showed positive relationships between agricultural land cover and both pollinator generality and robustness to extinctions under several extinction scenarios. The results also showed that crop-pollinator networks are significantly more robust to simulated extinction scenarios than overall networks, supporting the contention of Kleijn et al. (2015) that strategies and initiatives based entirely on maintaining ecosystem services to crops may provide insufficient protection for wild pollinator communities overall.

Chapter 5 looks to the future, exploring the responses of beneficial insect communities to past, current and predicted future changes in land use (Vanbergen et al. 2013, Gill et al. 2016, Potts et al. 2016). I used citizen science data to build predictive species distribution models for a wide range of pollinator and natural enemy species, based on current spatial patterns in land cover, cropping patterns and climate data. I then constructed a series of spatially explicit future scenarios of change in land cover type and land use intensity, which could be applied separately or in combination, and explored their impacts on beneficial insect species richness and functional diversity. The results showed a wide range of possible consequences for beneficial insect species richness and functional diversity in the context of GB land use change. The results have a bearing on current conservation policy targets – for example, the models predicted that current policies aimed at restoring semi-natural grassland would increase richness and functional diversity of both pollinators and natural enemies, even if agricultural practices remain intensive on cropped land, whilst any expansion of arable land is likely to be accompanied by further declines in richness and functional diversity of beneficial insects, even if cropping practices become less intensive.

Chapter 6 discusses the implications of the results of the preceding three chapters for the management of landscapes for beneficial insects and insect-delivered ecosystem services, in the context of GB agricultural and conservation policy. I also outline some of the key benefits and remaining challenges of the approach to integrating spatial datasets taken by this thesis.

Figure 1.1 *Two beneficial insects which deliver ecosystem services in GB agricultural landscapes. On the left, a solitary bee (*Andrena flavipes*) pollinates a pear tree. On the right, a ladybird (*Adalia decempunctata*) hunts for aphids. Images credit J. Redhead.*

Chapter 2: A review of resilience concepts and metrics in agriculture and ecosystem services

When considering management or protection of ecosystem services in agricultural systems, the term ‘resilience’ is often encountered. This can be applied to the ecological systems of which beneficial insects form an integral part, the ecosystem services they provide or the agricultural system which these services benefit. Because the concept of resilience has evolved over several decades of ecological research, and remains the subject of controversy, it warrants further exploration to come to a working definition and some key metrics of resilience for use in for subsequent chapters.

2.1. Origins of resilience in ecology

Resilience outside of scientific usage describes the ability to recover quickly or easily from, or resist being affected by, a misfortune or shock (OED Online 2017). Within scientific parlance, resilience has long been in use in materials science to describe the energy required to deform a material to its elastic limit (e.g. Rankine 1876). In the early part of the 20th century, the term was used in psychology to describe the capacity for individuals to experience a positive outcome despite undergoing a negative experience, the most frequently researched example being childhood traumas (Rutter 1999, Tugade and Fredrickson 2004, Campbell-Sills et al. 2006). In this context, resilience is not a single character trait, but rather an emergent property recognisable by its outcome (Rutter 1999). The source of what is now termed the classical definition of ecological resilience is usually attributed to a seminal paper by Holling (1973), in response to varying outcomes from mathematical models exploring the link between biological diversity and stability (MacArthur 1955, Elton 1958, Lewontin 1969, May 1971). Holling recognized that ecosystems were complex, dynamic systems which could not be assumed to be in equilibrium. Therefore, definitions of stability pertaining to fluctuation around, or return to, an equilibrium state would be insufficient to adequately describe ecological systems. Instead, ‘engineering resilience’, which focuses on spatially or temporally localised stability, should be contrasted with ‘ecological resilience’, which encompasses the persistence of an ecological system over time and its ability to absorb change and disturbance and still maintain relationships between system variables – such as the populations of species, ecological processes or ecosystem functions (Holling 1973, Holling 1996). As in psychological definitions, ecological resilience was seen as an emergent property of a system, arising via multiple potential mechanisms and identifiable by its result in terms of persistence of an ecological system. Because systems can be highly stable (show little fluctuation) but nonresilient (have poor prospects for long-term persistence), the traditional focus of ecosystem management on stability (e.g. consistent populations or yields) risked undermining resilience and the potential for sudden and unpredictable collapse. Such collapses could be caused by the system shifting from one ‘alternative stable state’ to another (Lewontin 1969). Examples are a lake shifting from a clear- to a turbid-water state because of long-term changes in nutrient balances, or of a savannah from a grass- to a shrub-dominated community as a result of overgrazing. In both cases, the actual trigger for change lies within the range of environmental stochasticity usually experienced by the system, but the sensitivity of the system to the disturbance and/or its ability to resist, recover or reconfigure itself (collectively, its resilience) has been gradually eroded, resulting in a change in state. Once a system has shifted state, resilience of the new state may make restoration extremely difficult (Troell et al. 2005). These alternative stable states were originally illustrated with the system as a ball lying on a topographically varied surface, the ‘landscape’ of which represents the varying resilience of the system (Fig. 2.1), with ‘basins’ or ‘domains’ of attraction indicating the different states the system can occupy (Lewontin 1969). Although conceptually useful, this masks several important aspects of resilience including the potential for very different mechanisms governing the dimensions of the basins of attraction and the potential for systems to take different paths between change and recovery (‘hysteresis’) (Beisner et al. 2003, Standish et al. 2014).

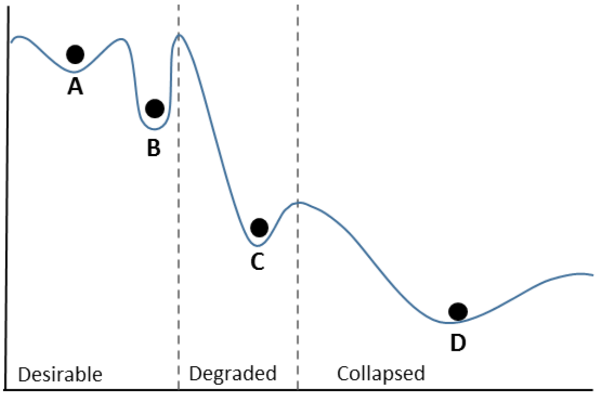

Figure 2.1. *Schematic visualising resilience as a topographic landscape, adapted from Standish et al. (2014). The x-axis represents variation in state space (divided by vertical dashed lines into desirable, degraded and collapsed based on ecosystem function). The black ball represents a system, whilst the blue line represents the resilience ‘landscape’, with each ‘basin’ being a state the system can occupy: A) a functionally desirable state which is relatively unstable but with high resilience; B) an alternative state with similar function but higher stability and lower resilience; C) has intermediate stability and resilience but reduced function; D) collapse to a state with low function, low stability and high (unhelpful) resilience.*

Over the next three decades, the concept of ecological resilience gradually grew in prominence (Gunderson and Allen 2010), following a variety of paths (Curtin and Parker 2014). Initially, many studies focussed on identifying ecological systems demonstrating alternative stable states (see reviews in Beisner et al. (2003); Carpenter et al. (2003); Folke et al. (2004); Schröder et al. (2005) and collected examples in Gunderson et al. (2010)). Other foci included the mechanisms underpinning resilience, including the importance of cross-scale interactions (Peterson et al. 1998, Sendzimir et al. 2002), extending the original concepts into heuristic models of ecological systems (Holling 1986, 2001, Gunderson and Holling 2002, Walker et al. 2006) and developing management and policy approaches based on ecological resilience concepts (e.g. Walters and Hilborn 1978).

As a result of these different streams of research and the complexities around defining and quantifying ecological resilience in different situations, by the end of the 20th century, ecological resilience was in a contentious position. Grimm and Wissel (1997) found multiple definitions of ecological resilience in the literature, including many uses of the engineering definition (e.g. Pimm 1984). Such findings stimulated ongoing debate over how to define resilience, from a property that should be quantified by standardised measures to a useful metaphor without a precise definition (Carpenter et al. 2001, Brand and Jax 2007, Standish et al. 2014, Newton 2016). Although the prevalence of resilience concepts in ecological research has continued to grow over the first decades of the 21st century (Myers-Smith et al. 2012, Ingrisch and Bahn 2018, Kéfi et al. 2019), a lack of widely accepted consensus remains. Many papers have used the term without definition or interpreted their results in a way inconsistent with their chosen definition (Myers-Smith et al. 2012). As a result, whilst the general concept of ecological resilience has been widely accepted, its usefulness in practice has remained contentious, especially in terms of its transition into policy (Klein et al. 2003, Brand and Jax 2007, Béné et al. 2012, Standish et al. 2014, Donohue et al. 2016, Newton 2016).

2.2. Resilience in agricultural and ecological policy

In a world which we know to be undergoing severe environmental changes it should be more efficient and less risky to build or preserve resilience in ecological systems rather than having to undo detrimental changes once they have occurred. Oliver et al. (2015a) simplify this by analogy into monitoring whether a bridge is still standing, as opposed to monitoring key parameters indicating its stability and making repairs. Of course, a bridge is an artificial structure for which we know exactly what parameters to monitor, how to repair damage if we find it and what the risks are of not doing so. None of these are necessarily true in ecological systems. Nevertheless, such compelling analogies are easily grasped and probably one of the reasons that the concept of building resilience has been integrated into a wide range of national and international policies in ecological and socioecological fields (Thompson et al. 2009, Defra 2011, European Commision 2012, IPCC 2014, CBD 2017). A further reason is the generally positive and pro-active vocabulary surrounding resilience (Sudmeier-Rieux 2014, Béné et al. 2016, Newton 2016). Agriculture in particular has seen a widespread uptake of resilience as a key goal of policy and research (Bennett et al. 2014, Reddy 2015, Tendall et al. 2015, Wilson and Lovell 2016, Bullock et al. 2017). Agricultural production is easily visualised as being underpinned by complex processes which regulate its vulnerability to environmental perturbation, since it involves the management of living organisms in open systems and because the effects of environmental perturbations such as floods, droughts, pests and diseases have an immediate and easily seen impact on food production and farmer’s livelihoods. In an agricultural context, resilience is often paired with sustainability (e.g. Brand 2009, Wilson and Lovell 2016) although there some overlap between the terms and, indeed, it is difficult to conceptualise a sustainable system that is not resilient or *vice versa*. Agriculture has also, especially in recent years, seen a focussing of resilience concepts around the concept of sustainable intensification, with an emphasis that enhancing biodiversity will enhance functional diversity and redundancy which in turn decreases the likelihood of a given ecosystem service suffering declines under environmental perturbation (Oliver et al. 2015a, Oliver et al. 2015b, Kleijn et al. 2019). Whether this is necessarily the case is the subject of much debate and ongoing research.

The widespread transition of resilience from ecological to policy contexts is not without potential pitfalls (Klein et al. 2003, Brand and Jax 2007, Brand 2009, Béné et al. 2012, Béné et al. 2016, Newton 2016). Although the term has a vernacular meaning and is readily explained by analogy, its precise definition in ecological terms remains contentious (Myers-Smith et al. 2012, Donohue et al. 2016). A general commitment to resilience-building, but without any means by which this can be measured over the large spatial and short temporal scales within which policies tend to be framed (Béné et al. 2016) is likely to be, at best, a waste of time. At worst, it may lead to the neglect of components of the system the policy is supposed to protect (Standish et al. 2014). Examples include the potential for failure of overly resilience-oriented management to address the mechanisms of biodiversity loss (Newton 2016) or poverty (Béné et al. 2012) because the view of resilience around which the policy is built neglects these specific components of the system. A further issue is that policies seldom acknowledge that resilience is not necessarily positive. This is understandable, as the vernacular and psychological usages of the term focus on positive outcomes under challenging circumstances. However, the potential for systems (both ecological and socioeconomic) to become entrenched in undesirable states despite efforts to change them (Holling 2001, Walker et al. 2006) is widely recognised (Béné et al. 2012, Béné et al. 2016, Redhead et al. 2018a). For example, the current reliance of intensive agriculture on prophylactic use of synthetic pesticides simultaneously damages resilience of the agricultural system as a whole (via detrimental impacts on beneficial insects and creating resistant pests), masks declines in resilience of crop production (by insulating it from environmental factors) and, as a farming paradigm, is proving highly resilient to change despite mounting evidence of its long-term unsustainability (Wilson and Tisdell 2001).

2.3. Functional resilience and the resilience of ecosystem services

The context of ecosystem services may help to simplify some of the complexities around defining and quantifying resilience in agricultural systems. The integration of the concepts of ecosystem services and of ecological resilience has a long history. Holling (1973) cited examples of timber and fisheries management, which would now be classed as ecosystem services, noting that the most resilient systems were not necessarily the most biodiverse nor those with highest levels of service delivery, whilst Peterson et al. (1998) stated the importance of resilience to "the services that support humanity and other life".

To be meaningful, it is important that any assessment of resilience states the "resilience *of* what, *to* what" (Carpenter et al. 2001, Cumming et al. 2005, Hodgson et al. 2015, Quinlan et al. 2016). In practice, this means defining the system state under examination, the disturbances to which resilience is being assessed and the temporal and spatial scales over which this is being performed. However, deciding which variables define the system state and drive its resilience remains challenging. Many drivers of resilience are likely to be 'slow' variables (Carpenter et al. 2001), where changes occur over long timescales and are difficult to detect. By the time the importance of such variables has been recognised, resilience may have been undermined to a degree that state change is inevitable (Carpenter et al. 2001). In many ecological systems, the only way to identify a threshold may be to cross it (Carpenter et al. 2003). Because of these issues, Cumming et al. (2005) suggested a change of emphasis from system structures, processes and states to system *identity*. This could then be based on a relatively few key variables describing the system state, be they related to species, communities or ecological processes. Crucially, as resilience concepts have developed, ecosystem functions have become recognized as an aspect by which to define the identity of system for which resilience is being assessed. Ecosystem functions can often be directly linked to ecosystem services. This is very much the case for insect-delivered ecosystem services, as pollinating and pest-controlling insects are readily identifiable as key functional groups involved in delivering them. In many cases, the ecosystem functions which determine system identify can be selected on the basis of an overarching goal of maintaining ecosystem service delivery. For example, the identity of resilient systems in the context of food security is determined by multiple ecological functions including pollination, pest-control and soil health (Béné et al. 2016, Bullock et al. 2017). These operate over a wide range of spatial scales and levels of ecological organisation (Bullock et al. 2017, Kéfi et al. 2019), from fields, to farms, landscapes, regions, nations and the global food system as a whole. Whether resilience is helpful or unhelpful and the practices we might use to promote resilience where desirable become much easier to define when focussing on a single scale and set of functions. This also helps us to be explicit about which ecosystem parameters are of interest (Cumming et al. 2005) and aids in selecting likely indicators or surrogates of resilience. For example, we can use experimental evidence to infer relationships between the abundance, richness, diversity or traits of known functional groups and particular aspects of resilience of function (Folke et al. 2004, Fischer et al. 2006, Van Ruijven and Berendse 2010, Allan et al. 2011, Gallagher et al. 2013, Mouillot et al. 2013, Isbell et al. 2015, Oliver et al. 2015b). Field experiments have revealed losses of functional diversity in degraded systems (Standish et al. 2014) or systems undergoing biodiversity declines in response to anthropogenic drivers (Oliver et al. 2015b), supporting the suggestion that functional surrogates are responsive to the kind of disturbances we wish to understand. Because the delivery of many ecosystem functions depends on mutualistic or trophic interactions (e.g. pollination, consumption of pests), there is also scope to investigate the properties of ecological networks as indicators of functional resilience. Ecological network approaches offer a powerful way to move beyond considering species in isolation and bring the opportunity to examine aspects of resilience by simulating disturbances to networks and examining the impacts on network structure (Memmott et al. 2004, Memmott et al. 2007, Kaiser-Bunbury et al. 2017, Vanbergen et al. 2017).

2.4. Quantifying resilience

Early work on resilience recognised that it was likely to be a quality which was extremely difficult to measure (Holling 1973). Being an emergent property, it has multiple aspects compounded of the absorptive (resistance), adaptive (recovery) and transformative (reorganisation) capacities of the system (Béné et al. 2016). One approach is to identify ‘indicators’ (Carpenter et al. 2001) or ‘surrogates’ (Carpenter et al. 2005, Cumming et al. 2005) of resilience. These can be known drivers towards a more or less resilient state (e.g. slow variables) or likely correlates with aspects of resilience inferred from ecological theory

(McClanahan et al. 2012, Oliver et al. 2015a). However, in practical terms there is still potential for confusion over exactly which aspect of resilience any one surrogate is measuring and thus where to target efforts at management or conservation. Where resources are limited or trade-offs occur, the need to prioritise different aspects of resilience (Hodgson et al. 2015) is also problematic. For example, Côté and Darling (2010) argued for a focus on resistance in coral reef systems, suggesting there is “no role for recovery”, whilst Graham et al. (2015) showed that reef recovery can and does occur.

Some authors have proposed a unifying framework by which resilience is measured via standardised measurements of resistance, quantifiable as the amount of change a system can experience before changing state, and recovery, quantifiable as the time it takes the system to return to a pre-disturbance state (Klein et al. 2003, McClanahan et al. 2012, Hodgson et al. 2015, Ingrisch and Bahn 2018). However, in practice there is a complex interplay between resistance and recovery, with sufficiently rapid recovery (Oliver et al. 2015a) or reorganisation (Folke 2006) appearing as resistance. The suggested methods of quantification also assume a stable state against which to measure change or return time. It therefore becomes much harder (if not impossible) to assess resilience to long-term disturbances (Pimm 1984, Myers-Smith et al. 2012), which are of especial concern in many systems (e.g. climate change). Where we have knowledge of desirable or historic levels of ecosystem function these can act as thresholds by which to measure resistance and recovery, or the degree to which change is moving the system from a desirable to an undesirable state. Measuring resilience (or lack thereof) in terms of surpluses and deficits of an ecological function (see Fig. 2.2) is then feasible (Oliver et al. 2015a, Bullock et al. 2017).

However, without a clear understanding of the mechanisms behind resilience measured in this way, whilst we can compare relative resilience between systems (Fig. 2.2), we cannot infer much about the resilience of any one system in isolation or resilience to types and levels of disturbances other than those the systems have already experienced. It therefore remains important to define the boundaries of the system under consideration (“resilience *of*...”) and the perturbation to which resilience is being assessed (“resilience *to*...”) (Carpenter et al. 2001, Cumming et al. 2005). Several studies assessing resilience by functional proxies do not clearly define either of these, by assuming that large-scale trends in functional groups are indicative of changes in general resilience to a wide variety of potential perturbations (Gallagher et al. 2013, Oliver et al. 2015b). This assumption may or may not be true, but it limits the usefulness of the findings in terms of predicting impacts under specific changes or developing and targeting management or policy mitigation actions.

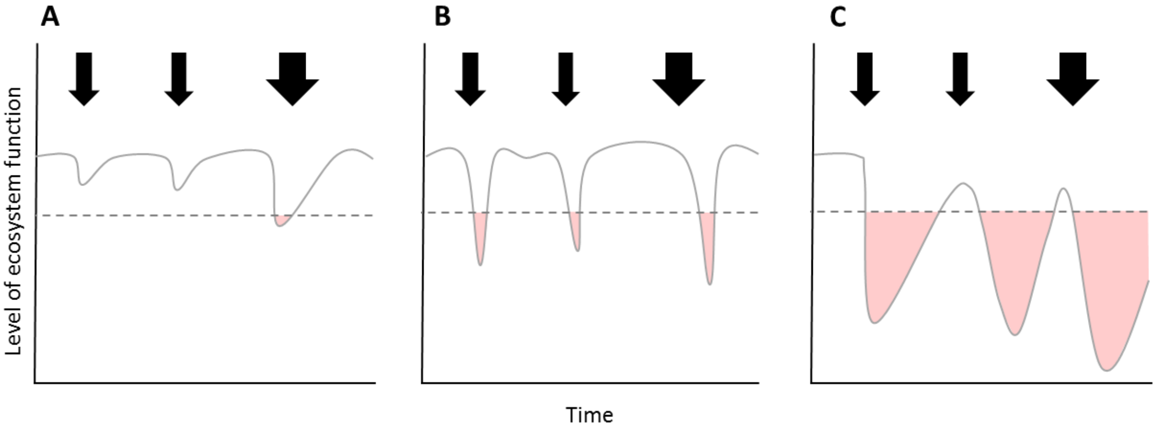

Figure 2.2. *Schematic of identifying varying levels of resilience from changes in ecosystem function, adapted from Oliver et al. (2015a). Black arrows indicate environmental perturbations. Horizontal dashed line indicates a threshold level of function identified by human values. Portions of the curves below this line (pink shading) thus indicate a deficit of function. The three panels represent three different systems: A) shows relatively high resistance and rapid recovery; B) shows lower resistance but more rapid recovery; C) shows low resistance and slow recovery and can be inferred to be the least resilient.*

2.5. Towards a working definition of resilience

Given all of the complexities outlined above, the most all-encompassing definition of resilience in the context of ecosystem services would appear to remain closely akin to the one given by Holling (1973), along the lines of “the capacity of system to persist in the face of environmental perturbation, encompassing its ability to resist, recover from and adapt to change”. This definition can be applied at the multiple spatial scales and levels of ecological organisation involved in the agricultural system (Bullock et al. 2017) and can be equally applied to ecosystem functions, ecosystems services, farm systems, agro-ecosystems and the global food system as a whole. As Bullock et al. (2017) suggest, resilience is not necessarily required or desirable at all scales or in all contexts. Therefore, when analysing resilience in agricultural systems it is important that the study system and its boundaries should be clearly defined (“resilience *of*...” and “resilience *to*...”). It is acceptable to state this in very general terms (e.g. “Climate resilient agriculture for ensuring food security” (Reddy 2015)) if the aim is provide an overarching framework, but caution should then be used in speculating about what actually comprises a resilient system. In contrast, if the system is very specifically defined (e.g. Bronstein and Hossaert-McKey 1995, Gerisch et al. 2012, Lukac et al. 2012) then we should be equally cautious in making inferences about the implications of resilience in single system component for resilience at larger spatial scales or the system as a whole.

If attempting to measure resilience from levels of a function, several metrics of resilience should, ideally, be analysed in conjunction (Walker et al. 2006, Standish et al. 2014, Kéfi et al. 2019), spread across the system’s capacity for resistance, recovery and reorganisation (Béné et al. 2016). Studies analysing multiple indicators of the resilience of ecosystem functions or services are rare at present and often focus on simple metrics relating to stability or resistance (Kéfi et al. 2019). However, analysing multiple aspects offers the greatest potential for insight into the multidimensional nature of resilience (Donohue et al. 2016) and thus how it might best be maintained in agricultural systems. The ability to demonstrate direct effects of management practices which increase or maintain biodiversity on the resilience of key agricultural output parameters (such as crop yield, quality, or farm profitability) is also one of the most important drivers in encouraging the uptake of sustainable intensification (Kleijn et al. 2019) and overcoming the undesirable resilience of the current intensive agricultural paradigm to the increasing evidence of its damaging effects and long-term unsustainability.

Chapter 3: The influence of landscape composition and configuration on crop yield resilience[1]

3.1. Abstract

Sustainable agriculture aims to produce sufficient food whilst minimising environmental damage. To achieve this, we need to understand the role of agricultural landscapes in providing diverse ecosystem services and how these affect crop production and resilience, i.e. maintaining yields despite environmental perturbation.

I used ten years of English wheat yield data to derive three metrics of resilience (relative yield across the time series, yield stability around a moving average and resistance to an extreme weather event) at 10km × 10km scale. I used remotely-sensed maps to calculate measures of landscape structure, including composition (proportions of different land cover types) and configuration (metrics of connectivity and proximity), known to affect ecosystem service delivery (e.g. control of pests by beneficial invertebrates). I then used an information-theoretic approach to identify the best-fitting combination of landscape structure predictors for each resilience metric, using a potential yield model to account for the effects of climate and soils.

Relative yield showed a strongly positive relationship with area of arable land. For yield stability, this relationship was evident but alongside other landscape structure variables in the best-fitting model. No relationship with arable land was evident for resistance. Yield stability showed a strongly positive effect of proximity to semi-natural habitats. For resistance, the best-fitting model included positive relationships with the cover of semi-natural habitats and proximity to semi-natural grasslands.

Our results showed a general trend of increasing importance of semi-natural habitat and decreasing importance of arable land as resilience metrics were derived from shorter portions of the time series. This likely to be driven by the complex interplay between landscape structure, agricultural management, and ecosystem services. The results demonstrate that measurements of relative levels of yield over time may be insufficient to capture the full effect that non-arable components of the landscape, and the ecosystem services they deliver, has on stability or resistance to extreme events. This suggests that there are trade-offs in the management of arable landscapes to maintain resilience over shorter vs. longer timescales.

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3.2. Introduction

Global food systems are under pressure to produce sufficient food for a growing human population (Godfray et al. 2010). Agriculture has long aimed to address this challenge by maximising crop yields (Curtis and Halford 2014, Mitchell and Sheehy 2018). However, intensive approaches to achieving this have driven severe declines in biodiversity (Green et al. 2005, Reidsma et al. 2006, Butler et al. 2007) and other adverse environmental impacts (Tilman et al. 2002, Tsiafouli et al. 2015).

Sustainable intensification aims to increase agricultural productivity, whilst also maintaining or bolstering biodiversity (Bommarco et al. 2013, Garnett et al. 2013, Kleijn et al. 2019). This approach has been driven in part by increasing awareness that biodiversity provides vital ecosystem services which maintain the viability of agricultural systems (Bommarco et al. 2013), including crop pollination and natural pest control (Naylor and Ehrlich 1997, Kremen and Chaplin-Kramer 2007). If sustainable intensification is to succeed, we need detailed knowledge on how to manage agricultural landscapes to ensure optimal, long-term provision of these services (Gagic et al. 2017, Kleijn et al. 2019). Landscape structure has been repeatedly identified as a key driver of ecosystem service delivery. I here define landscape structure as being comprised of composition (i.e. number and proportions of different land cover types) and configuration (i.e. spatial arrangement of those land cover types), after (Fahrig et al. 2011). Whilst many studies have demonstrated relationships between landscape structure and service indicators such as beneficial invertebrate communities or crop pest populations (Bianchi et al. 2006, Chaplin-Kramer et al. 2011, Rusch et al. 2013, Haan et al. 2019), few have directly examined effects on crop yield (Holland et al. 2016, Holland et al. 2017, Karp et al. 2018). Those that do (e.g. Martin et al. 2016, Martin et al. 2019) mostly focus on average yields over time.

However, average yields are not necessarily indicative of long-term sustainability or ‘resilience’. Holling (1973) defined ecological resilience as a “measure of the persistence of systems and of their ability to absorb change and disturbance”. The guiding principle is therefore to consider not just the absolute quantity of a single function (e.g. crop yield) but also its ability to persist over time by resisting, recovering from and adapting to perturbations (Oliver et al. 2015a). In the case of crop yield, such perturbations include extreme weather events, pest outbreaks or diseases. These can have substantial impacts on livelihoods even if average yields are high (GFS 2015). Resilience is underpinned by complex interactions between environmental factors (e.g. climate, soil health, communities of beneficial organisms) so the landscapes which deliver high average yields under normal conditions are not necessarily those which are most stable or most resistant to extreme events. The need to identify and develop resilient cropping systems has been embraced in research (Altieri et al. 2015, Bullock et al. 2017) and policy (Defra 2018a), but the question of how landscapes and the ecosystem services they deliver affect the resilience of agricultural systems remains a key knowledge gap preventing the widespread uptake of sustainable intensification (Kleijn et al. 2019).

In this paper I explore relationships between landscape structure and crop yield resilience. I used a ten-year time series of wheat yields from a national survey of English farms to derive metrics relating to different aspects of resilience. I analysed relationships between these metrics and aspects of landscape structure known to affect provision of biodiversity-mediated ecosystem services. I hypothesised that:

a) Area of arable land would have a positive effect on resilience, as it is indicative of the intensity of, and investment in, agricultural management
b) Semi-natural habitats would also have a positive effect on resilience as they act as reservoirs of beneficial organisms providing ecosystem services
c) Metrics relating to different aspects of resilience would differ in the strength of these relationships and the relative importance of landscape composition and configuration

3.3. Methods

YIELD DATA FROM A NATIONAL SURVEY

Wheat yield data were obtained from Defra's cereals and oilseeds production survey, part of an annual survey of the English agricultural industry based on a stratified random sample of farms. Survey methods can be found in Defra (2018b). Data were available for 10 years (2008-2017), comprising average winter wheat yield per farm and coordinates locating each to 1km. Data were cleaned to remove anomalous yield values, giving around 22,000 individual samples (Appendix A1).

Because a new random sample of farms is drawn each year, few had consecutive data across 10 years. To analyse yield variation over time and account for local spatial variation in farming practices I therefore aggregated data to mean annual yield per 10km x 10km grid cell ('hectad'). From this dataset, hectads were identified with sufficient samples per year for analyses of resilience (Appendix A1). I ensured that the selection of well-sampled hectads did not bias the dataset towards particular landscape structures (Appendix A, Fig. A2). From 315 hectads with at least one sample per year, 137 met the criteria for sufficient sampling. All data handling and analysis was performed in R (v3.4, R Core Team 2017).

CONSTRUCTING METRICS OF RESILIENCE

I here use a broad definition of crop yield resilience as “any quantification of the agricultural system’s ability to maintain consistent delivery of yields despite environmental perturbation”. There are many potential ways of quantifying resilience from temporal and spatial variability in yield. Some studies have begun to explore links between environmental drivers and aspects of yield resilience (Di Falco and Chavas 2008, Gaudin et al. 2015, Iizumi and Ramankutty 2016, Knapp and van der Heijden 2018) but these often use only a single metric. However, resilience is conceptually complex (Donohue et al. 2016, Ingrisch and Bahn 2018, Kéfi et al. 2019), with multiple facets derived from the capacity of a system to resist, recover from and adapt to environmental change (Béné et al. 2016, Ingrisch and Bahn 2018), so metrics vary in which aspects of resilience are examined and the timescales over which these are measured. Single metrics may therefore be insufficient to fully understand the effects of landscape structure (Isbell et al. 2015). For every hectad with sufficient data, I calculated three metrics capturing different aspects of resilience:

i. **Relative yield across the time series**. Average difference between annual and national average annual yield (Fig. 3.1A). This combines average magnitude and variability over the time series, accounting for surpluses (when yield exceeds the national average) and deficits (*vice versa*), in line with the functional resilience metric proposed by Oliver et al. (2015a).

ii. **Yield stability around a moving average**. Inverse of absolute percentage difference between yield in any one year and average yield over the years either side (Fig. 3.1B), averaged across the time series (Iizumi and Ramankutty 2016). This metric is sensitive to fluctuation of yield over shorter timescales and incorporates aspects of resistance and recovery.

iii. **Resistance to a specific event**. Inverse proportional change in yield between 2012 and the pre-2012 mean (Fig. 3.1C). Exceptionally heavy spring and summer rainfall in 2012 caused poor wheat yields (Defra 2012, Impey 2012), with a mean 14% decrease compared to previous years (from survey data).

All metrics were calculated such that larger values imply greater resilience (i.e. use of inverse values). I explored intercorrelations between metrics and correlations with mean yield, i.e. average yield per hectad across all years in the time series (Appendix A2). Although conceptually a measure of resilience (i.e. ability to deliver yields exceeding the national average despite environmental fluctuations) the metric of relative yield was in practice strongly correlated with mean yield (Appendix A2).

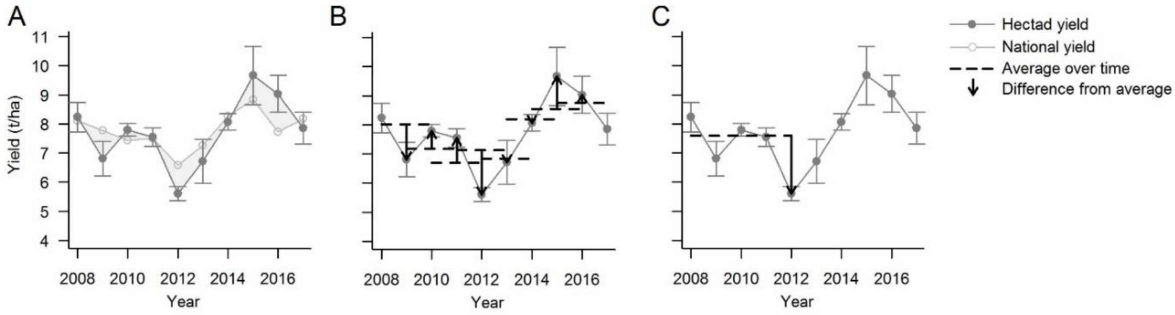

Figure 3.1. *Schematic showing derivation of metrics of resilience from an example time series.* ***.*** *A) Relative yield, the average difference between hectad and national average yields across the time series. B) Yield stability, the difference between any one year and the average over the two years on either side. C) Resistance, the proportional decrease in 2012 from the pre-2012 mean. The inverse of the latter two metrics was taken such that higher values indicate higher resilience in all cases.*

ACCOUNTING FOR CLIMATE AND SOIL EFFECTS

To explore relationships between metrics of yield resilience and landscape structure, I first controlled for the effects of meteorological and soil variables. Because the way in which these interact to influence crop yields is complex, I condensed them into a single metric of potential yield. I modelled potential yield from temperature, precipitation and solar radiation (Agri4Cast data, Biavetti et al. 2014) and soil water holding capacity (Bell et al. 2018), based on approaches in Sylvester-Bradley and Kindred (2014) and Lynch et al. (2017). The model has three main stages: 1) estimation of green area index from accumulated growing degree days, 2) interception of solar radiation and water-limited conversion to biomass, 3) apportioning accumulated biomass to grain yield. For a full description see Appendix A3. For each resilience metric, the equivalent metric for potential yield was included as a covariate in statistical models (see below). I also accounted for any further impacts of regional variation in soils and climate by assigning each hectad to an environmental zone, using a pre-existing classification (Bunce et al. 2007), included as a random effect in statistical models (see below).

LANDSCAPE COMPOSITION AND CONFIGURATION

I used a satellite-derived land cover map (LCM2015, 25m raster, Rowland et al. 2017) to determine the composition and configuration of land cover types per hectad. I analysed three land cover classes: arable land, semi-natural habitats and semi-natural grasslands. Semi-natural habitats included semi-natural grassland, broadleaf woodland, heathland and wetland as these are known to affect ecosystem services relevant to crop production (Tscharntke et al. 2005, Rand et al. 2006, Blitzer et al. 2012, Rusch et al. 2013, Holland et al. 2017, Martin et al.

2019). I also analysed semi-natural grasslands separately as these are structurally more similar to arable land and may be especially important in providing ecosystem services (Duflot et al. 2015, Bengtsson et al. 2019).

For each land cover class, I calculated three largely independent metrics of landscape composition and configuration. These were: percentage area, mean edge:area index and mean distance to the nearest patch. These were drawn from a variety of composition and configuration metrics widely used in assessments of landscape impacts on ecological processes (Cushman et al. 2008, Chaplin-Kramer et al. 2011, Haan et al. 2019, Martin et al. 2019) explored in preliminary analyses (Appendix A4). Mean edge:area index and distance to the nearest patch were transformed to indices of 'connectivity' and 'proximity' (Appendix A4) to aid interpretation of regression coefficients. Structure metrics were calculated in ArcGIS (v10.4, ESRI, CA) and the *landscapemetrics* R package (Hesselbarth et al. 2019).

STATISTICAL ANALYSIS AND MODELLING

All statistical analyses were undertaken in R. I used an information-theoretic approach to identify the best-fitting combination of landscape structure predictors for each resilience metric (i.e. relative yield, yield stability, resistance). For each metric, I first used the *nlme* package (Pinheiro et al. 2017) to construct a global linear mixed effects model containing the random effect of environmental zone and all other explanatory variables as fixed effects (i.e. cover, connectivity and proximity of each of arable, semi-natural habitats and semi-natural grasslands, and potential yield). The model included a spherical spatial autocorrelation structure, which preliminary analyses found to increase model fit, as determined by Akaike's Information Criterion adjusted for small sample sizes (AICc). I then ran all possible subsets of explanatory variables from the global model using the *MuMIn* package (Barton 2016) and ranked models using AICc. Models were constrained to include the random effect and potential yield variable and to exclude pairs of highly intercorrelated predictors (Fig. A5). Where ΔAICc amongst top ranked models was <2, the model with the smallest number of parameters was defined as the 'best' model. I then repeated the ranking procedure with all quadratic terms and pairwise interactions between variables in the 'best' model, defining a new 'best' model if ΔAICc >2. I confirmed the explanatory power of the 'best' model by calculating pseudo-R^2 values and checked for overfitting using a 200-fold cross-validation test, comparing pseudo-R^2 to the distribution from cross validation. Because the 'best' model may exclude potentially important predictors where several models had ΔAICc <2, I calculated model averaged coefficients across all possible subsets (Harrison et al. 2018) to check that these confirmed the 'best' model. I also ran individual models (with autocorrelation and random effects as described above) for each variable in the 'best' model, to explore whether relationships were evident when analysed independently of other predictors.

3.4. Results

The 'best' models for all three resilience metrics contained at least one landscape structure variable and had ΔAICc of >2 from the null model (random factor and autocorrelation structure only) and from models with the potential yield variable only (Table 3.1). Cross-validation of pseudo-R^2 did not suggest significant overfitting for any 'best' model. In all cases, models including interaction terms did not result in ΔAICc >2.

Table 3.1 *Properties of 'best' models as defined by minimum AICc from all possible subsets. The table shows the number of candidate models with ΔAICc <2, ΔAICc from a null model containing random effect and spatial autocorrelation structure only, and ΔAICc from a model including potential resilience only. Also shown are pseudo-R^2 and p-value from cross-validation (values of p <0.05 suggest significant overfitting).*

Resilience metric	N models	ΔAICc from null model	ΔAICc from potential model	pseudo-R^2	Cross validation p- value
Relative Yield	7	-11.790	-8.565	0.182	0.458
Yield Stability	4	-7.199	-5.837	0.155	0.163
Resistance	5	-11.096	-8.899	0.392	0.184

RELATIVE YIELD ACROSS THE TIME SERIES

The 'best' model for this resilience metric included a strong positive effect of arable cover (Table 3.2, Fig. 3.2A). This suggests that the highest relative yields are obtained where a higher proportion of the landscape is farmed. Results from model averaging strongly supported this predominance of arable cover, with a weight of 0.7 (Table 3.3). Other landscape variables generally had low weights, and a mixture of positive and negative coefficients. Relative yield also showed a strong, positive, non-linear relationship with modelled potential yield, suggesting a major influence of climate and soils, up to a point when yield becomes limited by other factors.

YIELD STABILITY AROUND A MOVING AVERAGE

Yield stability showed a positive relationship with cover of arable land and proximity to semi-natural habitats in the 'best'-fitted model (Table 3.2, Fig. 3.2B). This suggests that yields are most stable in landscapes with both a high coverage of arable land and with semi-natural habitats evenly distributed throughout the landscape (e.g. Fig. 3.3B). The effect of proximity to semi-natural habitat was only evident in the ‘best’ model containing the effect of arable land, not in individual models (Table 3.2). The relationship with potential yield stability was weaker than that between relative yield and potential yield, suggesting that areas with more variable climate did not necessarily experience the most variable yield, and that landscape factors potentially have a greater moderating effect. Results from model averaging (Table 3.3) were again supportive of those from the ‘best’ model, although semi-natural habitat connectivity showed a moderate weight (0.56).

Table 3.2 *Coefficients (±1 S.E.) of landscape structure variables in the ‘best’ (defined by minimum AICc) mixed models for each yield resilience metric. Models were constrained to include potential yield (to account for weather and soil effects). Coefficients are given as unstandardized and standardised for comparison, alongside unstandardized coefficients from individual models including only a single predictor. SNH =all semi-natural habitats, SNG =semi-natural grassland. P-values are calculated from ratios between estimates and their standard errors, and the associated value from a t-distribution, as returned by summary.lme R function.*

	‘Best’ model			**Individual models**	
	Unstandardized Coefficient	**Standardised Coefficient**	**p value**	**Coefficient**	**p value**
Relative Yield					
Intercept	672.47 (202.55)	-	0.001	-	-
Potential	-10.33 (3.53)	-7.44 (2.54)	0.004	-9.24 (3.56)	0.013
Potential^2	0.05 (0.02)	7.68 (2.54)	0.003	0.04 (0.02)	0.008
Arable cover	0.06 (0.02)	0.25 (0.1)	0.012	0.06 (0.03)	0.031
Yield Stability					
Intercept	54.17 (12.71)	-	<0.001	-	-
Potential	0.01 (<0.01)	0.12 (0.1)	0.209	0.01 (<0.01)	0.050
Arable cover	0.04 (0.01)	0.31 (0.1)	0.004	0.03 (0.01)	0.009
SNH Proximity	35.08 (13.23)	0.28 (0.11)	0.009	10.41 (12.12)	0.392
Resistance					
Intercept	-33.75 (6.77)	-	<0.001	-	-
Potential	-0.14 (0.16)	-0.07 (0.08)	0.396	0.33 (0.15)	0.042
SNH Cover	0.58 (0.25)	0.2 (0.09)	0.023	0.77 (0.25)	0.002
SNG Proximity	21.64 (8.98)	0.23 (0.1)	0.017	28.88 (8.28)	0.001

RESISTANCE TO A SPECIFIC EVENT

Resistance was the only metric not to show a positive relationship with area of arable land in the ‘best’ model (Table 3.2) and there was no support from model averaging to suggest such a relationship (Table 3.3). Instead, resistance showed a strong, positive relationship with cover of semi-natural habitat and proximity to semi-natural grassland (Table 3.1). This suggests that landscapes exhibiting the highest resistance to the poor conditions of 2012 were those with large extents of semi-natural habitat and where arable land was generally in close proximity to grassland in particular (e.g. Fig. 3.3C). Although resistance showed a positive relationship with potential resistance in individual models (Table 3.2), suggesting that the severest decreases were in areas which experienced the most detrimental weather conditions, this relationship was not evident in the 'best' model, suggesting that the positive effects of semi-natural habitats can mitigate against climatic impacts. Support from model averaging for the coefficients in the 'best' model was high (Table 3.3).

Table 3.3 *Model averaged standardised coefficients and average Aikaike weights across models containing each landscape structure variable - i.e. percentage cover, connectivity index (Conn.) and proximity index (Prox.) for each of arable land, all semi-natural habitats and semi-natural grassland.*

	Arable land			**Semi-natural habitats**			**Semi-natural grassland**		
	Cover	**Conn.**	**Prox.**	**Cover**	**Conn.**	**Prox.**	**Cover**	**Conn.**	**Prox.**
Relative Yield									
Coefficient	0.222	-0.037	0.036	-0.074	0.105	0.051	-0.050	0.031	-0.263
Weight	0.696	0.268	0.256	0.240	0.382	0.098	0.209	0.162	0.425
Yield Stability									
Coefficient	0.270	0.071	-0.028	0.104	-0.165	0.261	-0.014	0.022	0.021
Weight	0.862	0.307	0.252	0.286	0.562	0.655	0.177	0.109	0.089
Resistance									
Coefficient	-0.020	-0.001	0.097	0.212	-0.126	0.228	0.101	-0.077	0.237
Weight	0.254	0.242	0.417	0.727	0.423	0.227	0.109	0.203	0.648

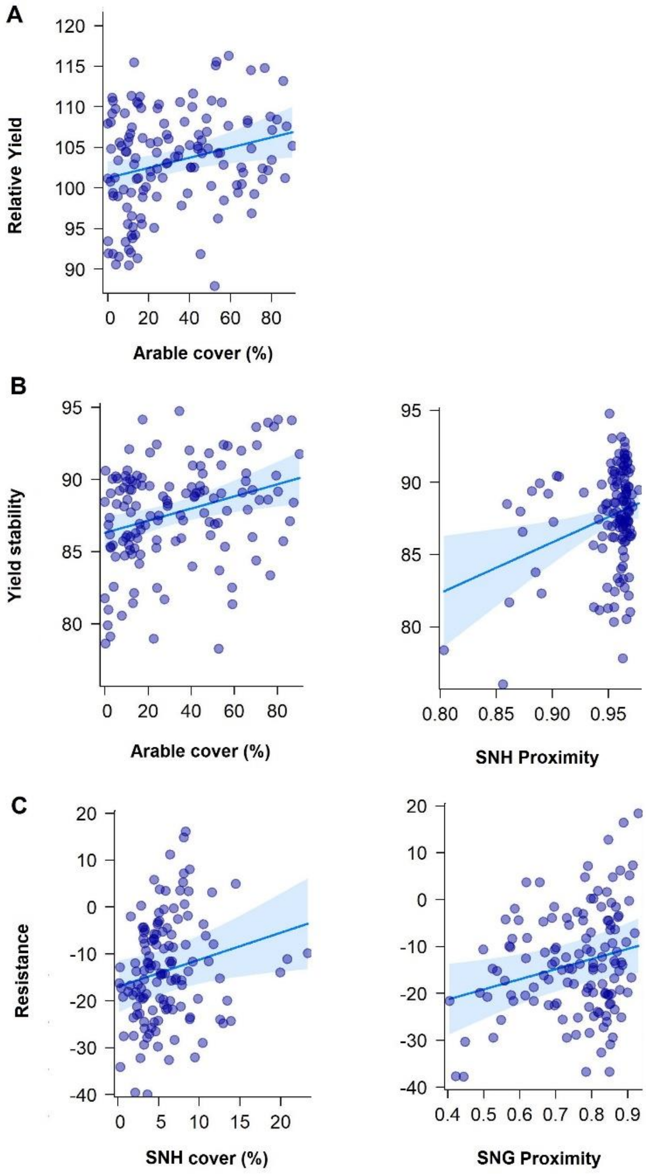

Figure 3.2. *Partial residual plots of landscape structure variables in the 'best' models for each resilience metric: A) relative yield, B) yield stability, C) resistance**.** Plots show the effect of a given variable after removing variance from other effects in the model. Higher values on the y-axes indicate increased resilience and are thus considered favourable for agricultural productivity. SNH =semi-natural habitat, SNG =semi-natural grassland.*

3.5. Discussion

RELATIONSHIPS WITH LANDSCAPE STRUCTURE

All three resilience metrics showed relationships with landscape structure. In support of the first hypothesis, two of them showed a positive effect of higher coverage of arable land. Higher relative yield (i.e. relative difference between local and national yield across the time series) was strongly associated with landscapes dominated by arable land. Although the metric of relative yield is conceptually indicative of resilience to wide range of perturbations over time (Oliver et al. 2015a), in practice it correlates strongly with mean yield. Mean yield is in turn highly likely to correlate with coverage of arable land because farming systems in England have long developed to exploit the most productive land (Chambers and Mingay 1966) and these areas typically receive the greatest investment in agricultural inputs. This may have a masking effect on the role of ecosystem services and the non-arable components of the landscape (Pywell et al. 2015, Gagic et al. 2017, Martin et al. 2019). A positive relationship between yield stability and cover of arable land to was also evident but resistance to the poor weather of 2012 showed no evidence such a relationship, exemplifying that average or relative yield is not necessarily indicative of the full extent to which landscape structure affects crop yield resilience.

Two metrics showed a positive effect of cover or configuration of semi-natural habitats. This supports the second hypothesis that semi-natural habitat has a role in contributing to the resilience of crop yields to environmental perturbation. The most probable mechanism underpinning the positive effect of semi-natural habitats is that they provide reservoirs of organisms providing beneficial ecosystem services (Martin et al. 2019), including those involved in natural control of pests and pathogen vectors (‘natural enemies’). Although semi-natural habitats may also have other characteristics that influence yield resilience (e.g. favourable microclimates, retention of water, reduction of soil and nutrient runoff) these are likely to be influential at finer spatial scales than the hectads analysed here. Many studies have previously demonstrated positive relationships between semi-natural habitats and the abundance and richness of natural enemies (Tscharntke et al. 2005, Bianchi et al. 2006, Chaplin-Kramer et al. 2011, Rusch et al. 2013, Holland et al. 2016, Martin et al. 2016, Holland et al. 2017). However, natural enemies comprise a great diversity of organisms, each with their own, complex relationships with landscape structure and with one another (Plantegenest et al. 2007, Chaplin-Kramer et al. 2011, Martin et al. 2013, Martin et al. 2016, Karp et al. 2018). These relationships are often highly context-dependent (Haan et al. 2019). For example, dispersing the same amount of semi-natural habitat throughout the landscape simultaneously increases the potential for movement into arable land (Tscharntke et al. 2005, Rand et al. 2006, Blitzer et al. 2012) and lessens the value of individual patches (Mitchell et al. 2015). Such trade-offs affect both natural enemies and the pests and pathogens which they help to control (Plantegenest et al. 2007, Karp et al. 2018). Effects of natural enemies can also be counterintuitive, for example by promoting increased movement of pathogen vectors (Clark et al. 2019, Crowder et al. 2019). The complexity of these interrelationships means that positive effects of semi-natural habitat on natural enemy abundance and richness do not always translate to improved pest regulation or enhanced yields (Martin et al. 2013, Mitchell et al. 2014, Tscharntke et al. 2016, Karp et al. 2018, Martin et al. 2019, Smith et al. 2020). By examining effects on yield of a single crop I focus directly on the outcome of this suite of complex interactions and the results show that amount and proximity of semi-natural habitats have an overall positive effect on yield stability and resistance. Although I do not have direct evidence for the mechanisms underlying these relationships, demonstrable links between semi-natural habitat and variations in crop yield are the most directly compelling evidence for farmers of the importance of semi-natural habitat for agricultural production (Holland et al. 2017, Kleijn et al. 2019).

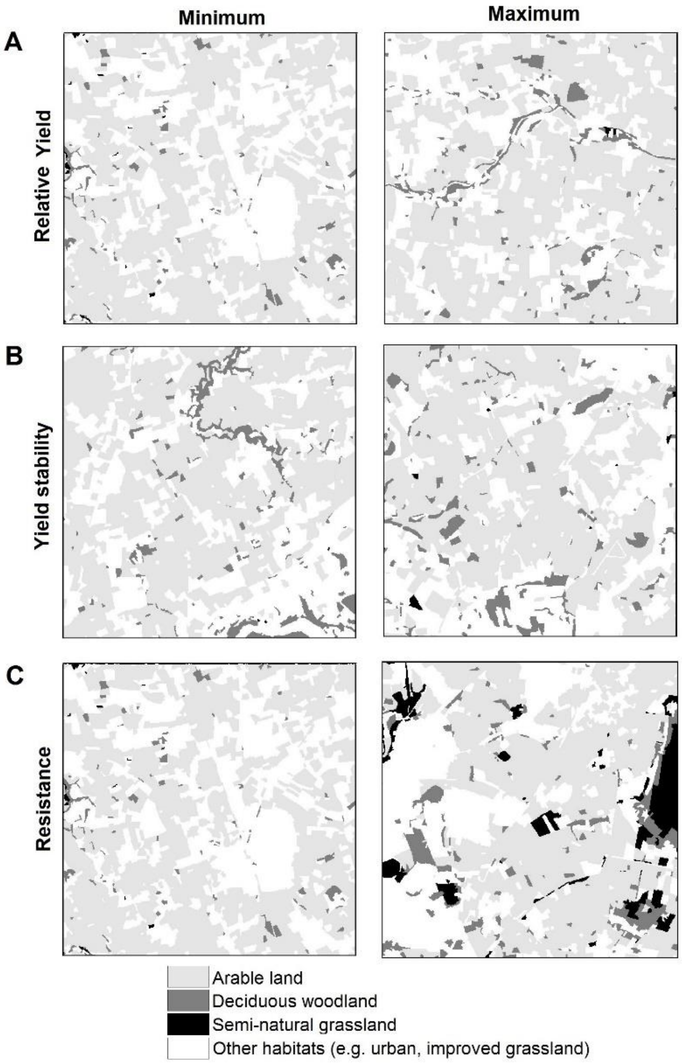

Figure 3.3. *Example hectads from a single environmental zone with the maximum and minimum predicted values for each resilience metric.*

DIFFERENCES BETWEEN RESILIENCE METRICS

Given the aforementioned complexities of the relationships between landscape structure, ecosystem services and yield, it is unsurprising that there were clear differences in the relationships between landscape structure and the different metrics of resilience (Haan et al. 2019). As described above, the results showed a general trend of increasing importance of semi-natural habitat and decreasing importance of arable land as resilience metrics were derived from shorter portions of the time series. There are two possible explanations for this.

Firstly, over shorter timescales, a narrower range of environmental fluctuations are likely to be encountered. This means that the ecosystem services with greatest impact on crop yield are likely to be more limited, and thus that relationships with specific landscape structure variables are more likely to be consistent. In a single, extreme year the mechanisms governing resistance, and hence relationships with landscape structure, are likely to be even more specific. Indeed, the resistance metric showed a positive effect of not just semi-natural habitats but semi-natural grassland in particular. Grasslands are more similar to arable land, structurally and in community composition, than other semi-natural habitats (e.g. woodland). This makes them particularly important as reservoirs of beneficial species (Duflot et al. 2015, Bengtsson et al. 2019), presumably including those conferring resistance to the specific perturbation explored here.

Secondly, it is likely that many effects of the non-agricultural components of landscape structure are only made obvious when extreme perturbations occur. The reliance of English agriculture on intensive management such as the prophylactic use of agrochemicals (Hillocks 2012) may, under normal circumstances, mask (or even suppress) potential benefits from ecosystem services (Gagic et al. 2017). It thus requires an extreme event where farming practices cannot fully compensate for environmental fluctuations for the value of ecosystem services to become evident.

Of course, these two explanations are not mutually exclusive. The precise mechanisms controlling the relationships between resistance and semi-natural habitat vary with spatial and temporal context (Haan et al. 2019). So a particular extreme (e.g. high rainfall, as in 2012) might increase populations of specific pests beyond the capacity of agricultural management to control them (e.g. molluscs) making resistance highly dependent on landscape factors which most affect their predators (e.g. carabids). However, another extreme year with different conditions might promote another set of pests, which are in turn controlled by different natural enemies with different responses to landscape structure (Martin et al. 2019), leading to a lack of clear response if the two extreme years were analysed in conjunction.

Overall, the results clearly demonstrate that a single metric of resilience (especially one based on average levels of function over longer timescales) is unlikely to adequately capture the full effect of landscape structure or the benefits of ecosystem services to agriculture (Benton and Bailey 2019). The responses of resistance and shorter-term stability are indicative of where current farming practices cannot fully compensate for environmental fluctuations. Extreme weather events, as encountered in 2012, are likely to become more frequent (Rosenzweig et al. 2001, Trnka et al. 2014). Other changes may have similar consequences, reducing the ability of the agricultural system to mitigate against environmental impacts, such as the regulatory loss of pesticide active ingredients (Hillocks 2012). Such shifts may make farmers increasingly reliant on natural pest control and thus increase the importance of landscape context – it has been demonstrated that organic farming systems exhibit greater fluctuations in yield than conventional ones, and show an increased dependency on landscape-mediated ecosystem services (Knapp and van der Heijden 2018, Smith et al. 2020).

CONCLUSIONS AND IMPLICATIONS FOR LANDSCAPE MANAGEMENT

The results confirm that semi-natural habitats in arable landscapes have a role for society that extends beyond simply supporting agricultural biodiversity to enhancing the long-term viability of farming systems. At the scale I analysed, this is relevant to national or regional policy-making, including agri-environmental funding for creating, restoring and maintaining semi-natural habitats (Critchley et al. 2004). Although the sampled landscapes do not cover the full national range of possible agricultural landscape structures, they include a wide variety with moderate to high coverage of agricultural land such as dominate much of lowland England.

Differences in the relative strength of the responses to arable land, semi-natural habitat and its configuration suggest that there are potential trade-offs to be made in managing landscapes for resilience over shorter vs. longer timescales. The results also have a bearing on the relative merits of strategies based on land-sharing vs. land-sparing. Whilst land-sparing is often determined to be preferable in terms of maximising average delivery of biodiversity and crop yield (Ekroos et al. 2016, Lamb et al. 2019), the results suggest that whilst land-sparing might maximise relative yields, at least some degree of land-sharing (i.e. intermixtures of semi-natural habits and arable land within hectads) is required to maximise stability and resistance. Given the increased risk of extreme events under climate change and concerns over the current reliance on agrochemicals, the finding that landscapes which most enhance relative yield are not necessarily those which confer increased stability or resistance to environmental perturbations is an important challenge to address in developing sustainable agricultural systems.

3.6. Chapter acknowledgements

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Chapter 4: Potential landscape-scale pollinator networks across GB: structure, stability and influence of agricultural land cover[2]

4.1. Abstract

Understanding spatial variation in the structure and stability of plant-pollinator networks, and their relationship with anthropogenic drivers, is key to maintaining pollination services and mitigating declines. Constructing sufficient networks to examine patterns over large spatial scales remains challenging. Using biological records (citizen science), I constructed potential plant-pollinator networks at 10km resolution across Great Britain, comprising all potential interactions inferred from recorded floral visitation and species co-occurrence. I calculated network metrics (species richness, connectance, pollinator and plant generality) and adapted existing methods to assess robustness to sequences of simulated plant extinctions across multiple networks. I found positive relationships between agricultural land cover and both pollinator generality and robustness to extinctions under several extinction scenarios. Increased robustness was attributable to changes in plant community composition (fewer extinction-prone species) and network structure (increased pollinator generality). Thus, traits enabling persistence in highly agricultural landscapes can confer robustness to potential future perturbations on plant-pollinator networks.

4.2. Introduction

Insect pollinators face many threats that may jeopardize the crucial ecosystem service they provide to crops and wild plants (Vanbergen et al. 2013, Gill et al. 2016, Potts et al. 2016). The stability of pollinator communities and the service they deliver is mediated by the structure of ecological networks formed by interactions between pollinator and plant species (Vázquez et al. 2009, Vanbergen et al. 2017). Understanding such networks is important to predict the risks associated with threats to pollinators (Gill et al. 2016). Analysis of plant-pollinator networks has provided insights into their structure and potential stability under actual or simulated environmental change, including extinctions (e.g. Memmott et al. 2004, Kaiser-Bunbury et al. 2010), climate change (e.g. Memmott et al. 2007), habitat change (e.g. Forup et al. 2008, Vanbergen et al. 2017) and restoration (Kaiser-Bunbury et al. 2017).

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Studies traditionally rely on obtaining well-characterised networks from field surveys, which are time consuming and costly to construct (Vázquez et al. 2009, Burkle and Alarcón 2011). Constructing networks replicated across larger spatial scales remains a daunting prospect (Burkle and Alarcón 2011), particularly at the regional and national scales relevant to land use and conservation policy-making. Although broad geographic patterns in plant-pollinator network properties have been identified across biomes (Olesen and Jordano 2002, Welti and Joern 2015) or within landscapes (Burkle and Alarcón 2011, Carstensen et al. 2014, Trøjelsgaard et al. 2015, Kaiser-Bunbury et al. 2017), these still rely on a comparatively limited number of empirical plant-pollinator networks.

Of particular interest in understanding spatial variability in plant-pollinator networks is the contrast between the benefits of insect pollinators to agricultural crops (Kremen et al. 2002, Winfree 2008, Eilers et al. 2011) and the negative impacts of intensive agriculture on pollinators (Kluser and Peduzzi 2007, Potts et al. 2010, Gill et al. 2016). However, we have very little knowledge of how plant-pollinator networks are affected by agriculture at landscape scales (e.g. >1km^2) or whether networks comprising species that pollinate agricultural crops are representative of the wider pollinator community (Kleijn et al. 2015, Gill et al. 2016).

Lack of information on ecological interactions across larger spatial, temporal and taxonomic scales, termed the ‘Eltonian shortfall’, represent key gaps in the large-scale knowledge of biodiversity (Hortal et al. 2015). Moreover, there are limitations on the extent to which different data sources can be combined to analyse multiple networks because data collection methods can introduce potential biases (Hortal et al. 2015). Whilst there are exciting possibilities for molecular techniques to increase the speed and accuracy with which plant-pollinator networks can be constructed (Keller et al. 2015, Richardson et al. 2015, Bohan et al. 2017, Pornon et al. 2017) these are yet to be realised across larger spatial scales.

Biological records (i.e. records submitted to voluntary recording schemes, a form of ‘citizen science’) provide a valuable resource for analysing large-scale patterns in time and space (Bishop et al. 2013, Tulloch et al. 2013, Powney and Isaac 2015). Records consist of species’ identification, date and location (hereafter ‘occurrence’ data) and provide large volumes of data over a wide spatial coverage, equivalent to innumerable hours of field survey. Methods to control for variation in recorder effort and to infer ecological signals from occurrence data are rapidly emerging (e.g. Isaac et al. 2014, Dyer et al. 2016), but hitherto their potential as a source of data on ecological networks is untapped (Gray et al. 2014).

Here, I constructed potential plant-pollinator networks for every 10km-by-10km grid square ('hectad') in Great Britain (GB) using interactions from a 30-year, long-term national dataset of occurrence records of pollinating insects (bees, butterflies and hoverflies). Instead of inferring species interactions from spatial co-occurrence (Morales-Castilla et al. 2015, Morueta-Holme et al. 2016) I used metadata from records that detailed flower visitation as a proxy of pollination (Ballantyne et al. 2015). These networks are 'potential' in that I acknowledge their limitations in terms of assumptions that constrain their biological realism. However, whilst the structure of each potential network may be subject to errors, I aimed to minimise bias affecting comparisons across replicate networks. I used these potential networks to address three questions. First, does network structure and stability vary spatially across GB? Second, is network stability reduced by greater agricultural land cover, a major driver of plant and pollinator declines (Kluser and Peduzzi 2007, Potts et al. 2010, Vanbergen et al. 2013, Ollerton et al. 2014)? Finally, are the structure and stability of networks comprising crop-pollinator species consistent with those of the wider pollinator community?

4.3. Materials and Methods

CONSTRUCTING A PLANT-POLLINATOR INTERACTIONS DATABASE

I constructed a national-scale (GB) plant-pollinator interaction database defining which species of pollinator visit which species of plant (Fig. 4.1). Data were mostly (73%) sourced from biological records. Specifically, these were species observations submitted to the Bees, Wasps and Ants Recording Society (BWARS), Butterflies for the New Millennium (BNM, Asher 1997) and Hoverfly Recording Scheme (HRS), with plant interactions recorded as incidental metadata.

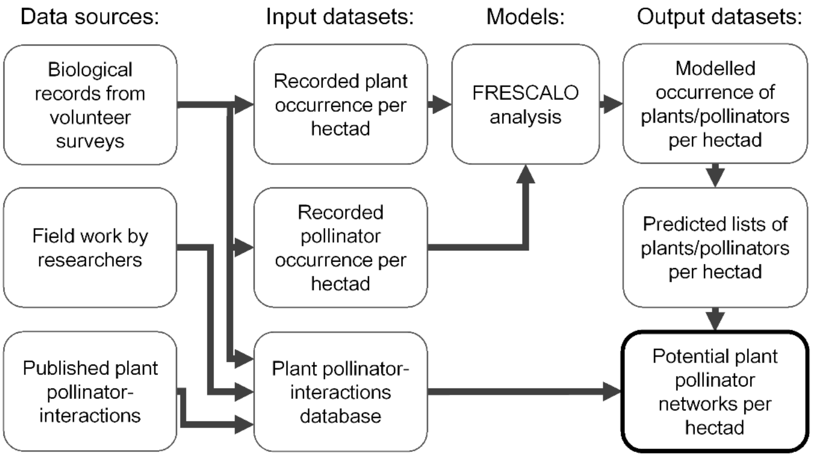

Figure 4.1. *Schematic showing steps in construction of potential plant-pollinator networks for every 10 x 10km cell ('hectad') in Great Britain from biological records*

Interactions were inferred by algorithmically screening metadata for valid scientific or vernacular plant names (or widely used synonyms or abbreviations thereof), followed by data cleaning (see Appendix B1). Remaining interaction data were obtained from books (e.g. Morris 1998), papers (e.g. Carvell 2002) and unpublished experimental data. Where interactions were recorded only to plant genus I assumed, given the rarity of pollinators specialised to the level of individual plant species (Waser et al. 1996, Minckley and Roulston 2006), that these were indicative of interactions with all plant species within the genus that were present in the dataset (full details in Appendix B1). These inferred interactions comprised 6487 unique interactions (39%) within the full dataset.

The final plant-pollinator interactions database contained 16,712 unique interactions, involving 485 pollinator species (206 bees, 56 butterflies, 223 hoverflies) and 499 plant species. These totals comprise approximately 76, 92, 81 and 55% of GB bee, butterfly, hoverfly and insect-pollinated plant species, respectively (Fitter and Peat 1994, Stubbs and Falk 2002, Thomas 2010, Falk 2015). I explored the completeness of the interactions database by calculating interaction accumulation curves across all records used to construct the database (i.e. pollinator occurrences where it was possible to able to identify a valid plant interaction) and for each plant and pollinator species separately (Appendix B2). Results suggested that the database captured around 60% of estimated total interactions (mean 62% for pollinators, 57% for plants), comparable to studies which performed high-effort, multi-temporal field sampling of individual networks (Chacoff et al. 2012, Falcão et al. 2016).

MODELLING PLANT AND POLLINATOR OCCURRENCE

For all species in the interactions database, I obtained occurrence data from BWARS, HRS, BNM and, for plants, the Botanical Society of Britain and Ireland (Fig. 4.1). Data records were restricted to 1985 onwards, covering the vast majority of records while excluding occurrences of species that may have been more widespread prior to major changes in GB land use (Robinson and Sutherland 2002, Ollerton et al. 2014). Occurrence data were modelled to account for spatial bias in recorder effort using the FRESCALO algorithms (Hill 2012), implemented in the *Sparta* (v0.1.30 August et al. 2015b) package of R (v3.4.0 R Core Team 2017). FRESCALO weights by recorder effort to estimate trends and probability of occurrence in under-recorded areas (for validation of FRESCALO for different groups and through simulation see Hill 2012, Fox et al. 2014, Isaac et al. 2014, Dyer et al. 2016). I used the CEH Land Cover Map (LCM2007, Morton et al. 2011) as input data for FRESCALO’s calculation of neighbourhoods of ecologically similar hectads (see August et al. 2015b, Dyer et al. 2016). For each species, FRESCALO produces a probability of occurrence per hectad. To transform this to presence/absence, I assigned a species as present in a hectad if its probability of occurrence was greater than a set threshold (see Appendix B3).

CONSTRUCTING POTENTIAL NETWORKS

I used lists of modelled plant and pollinator species presence per hectad to filter the interactions database (as derived from plant associations in biological records) and create a potential plant-pollinator network for each hectad (Fig. 4.1). Networks were unweighted (i.e. interaction matrices consisting of ones and zeros), this being the most conservative interpretation of the interaction data because the frequency with which an interaction was recorded is unlikely to provide reliable quantitative information on abundance, due to differences in detectability, recorder bias and data sources.

NETWORK STRUCTURE METRICS

From the networks constructed in each of 2823 GB hectads I used the R package *bipartite* (v2.07, Dormann et al. 2009) to calculate the following metrics (Bersier et al. 2002, Dunne et al. 2002, Tylianakis et al. 2007):

i. Species richness: total number of plant and pollinator species in the network
ii. Connectance: proportion of possible links which are realised
iii. Pollinator generality: mean number of plants per pollinator
iv. Plant generality: mean number of pollinators per plant

Whilst other, more complex metrics of network structure (e.g. nestedness, modularity) have been implicated in stability they can be comparatively insensitive to spatial or temporal change (Kaartinen and Roslin 2012, Morris et al. 2014, Kemp et al. 2017). Preliminary analyses confirmed that nestedness and modularity showed little variation even for networks greatly differing in the metrics listed above.

ROBUSTNESS TO SIMULATED EXTINCTIONS

To derive a metric of network stability, I assessed the impact of simulated extinctions of plants. This was a measure similar to robustness (following Memmott et al. 2004, Burgos et al. 2007), but differing in that sequential simulated extinctions were ordered according to a complete 'global' list of plants (i.e. across all hectads) and not just those in each 'local' network (i.e. individual hectad) (Fig. 4.2). This approach meant the same extinction scenario was universally applied across hectads and enables comparisons across networks with different plant communities. I term this approach and the resulting metric "robustness to global simulated extinctions" (R_g from hereon) to avoid confusion with the usual approach. For comparison, I also calculated 'local' robustness (R_l from hereon) following Memmott et al. (2004) with randomised extinction of plants within each hectad. I focussed on simulating plant extinctions because many of the major impacts of agriculture indirectly affect pollinators via altered plant communities (Potts et al. 2010, Vanbergen et al. 2013, Vanbergen et al. 2017), as would restoration of agricultural plant-pollinator networks in practice (Kremen et al. 2002, Forup et al. 2008, Menz et al. 2011, Kaiser-Bunbury et al. 2017).

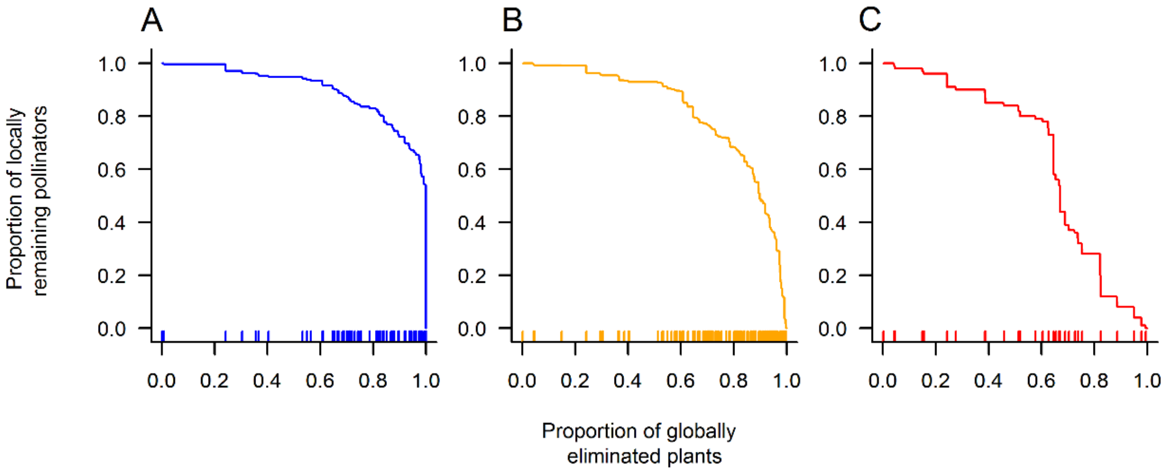

Figure 4.2. *Example extinction curves (coloured lines) for three hectads with different plant-pollinator communities and correspondingly different robustness to global simulated extinctions as measured by area under extinction curve (A: R_g =0.90, B: R_g =0.82, C: R_g =0.66). Plant extinctions are ordered by trend (i.e. most strongly declining are eliminated first). Tick marks along the x-axis indicate where simulated plant extinction from the global list resulted in an extinction from the hectad.*

As well as randomised plant extinctions from the global list ($R_{g\,R}$), I conducted simulated extinctions by ordering the complete list of 499 plant species according potential predictors of future plant declines under three scenarios:

a) historic distribution trend (1985-2015) estimated using FRESCALO (Hill 2012, Isaac et al. 2014), extinctions occurring first for plants showing the greatest historic decline ($R_{g\,Trend}$);

b) soil fertility tolerance based on Ellenberg N values (Hill et al. 2004), extinctions occurring first for plants preferring low soil fertility, as historically observed in GB flora (Stevens et al. 2006, Maskell et al. 2010) ($R_{g\,N}$);

c) drought tolerance based on Ellenberg F values (Hill et al. 2004), extinctions occurring first for plants preferring moister conditions expected to suffer under climate change (Thuiller et al. 2005, Watts et al. 2015) ($R_{g\,F}$).

For each hectad-level network, plants were sequentially extirpated from the global list in the order determined by each scenario. After each plant extinction any pollinator species with no remaining links were removed from the network. I assessed R_g as the area under the curve (Burgos et al. 2007) of pollinators remaining in the local network against plants removed from the global sequence (Fig. 4.2). This process was repeated 100 times per scenario, with random ordering of plant species with tied trends or Ellenberg values (or of the entire list for randomised plant extinctions; $R_{g\,R}$).

Following individual plant extinctions, there is potential for pollinators to switch between plants and rewire networks (Thomsen et al. 2017). Other authors have used regional information to inform the likelihood of rewiring in local networks (Kaiser-Bunbury et al. 2010). However, the potential networks already implicitly incorporate some of this capacity for rewiring because each local network contains information from all recorded interactions across GB over three decades. Another approach is to create putative novel interactions from plant-pollinator traits but, given the assumptions and uncertainties involved, it is difficult to assess whether such rewiring scenarios are more ecologically meaningful than using only observed interactions. I conducted supplementary analyses exploring additional trait-based network rewiring scenarios but found that spatial patterns in robustness metrics were largely unaffected (Appendix B4).

Two main sources of error in the hectad-level potential networks are the methods used to model occurrence and the database used to assign interactions. Consequently, I assessed the impact of these sources of uncertainty independently and in combination by performing, for each hectad, 100 randomised resamples of species according to FRESCALO probability of occurrence, and of interactions proportional to the number of times they were recorded (see Appendix B5).

CROP-POLLINATORS

I repeated the analyses calculating hectad-level network metrics, including R_g and R_l, for potential networks consisting solely of interactions involving known crop-pollinators. This allowed me to explore whether the structure and stability of crop-pollinator networks was similar to the wider plant-pollinator networks in which they were embedded. Bees are generally considered the most important contributors to crop pollination (Free 1993, but see Rader et al. 2016) and their predominance in the pollination of GB crops is well supported (Woodcock et al. 2013, Garratt et al. 2014). Crop-pollinators were determined from a published list of bee species with the highest contribution to crop production value (Kleijn et al. 2015) for major GB insect-pollinated crops (oilseed rape, field bean, apple and strawberry). The interactions database included 23 such species from 5 genera (see Appendix B, Fig. B5 for full species list). I then compared metrics for crop-pollinator networks, overall plant-pollinator networks and bee-only networks. Because crop-pollinator networks are considerably less speciose, I resampled the bee-only network for each hectad 100 times, with a random selection of pollinators equal in number to crop-pollinator species in the hectad, and then calculated mean resampled network metrics for comparison. The number of plants in each resampled network was allowed to vary depending on interactions with the selected pollinators, as attempting to limit plants to the number in the crop-pollinator networks would severely restrict the number of resampled networks and constrain resultant network metrics.

STATISTICAL ANALYSIS

Network metrics were modelled independently against agricultural coverage, using linear mixed-effects models in the *nlme* R package (v3.1 Pinheiro et al. 2017). I derived coverage of agricultural land (arable + improved grassland) per hectad from LCM2007 and used this as a fixed effect explanatory variable, along with an optional quadratic term, which was retained in models if significant. To account for the potential influence of other environmental variables on network structure and response to agricultural coverage, I assigned each hectad to an environmental zone, using a pre-existing classification (Bunce et al. 2007). Environmental zone was then included as a random factor in all models, with variable slope and intercept. Some of the network metrics I used are sensitive to the size of the network (Jordano 1987, Olesen and Jordano 2002, Forup et al. 2008, Morris et al. 2014), so models were compared with and without total species richness as a fixed covariate. Environmental zones represented by <30 hectads were considered to have insufficient sample size for robust analysis and were excluded, as were hectads with >50% coverage of sea, giving a final sample of 2290 hectads. All variables were standardised to mean of zero and standard deviation of one, to facilitate comparison of model coefficients. Each model was compared using a likelihood-ratio test against a model consisting only of the random effect and species richness, to determine the impact of incorporating agricultural coverage on model fit. I also applied randomisation tests (Fortin and Jacquez 2000) to account for potential complex spatial autocorrelation patterns arising from how FRESCALO defines neighbourhoods based on spatial proximity and biological similarity (see Appendix B6).

4.4. Results

SPATIAL PATTERNS IN NETWORK PROPERTIES

Variation in plant and pollinator species richness conformed to known clines across GB (i.e. higher richness in the south and at lower altitudes, Fig. 4.3). Spatial patterns for connectance, pollinator generality and plant generality showed similar latitudinal and altitudinal trends to species richness (Fig. 4.3), and a significant correlation with total plant-pollinator species richness (Pearson's r =-0.95; 0.82; 0.97, respectively, n =2290, p <0.001 in all cases).

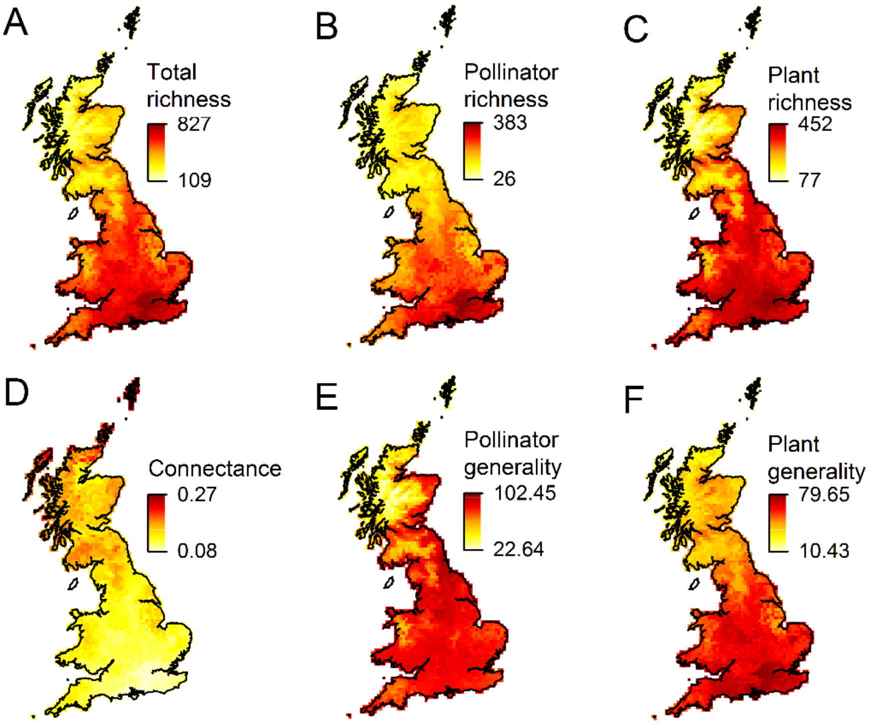

Figure 4.3 *Network properties per hectad across GB: A) total species richness of plants and pollinators combined, B) richness of pollinators and C) richness of plants, D) network connectance, E) pollinator generality, F) plant generality. Lighter colours indicate lower values, darker colours indicate higher, with linear colour stretch from maximum to minimum values.*

Robustness to global simulated extinctions (R_g) also showed spatial variation across GB, with more variation than would be expected under simple conformity to species richness, latitude or altitude (Fig. 4.4A, C, E, G and I). The different extinction sequences gave mean R_g scores across hectads of 0.84, 0.92, 0.85 and 0.93 for extinctions ordered by trend ($R_{g\ Trend}$), Ellenberg N ($R_{g\ N}$), Ellenberg F ($R_{g\ F}$) and randomised extinctions ($R_{g\ R}$), respectively (range across hectads 0.66-0.97 across all four R_g measures), but with varying spatial patterns (Fig. 4.4). Robustness to randomised local extinctions (R_l) showed a very similar range of values and spatial patterns to $R_{g\ R}$ (Fig. 4.4I).

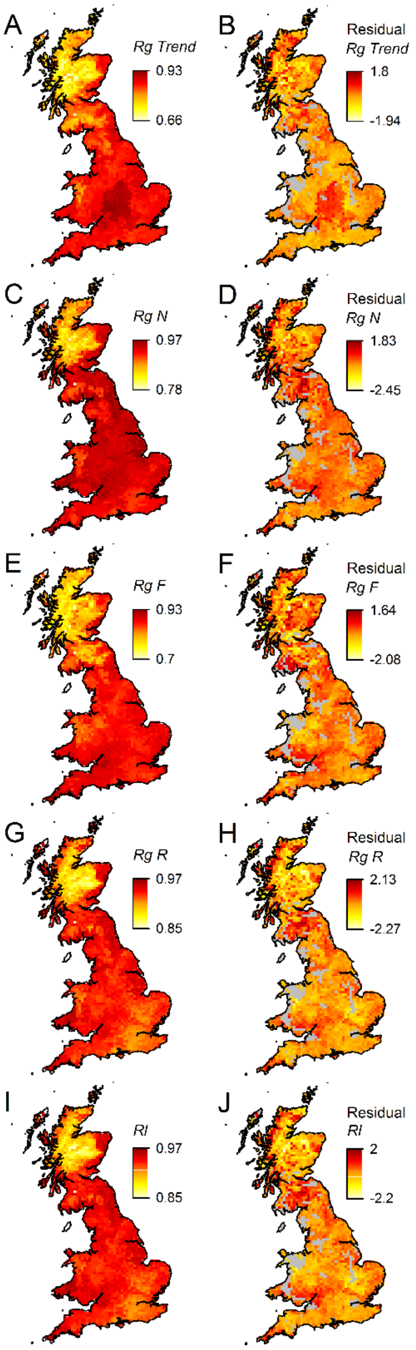

Figure 4.4 *Spatial patterns in robustness to global simulated extinctions (R_g) as measured by area under extinction curve. Panels A, C, E, G and I show R_g with extinctions ordered by historic plant occurrence trend ($R_{g\ Trend}$), fertility tolerance ($R_{g\ N}$), drought tolerance ($R_{g\ F}$), globally randomised extinctions ($R_{g\ R}$) and locally randomised extinctions (R_l), respectively. Panels B, D, F, H and J show residuals from linear mixed models of $R_{g\ Trend}$, $R_{g\ N}$, $R_{g\ F}$, $R_{g\ R}$ and R_l, respectively, against species richness and environmental zone. Grey shaded cells indicate environmental zones with <30 cells excluded from mixed models. For all panels, darker colours indicate higher values, with a linear colour stretch between maximum and minimum values.*

Pollinator generality and all five measures of robustness to simulated extinctions showed significant positive relationships with agricultural coverage (Table 4.1). All relationships apart from $R_{g\,F}$ included a significant negative quadratic term (Table 4.1) indicating a levelling off of the relationship as agricultural coverage approaches 100% (Fig. 4.5A, B, C, E, F). These results suggest that pollinator communities in more highly agricultural landscapes are more generalist and that, under all the extinction scenarios, hectads with a higher coverage of agricultural land lost pollinators less quickly than other hectads in the same environmental zone. This effect appeared most pronounced for $R_{g\,Trend}$ and $R_{g\,N}$ (Fig. 4.5B and C). Neither plant generality nor connectance showed any significant relationship with proportion of agricultural coverage (Table 4.1).

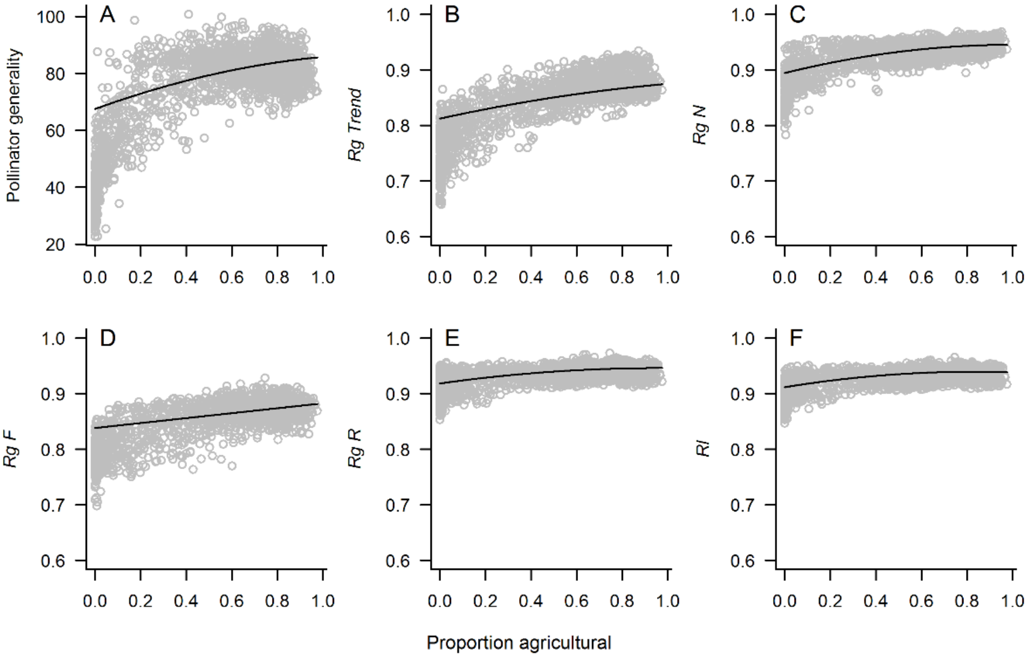

Figure 4.5 *Relationships with proportion of agricultural land cover for six network properties: A) pollinator generality B) robustness to simulated global extinctions ordered by historic plant trend ($R_{g\,Trend}$), C) robustness to simulated global extinctions ordered by Ellenberg N ($R_{g\,N}$), D) robustness to simulated global extinctions ordered by Ellenberg F ($R_{g\,F}$), E) robustness to simulated global extinctions ordered at random ($R_{g\,R}$), F) robustness to simulated local extinctions ordered at random (R_l). All relationships are statistically significant (see Table 4.1). Slopes were back transformed from the full model (i.e. with agricultural land cover, species richness and environmental zone) and show the effect of agricultural land coverage on response variables once effects of species richness and environmental zone are accounted for.*

Table 4.1. *Results from linear mixed models of network metrics per hectad versus proportion of agricultural land and random effect of environmental zone for potential networks at hectad (10 × 10 km) scale across GB. Results are standardized slope coefficients (± standard errors) for linear and quadratic terms (the latter only retained where significant) with level of significance (*** <0.001, ** <0.01, * <0.05) and likelihood-ratio tests against a model consisting only of the random effect, and p value derived from comparing model results against 1000 randomisations. Model results are shown with and without species richness as a covariate.*

Metrics		**Species Richness**	**Agricultural cover (linear)**	**Agricultural cover (quadratic)**	**Likelihood-ratio test**		**Randomisation test**
		Slope ± SE	**Slope ± SE**	**Slope ± SE**	**χ^2**	**p value**	**p value**
Network Species richness	Total richness		0.06 (±0.12)		2.22	0.14	0.50
	Pollinator richness		-0.08 (±0.11)		2.01	0.16	0.09
	Plant richness		0.15 (±0.12)		0.78	0.38	0.23
Plant extinction scenario predictors per hectad	Mean historic trend		0.37 (±0.07) ***	-0.12 (±0.02) ***	29.33	<0.001***	<0.001***
	SD historic trend		0.14 (±0.12)		1.00	0.32	0.30
	Mean Ellenberg N		1.33 (±0.53) *	-0.1 (±0.02) ***	14.82	<0.001***	0.03*
	SD Ellenberg N		-0.54 (±0.08) ***	-0.22 (±0.04) ***	33.21	<0.001***	<0.001***
	Mean Ellenberg F		-0.23 (±0.07) **		5.07	0.02*	0.01**
	SD Ellenberg F		-0.05 (±0.11)		2.56	0.11	0.18
Network metrics (species richness not included as covariate)	Connectance		0.01 (±0.14)		2.14	0.14	0.27
	Pollinator generality		0.33 (±0.09) ***	-0.18 (±0.02) ***	52.29	<0.001***	0.00**
	Plant generality		0.08 (±0.11)		2.06	0.15	0.38
	$R_{g\,Trend}$		0.38 (±0.06) ***	-0.09 (±0.02) ***	19.89	<0.001***	<0.001***
	$R_{g\,N}$		0.49 (±0.05) ***	-0.14 (±0.02) ***	49.68	<0.001***	<0.001***
	$R_{g\,F}$		0.36 (±0.09) ***		10.33	0.00**	<0.001***
	$R_{g\,R}$		0.45 (±0.07) ***		18.65	<0.001***	<0.001***
	R_I		0.42 (±0.07) ***	-0.1 (±0.03) **	20.58	<0.001***	<0.001***
Network metrics (species richness included as covariate)	Connectance	-1.34 (±0.02) ***	0.12 (±0.05) *		0.68	0.41	0.13
	Pollinator generality	0.53 (±0.02) ***	0.34 (±0.07) ***	-0.07 (±0.02) **	13.84	<0.001***	<0.001***
	Plant generality	0.96 (±0.01) ***	0.01 (±0.03)		4.90	0.03*	0.32
	$R_{g\,Trend}$	0.21 (±0.03) ***	0.38 (±0.05) ***	-0.05 (±0.03) *	19.70	<0.001***	<0.001***
	$R_{g\,N}$	-0.12 (±0.03) ***	0.49 (±0.05) ***	-0.16 (±0.02) ***	54.18	<0.001***	<0.001***
	$R_{g\,F}$	-0.12 (±0.03) ***	0.36 (±0.1) ***		8.62	0.00**	<0.001***
	$R_{g\,R}$	-0.68 (±0.04) ***	0.45 (±0.09) ***	-0.17 (±0.03) ***	24.10	<0.001***	<0.001***
	R_I	-0.57 (±0.04) ***	0.42 (±0.08) ***	-0.22 (±0.03) ***	42.18	<0.001***	<0.001***

While species richness was a significant covariate in models for all network metrics, its inclusion did not qualitatively change the relationships with agricultural coverage. For all models, likelihood ratio tests and randomisation tests generally corroborated the significance of the individual model coefficients for agricultural coverage (Table 4.1). There was no significant relationship between agricultural coverage and species richness of plants, pollinators or both combined, once environmental zones were accounted for (Table 4.1).

There were significant relationships between agricultural coverage and the mean values across the plant community per hectad of the trait and trend values used to order extinction sequences (Table 4.1). This indicates that agricultural coverage influences the relative position of the plant community in the global extinction sequences. Standard deviations in these values within hectads showed a significant, negative relationship only for Ellenberg N, suggesting hectads with higher agricultural cover not only host communities with higher average fertility tolerance, but show significantly less variation in fertility tolerance between plant species.

CROP-POLLINATOR NETWORKS

Subsets of networks consisting of only crop-pollinating bees and the plants they visit showed significant differences in their properties from complete hectad-level networks, or from randomly resampled networks of equivalent bee species richness. Crop-pollinator networks showed significantly higher plant species richness than the randomly resampled bee networks (pairwise t-test; t =133.57, p <0.001, df =2750), as well as higher connectance and pollinator and plant generalities (pairwise t-test; t =159.54, 155.48, 116.35 for connectance, pollinator generality and plant generality, respectively; df =2750 and p <0.001 in all cases). Robustness values for crop-pollinator networks were significantly higher than for full or resampled networks (Appendix B, Fig. B5), for all simulated extinction scenarios (pairwise t-test; t =152.22, 121.83, 132.14, 161.45, 155.72 for $R_{g\ Trend}$, $R_{g\ N}$, $R_{g\ F}$, $R_{g\ R}$ and R_I, respectively; df =2750 and p <0.001 in all cases). Crop-pollinator species were amongst the most widely occurring species in the database (median occurrence for crop-pollinators =60% of hectads, for all bees =30%, for all pollinators =43%).

4.5. Discussion

SPATIAL PATTERNS OF PLANT-POLLINATOR NETWORKS AND RELATIONSHIPS WITH AGRICULTURAL LAND COVER

The results revealed that national-scale spatial patterns were clearly evident in all network metrics. Those for pollinator and plant generality and for connectance largely reflected well-known latitudinal gradients in GB plant and invertebrate species richness (e.g. Woodcock et al. 2014). This is unsurprising as these metrics are a function of the connectedness between the two levels of a network and thus fundamentally affected by network species richness (Jordano 1987, Olesen and Jordano 2002, Thébault and Fontaine 2010).

Of greater interest in terms of implications for network stability were the more complex spatial patterns of the metrics of robustness to global simulated extinctions and the positive relationship with coverage of agricultural land evident under all the extinction scenarios. This positive relationship may, at first sight, seem surprising. Highly agricultural landscapes are often considered to have depauperate plant and pollinator communities (Kremen et al. 2002, Potts et al. 2010, Ollerton et al. 2014). As noted by Kleijn et al. (2015), this is often used as justification for pollinator conservation efforts under the assumption that continued crop pollination depends upon a diverse pollinator community. Whilst the results cannot directly shed light on the provision of pollination services, it is clear that plant-pollinator networks in landscapes with relatively high agricultural cover can exhibit higher robustness to extinction scenarios.

EXPLAINING HIGHER ROBUSTNESS OF PLANT-POLLINATOR NETWORKS IN AGRICULTURAL LANDSCAPES

Although it is somewhat counterintuitive that increased levels of anthropogenic disturbance (coverage of agriculture here) can lead to increased resilience to future perturbations (as estimated by the robustness metrics*),* similar relationships have been observed in other ecosystems (e.g. coral reefs, Côté and Darling 2010). This might be due to positive correlations between traits that confer tolerance to past and future disturbance (Vinebrooke et al. 2004). Exposure to previous stressors therefore acts as a filter either extirpating vulnerable species or favouring resistant ones to produce a community more resilient to future stress. The results suggest that the positive relationships between agricultural coverage and robustness may arise in this way from two interacting properties of the plant-pollinator networks.

First, I showed greater robustness to extinctions with increasing agricultural coverage even when extinctions were at random and irrespective of the relative vulnerabilities of the plant community to the trait- and trend-based extinction scenarios. This may be largely driven by the higher generality of pollinator communities in agricultural landscapes, thus being less reliant on individual plant species. Highly agricultural landscapes, where resources are spatially and temporally clustered and where travel between patches of resource is costly, favour the persistence of generalist pollinators (Waser et al. 1996). Conversely, there was no significant effect of agricultural coverage on plant generality, so the loss of each plant is no more likely to remove resources for multiple pollinators. In combination, increased pollinator generality and consistent plant generality insulate these networks against simulated extinctions.

Second, in landscapes with higher coverage of agriculture, plant communities are more liable to have already lost their most vulnerable plant species and gained more tolerant ones (evidenced by significant relationships between coverage of agriculture and mean historic trend in plant occurrence and Ellenberg values), such that global extinctions are less likely to have local impacts. Many of the severest historic declines in GB plant species are associated with agricultural expansion and intensification (Fuller 1987, Walker and Preston 2006). Therefore many plants showing strong historic declines have already disappeared from highly agricultural areas, being replaced by species which can persist in such landscapes and with stable or increasing historic trends (Carvalheiro et al. 2013), contributing to higher robustness to extinctions ordered by plant trend. Likewise, amongst the major, lasting impacts of modern agriculture are increases in soil fertility, so agricultural hectads would have undergone replacement of those plants with low fertility tolerance (Marrs 1993, Walker and Preston 2006, Walker et al. 2009, Redhead et al. 2014), contributing to higher robustness to extinctions ordered by fertility tolerance. Furthermore, plant communities in hectads with a higher coverage of agricultural land also showed a lower standard deviation in Ellenberg N, suggesting a homogenisation of fertility tolerances in agricultural landscapes.

Under extreme circumstances, where networks have completely extinction-prone plant communities or completely resistant ones, differences in robustness to global simulated extinctions might be driven by the second effect alone, regardless of network structure. However, this is unlikely in the data given the significant relationship with generality and robustness under randomised extinctions. Also, all hectads possessed plant communities with varying positions in the extinction sequences. For example, Figures 4.2A and 4.2C show extinction curves for the two hectads which were, respectively, most and least robust to extinctions ordered by plant trend. From the distribution of the tick marks denoting plant extinctions from the hectad on the horizontal axes it is clear that, whilst these two hectads have plant communities consisting of species with differing positions in the extinction sequence, neither hectad has all its plant species at either extreme.

Of course, the observed tendency of agricultural networks to require extreme plant extinction scenarios to collapse pollinator network structure does not mean that agriculture is without detrimental effects. Simple network metrics are insufficient to capture the myriad aspects of ecological stability (Grimm and Wissel 1997). Whilst the networks of agricultural landscapes may be more robust to the scenarios I examined, they may also have lower levels of functional diversity. Potentially, they may also have lower functional resilience due to a homogenisation of species traits in response to the selective pressures of intensive agriculture (Woodcock et al. 2014, Oliver et al. 2015b, Kaiser-Bunbury et al. 2017), as seen in the results for plant Ellenberg N.

In reality, extinctions are unlikely to proceed in a rigid linear sequence according to a single predictor. Extinction cascades (Vanbergen et al. 2017), rewiring (Thierry et al. 2011, Ramos-Jiliberto et al. 2012), climate change (Chen et al. 2011), disease (Smith et al. 2006) or invasive species (Bartomeus et al. 2008) can alter the stability of networks in unpredictable ways. However, the approach for calculating robustness to global simulated extinctions is sufficiently flexible that, where information on such effects exists, these could be incorporated into the extinction sequences.

CROP-POLLINATOR NETWORK PROPERTIES

The results showed that crop-pollinator networks are significantly more robust to simulated extinction scenarios than the overall networks of which they are a subset. This is probably due to the observed ubiquity and high generality of crop-pollinator species. These characteristics might be expected, as GB crop-pollinators are by definition those species pre-adapted to exploit the resource of non-native agricultural crop species growing in highly modified landscapes. The results support the contention of Kleijn et al. (2015) that strategies and initiatives based on conserving crop-pollinators will provide insufficient protection for wild pollinator communities overall. More generally, the results suggest caution where such functionally specific taxa are studied in isolation of the wider communities of which they are often only a small fraction. Obviously, crop-pollinators can be threatened by a wide variety of factors other than loss of nectar sources (Vanbergen et al. 2013, Gill et al. 2016, Potts et al. 2016). For example, preferential loss of crop-pollinators could be triggered if association with crops results in detrimental exposure to pesticides (Stanley et al. 2015, Woodcock et al. 2016b).

LIMITATIONS OF THE POTENTIAL NETWORK APPROACH

Constructing potential networks from biological records has a variety of limitations and assumptions that constrain their biological realism (hence ‘potential’ networks) and affect the uncertainty of results. Perhaps the most obvious limiting factor in the networks are the biological records from which they are constructed. In particular, the data are affected by shortfalls in the knowledge of species occurrence and of their interactions (Hortal et al. 2015).

Regarding occurrence, although FRESCALO accounts for variation in recorder effort, there are likely to be remaining inaccuracies for rare or under-recorded species, whilst conversion of FRESCALO's probabilistic outputs to binary presence/absence values may also introduce errors, particularly at species' range boundaries. Regarding interactions, I acknowledge that the coverage of GB plants, pollinators and the interactions between them are incomplete (see Appendix B2). The potential networks may exhibit either 'missing' or 'forbidden' links in some hectads (Olesen et al. 2010) as they do not account for variation in interactions due to flower phenology (Basilio et al. 2006, Rafferty and Ives 2011), pollinator life-history (Vieira and Almeida-Neto 2015, Vanbergen et al. 2017) or pollinator resource-switching (Thomsen et al. 2017).

The exploration of some of these sources of uncertainty (see Appendices B4 and B5) suggests that uncertainties arising from occurrence and/or interaction data affect hectad-level networks in ways that are relatively consistent across space. Whilst both sources of uncertainty affect the accuracy of individual potential networks they are far less likely to introduce a systemic bias which would affect the observed spatial patterns and relationships with agricultural land. Therefore, despite these limitations, I suggest that the potential networks properties and the spatial patterns I observe are broadly representative of real-world networks (see Appendix B5).

CONCLUSIONS

The results demonstrate the ability of potential networks constructed from biological records to provide new insights into spatial patterns of ecological networks across national scales that would be impossible to monitor using conventional direct observation approaches. The positive relationship between agricultural cover and robustness to a range of extinction scenarios supports previous observations that anthropogenic disturbance can result in ecological networks which are more robust to further perturbation. Furthermore, from the results, crop-pollinator networks are not representative of wider plant-pollinator networks, such that targeting landscape management for the retention of crop pollination may be entirely insufficient to conserve wider biodiversity (Kleijn et al. 2015).

The findings suggest potentially productive fields of further investigation, including further investigation of the mechanisms underpinning spatial patterns in network properties, validation of potential networks against those constructed from large-scale molecular data and exploration of more complex scenarios of extinction, invasion or restoration. In the future, the production of potential networks from biological records is likely to become easier and more accurate, as new technology and methods increase the quality and quantity of biological records (Tulloch et al. 2013, Gray et al. 2014, August et al. 2015a, Powney and Isaac 2015) and novel molecular techniques increase the potential for wide-scale validation (Keller et al. 2015, Richardson et al. 2015, Bohan et al. 2017, Pornon et al. 2017).

4.6. Chapter acknowledgements

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Chapter 5: Effects of future agricultural change scenarios on beneficial insects[3]

5.1. Abstract

Insects provide vital ecosystem services to agricultural systems in the form of pollination and natural pest control. However, there are currently widespread declines in beneficial insects which deliver these services (i.e. pollinators and 'natural enemies' such as predators and parasitoids). Two key drivers of these declines have been the expansion of agricultural land and intensification of agricultural production. With an increasing human population requiring additional sources of food, further changes in agricultural land use appear inevitable. Identifying likely trajectories of change and predicting their impacts on beneficial insects provides a scientific basis for making informed decisions on the policies and practices of sustainable agriculture.

I created spatially explicit, exploratory scenarios of potential changes in the extent and intensity of agricultural land use across Great Britain (GB), at a 10km (hectad) resolution. Scenarios covered 52 possible combinations of change in agricultural land cover (i.e. agricultural expansion or grassland restoration) and intensity (i.e. crop type and diversity). I then used these scenarios to predict impacts on beneficial insect species richness and several metrics of functional diversity. Predictions were based on species distribution models derived from biological records, comprising data on 116 bee species (pollinators) and 81 predatory beetle species (natural enemies).

I identified a wide range of possible consequences for beneficial insect species richness and functional diversity as result of future changes in agricultural extent and intensity. Current policies aimed at restoring semi-natural grassland should result in increases in the richness and functional diversity of both pollinators and natural enemies, even if agricultural practices remain intensive on cropped land (i.e. land-sparing). In contrast, any expansion of arable land is likely to be accompanied by widespread declines in richness of beneficial insects, even if cropping practices become less intensive (i.e. land-sharing), although effects of functional diversity are more mixed.

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5.2. Introduction

Beneficial insects deliver a wide variety of ecosystem services essential to human life (Schowalter et al. 2018). In agricultural systems, two of the most economically important services are pollination and natural control of crop pests (by predatory or parasitic ‘natural enemies’). Pollination services have been valued at US$235-577 billion (Lautenbach et al. 2012) and affect yield or quality of most globally important crop types (Klein et al. 2007, Gallai et al. 2009), whilst natural control of crop pests has been valued at over US$400 billion (Costanza et al. 1997) and is vital to many high economic value crops (e.g. Colloff et al. 2013, Classen et al. 2014).

There is increasing evidence of widespread declines in both pollinators (Kluser and Peduzzi 2007, Potts et al. 2010, Ollerton et al. 2014, Powney et al. 2019) and natural enemies (Kotze and O'Hara 2003, Brooks et al. 2012, Oliver et al. 2015b). A significant contributor to these declines has been the expansion of agricultural land and the intensification of agricultural production (Robinson and Sutherland 2002, Kotze and O'Hara 2003, Kluser and Peduzzi 2007, Potts et al. 2010), with the accompanying prevalence of agrochemicals (Basedow 1990, Woodcock et al. 2016b) and simplification of landscapes (Kotze and O'Hara 2003, Bianchi et al. 2006, Ollerton et al. 2014, Senapathi et al. 2015, Landis 2017). As insects themselves decline, so do the services they provide (Kremen et al. 2002, Oliver et al. 2015b) such that deficits are either already occurring (Garibaldi et al. 2011, Zhao et al. 2015) or predicted in the near future (Aizen et al. 2008).

With an increasing human population requiring additional sources of food (Godfray et al. 2010), further changes in agricultural land use appear inevitable. Simultaneously, international (CBD 2017) and national (Defra 2011, 2018a) policies incorporate significant commitments toward the restoration of intensively managed agricultural land. Future agricultural landscapes may therefore develop in many possible ways to meet these multiple goals. One of the most obvious distinctions is the contrast between ‘land-sharing’ and ‘land-sparing’ approaches (Green et al. 2005, Ekroos et al. 2016). Land-sharing integrates food production and biodiversity conservation on the same land, increasing the amount of farmed land but reducing intensity of agriculture. Land-sparing segregates food production and biodiversity conservation, compensating for a reduction in the farmed area by intensifying farming practices. Assessing the relative sustainability of these options, in terms of both food production and environmental impact, relies on empirical and theoretical knowledge of how changes in agricultural systems affect populations of beneficial insects, especially at the regional and national scales at which most agricultural policy is targeted and formulated. The majority of studies documenting the impacts of agriculture on beneficial insects have focused on the past (e.g. Robinson and Sutherland 2002, Kotze and O'Hara 2003, Brooks et al. 2012, Comont et al. 2014, Senapathi et al. 2015). While this provides evidence that the expansion of intensive agricultural practices has had largely negative impacts on beneficial insects, it has limited value in planning future agricultural policy, with comparatively few studies exploring potential future impacts over larger spatial scales (Reidsma et al. 2006). Furthermore, individual species differ in terms of functional characteristics that affect their capacity to exploit their environment. These differences affect not only on their response to environmental change but also in their capacity to deliver ecosystem services (Greenop et al. 2018, Woodcock et al. 2019). Exploring how changes in the occurrence of individual species impact on the functional diversity of the insect community thus provides additional information on how future agricultural changes may affect the capacity of beneficial insects to deliver ecosystem services (Hoehn et al. 2008, Greenop et al. 2018, Woodcock et al. 2019).

Here I develop national-scale scenarios of future change in the extent and intensity of agricultural land use to understand potential impacts on beneficial insects. The aim of scenario approaches is not to predict the future, but to better understand the range of potential outcomes, uncertainties and trade-offs between different responses (Moss et al. 2010, Holway et al. 2012). They provide a valuable method for engaging with policy makers (Audsley et al. 2006) and stakeholders (Tompkins et al. 2008) and a route for operationalising the ecosystem service concept into land use policy (Grêt-Regamey et al. 2017). Creating exploratory scenarios and modelling their impacts on key service indicators such as beneficial insect communities can thus be an important tool for designing and refining land use policy options (Holway et al. 2012), especially if these approaches can be based on widely available data and accessible models. The aims of this study were therefore:

i) To create multiple exploratory scenarios of potential future change in the extent of agricultural land cover and intensity of land use at national scale for Great Britain (GB)

ii) To use biological records to model the effect of existing patterns of land cover and land use on the distributions of pollinators (bees) and natural enemies (predatory beetles)

iii) To use these models to predict the impacts of all possible combinations of the scenarios on the species richness and functional diversity of beneficial insects

5.3. Methods

CREATING SCENARIOS OF FUTURE AGRICULTURAL CHANGE

Scenarios of agricultural land cover extent

I created two contrasting scenarios to explore changes in the extent of agricultural land, the balance of arable vs. pastoral farming, and the relative amounts of improved (i.e. intensively managed with agrochemical inputs and sowing of productive grass species) vs. semi-natural (i.e. retaining a diverse plant community, with low levels of management) grasslands:

i) Expansion of land under agricultural production. This was primarily driven by conversion of improved grassland to arable, with a smaller proportion from conversion of semi-natural grasslands to improved grassland (Fig. 5.1). Such changes may occur under increased demand for food (Godfray et al. 2010) and profitable farming (Defra 2018a).

ii) Restoration of grassland (i.e. retraction of agricultural land), converting improved grassland to semi-natural and arable to improved grassland (Fig. 5.1), in line with national (Defra 2018a) and international (European Commission 2011) policies for restoring semi-natural grasslands. Although GB semi-natural grasslands do have an agricultural role (extensive grazing) they are rare in the intensive arable systems which dominate Western Europe (Pedro Silva et al. 2008).

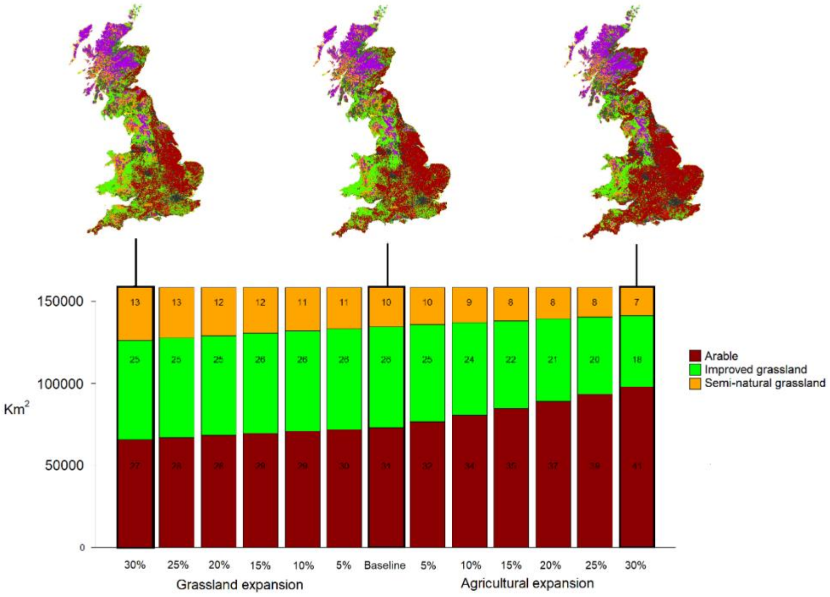

Figure 5.1. *Plot of areas of arable land, improved grassland and semi-natural grassland under each land cover scenario, and associated land cover maps for the baseline and two most extreme scenarios. Numbers on bars are percentage of GB covered by each land cover class under the scenario.*

Expansions were performed in sequential fashion, with 5% increments up to 30% change from the baseline (i.e. present-day land cover from the CEH Land Cover Map 2007 (LCM2007, Morton et al. 2011), creating scenarios with varying levels of expansion (Fig. 5.1). Because GB is already dominated by agricultural land (Morton et al. 2011) expansions beyond 30% are unlikely. For the grassland restoration scenario, expansions of up to 30% are sufficient to cover the ambition of 500,000 Ha of "additional wildlife-rich habitat" set out by Defra (2018a). The scenarios focussed on large scale changes if all other factors (e.g. climate, population growth) were to remain constant.

Scenarios were modelled using the Integrated Valuation of Ecosystem Services and Trade-offs (InVEST) Rule Based Scenario Generator tool (v3.3.3 Sharp et al. 2017). InVEST is a free, open-source suite of ecosystem service models (Sharp et al. 2017). The scenario generator tool ('the tool' from hereon) is a spatially explicit, multi-criteria, multi-objective evaluation tool (Tenerelli and Carver 2012) for generating user-defined scenarios of land cover or land use change. The tool determines relative suitability between grid cells for change by spatial overlay of multiple criteria provided by the user (Sharp et al. 2017). The parameters required by the tool are described in Table 5.1 for each land cover change scenario.

Table 5.1. *Parameters of the InVEST scenario generator tool and the data used for inputs under each of the two land cover change scenarios.*

		Input under each scenario	
Model parameter	**Description**	**i. Agricultural expansion**	**ii. Grassland restoration**
Baseline land cover	Raster map of land cover	CEH Land Cover map 2007 (LCM2007) at 1km resolution (Morton et al. 2011), simplified to ten aggregate classes (broadleaved woodland, coniferous woodland, arable, improved grassland, semi-natural grassland, mountain/heath/bog, saltwater, freshwater, coastal, built up)	
Quantity of Change	Required change in each land cover class	5% increments up to 30% increase in area of agricultural land cover	5% increments up to 30% increase in total area of grassland
Transition Likelihood	Matrix of likelihood of pairwise transitions between land covers	Historic changes from comparison of land utilisation survey (Stamp 1931) and LCM2007	Reverse of transitions used for scenario i
Priority	Relative priority of different land covers to break ties	Arable land > improved grassland	Semi-natural > improved grassland
Suitability Factors	Vector delineation of other known drivers of land suitability	Agricultural land classification (ALC, Soil Survey of Scotland Staff 1981, MAFF 1988, Natural England 2012, Welsh Government 2017) giving suitability of land for agricultural uses based on soils, topography, climate	
Proximity	Distance below which distance to existing cells affects suitability	Set to 10km. This is beyond the size of most farm management units where proximity to existing land determines likelihood of change.	
Constraints	Vector map of factors constraining change	Sites of Special Scientific Interest. Basic unit of GB statutory land protection, known to prevent change over long timescales (Ridding et al. 2015).	Not used

Transition likelihoods for the first scenario were parameterised by extrapolation of observed 20th century land cover changes. These were calculated by comparing the 1930s Dudley Stamp land utilisation map (Stamp 1931) and LCM2007, both at 1km resolution, determining the relative frequency of transitions between land cover classes and weighting transition likelihoods accordingly. The second scenario was more hypothetical, there having been no large scale grassland reversion in GB since the agricultural depression of the late 19th century (Best and Coppock 1962). Instead, the purpose of this scenario was to offer a contrast to agricultural expansion, assuming prioritisation of habitat restoration and biodiversity conservation.

The tool combines all parameter values (Table 5.1) via a weighted sum to gain an index of suitability per cell for each different land cover class. Cells are then converted sequentially, from most to least suitable, until the required level of change is met. Where two or more cells are of equal suitability, the tool selects at random. To assess uncertainty introduced by this random element, each scenario was run 100 times. Uncertainty was then quantified as the percentage of runs for which each cell was equal to its modal land cover across runs (see Appendix C2). To explore the sensitivity of the tool to the parameters and weightings, and to validate its ability to recreate known land cover change, I ran the tool using the 1km version of the Dudley Stamp map as a baseline to examine which combination of parameters most closely approached the actual configuration of the LCM2007 (see Appendix C3).

Scenarios of agricultural land use intensity

I used crop type and rotation as a proxy for agricultural intensity per 1km cell. Cropping patterns drive many aspects of intensity, including presence of monocultures, levels of agrochemical inputs, degree of landscape simplification and available resources for biodiversity. Because cropping patterns are highly variable over time and influenced by complex drivers such as market forces, government policies and societal preferences (Li et al. 2018) I did not use the approach of extrapolating from historic trends. Instead, I classified cropping patterns from an annual satellite-derived map of GB crops, CEH Land Cover® plus: Crops (CEH 2016). I used 3 years of data (2015-2017) to assign each 1km cell to one of three broad cropping classes (‘intensive’, ‘diverse’ or ‘extensive’) using a simple rule base (Appendix C, Table C1).

In general, cells with a predominance of winter-sown cereals and oilseed rape were considered ‘intensive’ because growing these crops without others in the rotation generally requires substantial use of synthetic pesticides and fertilisers (Sieling and Christen 2015) and is associated with increased mechanisation and homogeneous landscapes. These two crops have dominated GB agriculture over recent decades, with detrimental effects on biodiversity (Robinson and Sutherland 2002).

Cells with a large variety of crops or a predominance of root or legume crops, were considered ‘diverse’. Such landscapes are likely to show larger numbers of crop types over time as many of these crops can only be grown as part of more complex rotations. I follow the general usage of ‘crop diversification’ as cultivation of multiple crop types in a given area (Gurr et al. 2016, Aizen et al. 2019) rather than necessarily indicating structural heterogeneity or diversity in its ecological sense.

A prevalence of spring cereals or temporary grass leys was considered indicative of extensive agriculture. Spring sown cereals are generally beneficial for biodiversity in comparison to winter crops (Dicks et al. 2019) and often require lower inputs of pesticides (Robinson and Sutherland 2002), whilst the prevalence of temporary grass is likely to be indicative of farming systems utilising rotational pest and soil management and thus a reduced reliance on agrochemicals.

I constructed three scenarios, based on expansion of one of the three cropping classes into all areas where the ALC indicated the land was suitable to do so. A fourth scenario kept cropping patterns at their present-day baseline. I also predicted cropping intensity for cells which may become arable under one of the land cover change scenarios by taking the modal cropping class for all arable cells on land of the same ALC grade within 100km. Any cell which was dominated by arable land under the selected land cover scenario then received the appropriate cropping class from the selected cropping scenario. The scenarios did not account for configuration of crops within the landscape. Although this is known to affect beneficial insect communities (e.g. Martin et al. 2016, Hass et al. 2018, Haan et al. 2019, Sirami et al. 2019) I cannot predict the composition of a given landscape within a 1km cell using the scenario methods.

MODELLING RESPONSES OF BENEFICIAL INSECTS

To provide data on GB beneficial insect populations, I used biological records (i.e. records submitted to voluntary recording schemes, a form of ‘citizen science’). These provide large volumes of data on species’ identification, date and location (hereafter ‘occurrence’ data) and are a valuable resource for analysing large-scale patterns in time and space (Powney and Isaac 2015).

Occurrence data on bees at 1km resolution were extracted from the databases of the Bees, Wasps and Ants Recording Society held by the UK Biological Records Centre (BRC). The predominance of bees in pollination of GB crops is well supported (Garratt et al. 2014). For natural enemies, I focussed on carabid and coccinellid beetles. These are well-studied in agricultural systems (e.g. Cole et al. 2002, Woodcock et al. 2010, Comont et al. 2014, Woodcock et al. 2014) and sufficiently well-recorded to have large volumes of species-level data (unlike other natural enemy groups, e.g. parasitoid wasps). I compiled lists of predatory carabids and aphidophagous coccinellids (see Appendix C, Table C7 for references used to identify diets) and obtained occurrence data held by BRC from the Ground Beetle Recording Scheme and UK Ladybird Survey, respectively. Data were cleaned to remove species and data that might lead to erroneous or biased results (see Appendix C4 for data cleaning steps), resulting in 116 bee species, 16 coccinellids and 65 carabids for analysis (full list in Appendix C, Tables C5 and C6).

I used species distribution models (SDMs) to model the relationships between species occurrence and current patterns of land cover and agricultural intensity. SDMs are widely used to determine and make predictions from the relationships between occurrence and environmental variables (Elith and Leathwick 2009). SDMs were based on the ten LCM2007 aggregate land cover classes, with arable land subdivided into the current three cropping intensity types. They also included three climatic variables to ensure that modelled distributions were influenced by climatic constraints. These were mean January and July temperatures and mean annual precipitation, averaged across 2000-2012 at 1km resolution (Robinson et al. 2017). A logistic regression based SDM was run for each species of beneficial insect, with all land cover/use and climate variables included as standardised, explanatory variables. The models are thus of the form:

$$logit(\, Pr(Occ)\,) = \alpha + \beta_1\, LULC_1 + \beta_2\, LULC_2 + \beta_3\, LULC_3 + \ldots + \beta_{10}\, LULC_{10} + \beta_{TJan}\, TJan + \beta_{TJul}\, TJul + \beta_{Prec}\, Prec$$

Where Pr(Occ) is the probability of occurrence, α is the intercept and β is the regression coefficient for each covariate. Preliminary analysis supported logistic regression as performing as well as other, more analytically complex methods (Appendix C, Table C4), as also demonstrated in previous studies (Bradter et al. 2018). Models were run in R (v3.4.0 R Core Team 2017) using *Zoon* (August et al. 2017, Golding et al. 2018), with 1000 random background pseudoabsences and 5-fold cross-validation. Because spatial variation in recorder effort influences the probability that lack of occurrence indicates a genuine absence (Lobo et al. 2010) I used a threshold of species detection (Hickling et al. 2006, Redhead et al. 2015), with only cells with at least one other species permitted as pseudoabsences. See Appendix C (Table C4 & Fig. C1) for preliminary analyses used to determine this threshold.

PREDICTING SCENARIO IMPACTS ON SPECIES RICHNESS AND FUNCTIONAL DIVERSITY

Relationships with land cover and cropping intensity derived from the SDMs were then used to predict the occurrence of each species in each 10 x 10km grid cell (hectad) for all factorial combinations of land cover and cropping intensity scenarios (52 possible combinations = 2 land cover change scenarios × 6 expansion steps × 4 cropping intensity scenarios + 3 cropping intensity scenarios at baseline land cover + 1 baseline land cover and current cropping patterns). Climate layers were held constant across scenarios. For each scenario combination, occurrence probabilities were summed per hectad across species, giving an index of relative richness (Scherrer et al. 2018).

Functional diversity was calculated from traits compiled from sources listed in Appendix C, Table C5. Traits included body size (total length of thorax/elytra and intertegular distance (Cane 1987) for beetles and bees, respectively) because it is related to many functional roles including foraging range (Greenleaf et al. 2007), dispersal ability (Gutiérrez and Menéndez 1997) and life history (Peters and Peters 1986). For natural enemies I also included wing length (macropterous, brachypterous or dimorphic) as this is indicative of dispersal ability (Den Boer 1970) and thus species' vulnerability to disturbance and ability to exploit new habitats (Kotze and O'Hara 2003). I also included diet breadth (oligolectic or polylectic for pollinators; omnivore, generalist or specialist predator for natural enemies), which indicates both responses (vulnerability to changes in food resource availability) and effects (likelihood of feeding on species relevant to agricultural systems). For pollinators, which are highly seasonal in their life cycles, I also included seasonality (voltinism and flight season duration). I calculated two metrics of functional diversity for each hectad based on the species predicted to be found there under each scenario. These were: 1) Rao's quadratic entropy (RaoQ), which expresses the average difference in functional traits between two randomly selected individuals from a community, as calculated from average abundance-weighted pairwise trait differences between species (Botta-Dukát 2005); 2) functional evenness (F_{Eve}), which provides a measure of the evenness of species functional trait distribution (Mason et al. 2005). These two metrics were chosen because of their relative simplicity for calculation over large numbers of hectad and scenario combinations, and their representation of different aspects of functional diversity (Mason et al. 2005, Petchey and Gaston 2006, Mouchet et al. 2010). I also calculated community-weighted mean body size to directly explore one of the traits driving functional diversity responses. Body size is typically inter-correlated with many other characteristics (Gaston and Blackburn 1996, Gutiérrez and Menéndez 1997, Greenleaf et al. 2007, Rusch et al. 2015) and thus provides a core single-trait metric of community functional composition.

Functional diversity metrics were calculated using the *FD* package (Laliberté and Legendre 2010, Laliberté et al. 2014) and used predicated probability of occurrence from SDMs to weight traits in lieu of data on relative abundance (Woodcock et al. 2014).

5.4. Results

Under the baseline land cover and cropping scenarios, I found that the response metrics of species richness and functional diversity were generally inter-correlated to some extent (correlations with species richness were -0.79, 0.46 and -0.88 for pollinators and -0.58, 0.65, -0.71 for natural enemies, for each of RaoQ, F_{Eve} and community-weighted body size, respectively; Spearman's rho, n =2659, p <0.001 in all cases). Although these correlations are statistically significant across the entire dataset of all GB hectads, it was clear that a wide variation in functional diversity metrics per hectad is possible for any given value of species richness (Appendix C, Fig. C3). I therefore present results for species richness and each functional diversity metric separately.

IMPACTS OF LAND COVER SCENARIOS

The expansion of agricultural land cover had almost uniformly negative impacts on species richness, with declines in some hectads exceeding 20% (Fig. 5.2A and 5.2B). These were generally proportional to the degree of expansion, although there was some indication that these declines levelled off at higher percentage expansions. Effects on functional diversity were more mixed. For pollinators, roughly equivalent numbers of hectads showed increases and decreases in RaoQ whilst F_{Eve} was more consistently negatively affected (Fig. 5.2A). For natural enemies, both metrics tended to show decreases, as for species richness. In terms of community-weighted body size, arable expansion tended to favour larger-bodied pollinators and smaller-bodied natural enemies.

The grassland restoration scenario (Fig. 5.2C and 5.2D) was generally beneficial for species richness with widespread increases of up to 10% and very few decreases. The effect on all metrics of functional diversity was generally positive for natural enemies (Fig. 5.2D), whilst for pollinators 10-20% of hectads showed decreases of <1% in RaoQ (Fig. 5.2C). Community-weighted mean body size responded in the inverse manner to agricultural expansion, with a trend towards smaller-bodied pollinators and larger-bodied natural enemy communities.

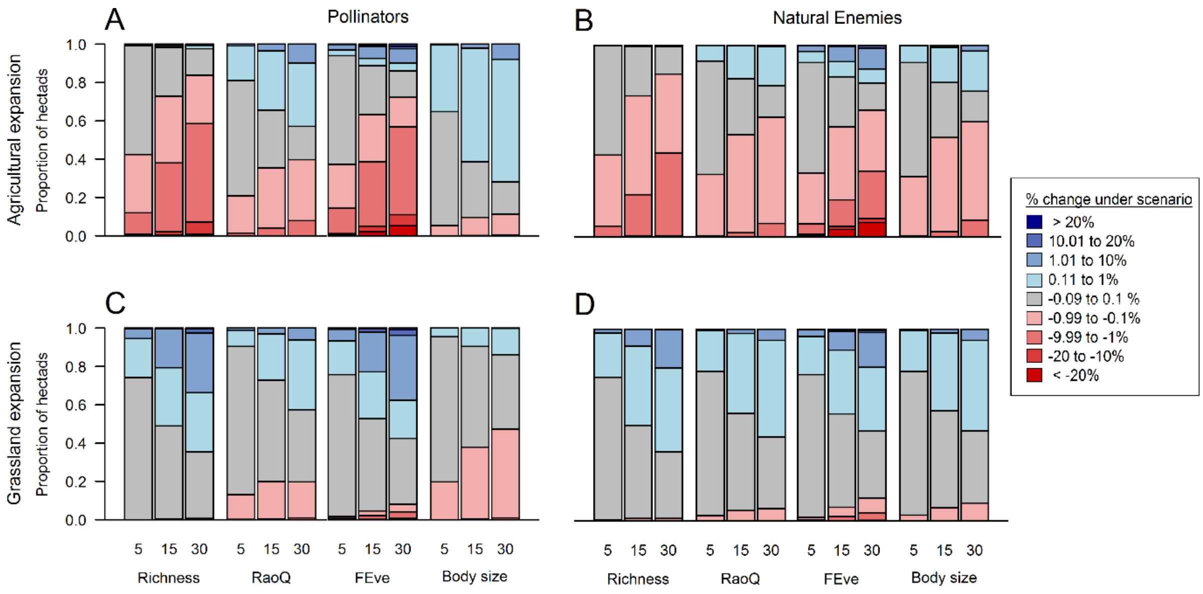

Figure 5.2. *Plots showing proportions of GB hectads with different levels of percentage change in species richness and functional diversity metrics under three levels of the two land cover expansion scenarios; agricultural expansion (A, B), and grassland restoration (C, D). Results are shown for pollinators (A, C) and natural enemies (B, D). Results for all levels of expansion are presented in Appendix C, Figs. C4-C7. RaoQ =Rao's quadratic entropy, FEve =functional evenness, Body size = community-weighted mean body size.*

IMPACTS OF CROPPING INTENSITY SCENARIOS

The intensification scenario had little impact on pollinators, with roughly equal numbers of hectads showing increases and decreases of <1% for most metrics (Fig. 5.3A). Natural enemies were slightly more prone to negative impacts, especially in terms of RaoQ, although these changes were still small (Fig. 5.3B). The diversification scenario was similar in its impacts, with impacts being generally negative but slight (Fig. 5.3C and 5.3D). In contrast, the extensification scenario had much more pronounced effects (Fig. 5.3E and 5.3F). These included widespread increases of up to 10% in beneficial insect species richness and RaoQ. Functional evenness tended to show strong decreases under the extensification scenario for both beneficial insect groups. Effects of the extensification scenario on community-weighted mean body size differed between pollinators and natural enemies - for pollinators (Fig. 5.3E) results varied widely between hectads, but for natural enemies there were widespread increases in community-weighted mean body size by up to 10% (Fig. 5.3F).

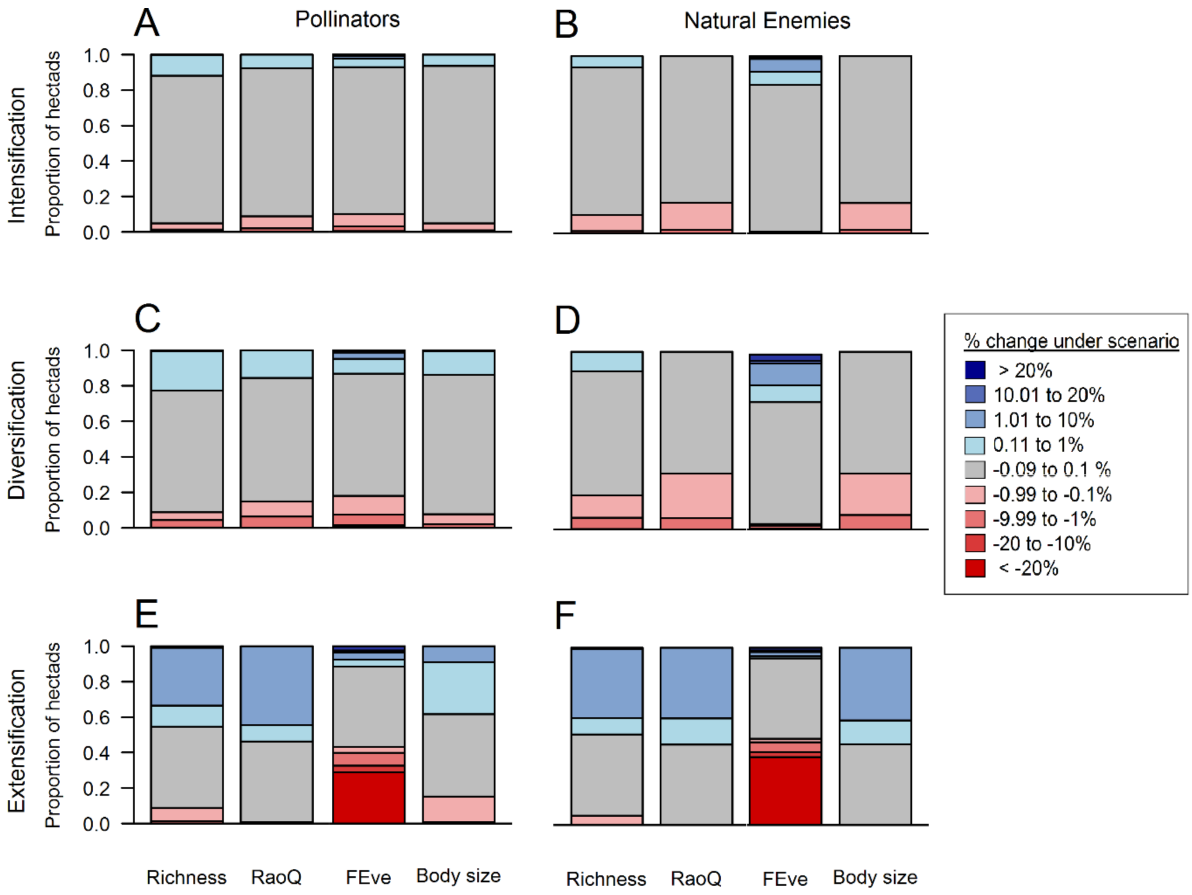

Figure 5.3. *Plots showing proportions of GB hectads with different levels of percentage change in species richness and functional diversity metrics under the three cropping intensity scenarios; intensification (A, B), diversification (C, D) and extensification (E, F). Results are shown for pollinators (A, C, E) and natural enemies (B, D, F). RaoQ =Rao's quadratic entropy, FEve =functional evenness, Body size = community-weighted mean body size.*

IMPACTS OF SCENARIO COMBINATIONS

There were 52 possible combinations of the land cover and cropping intensity scenarios. Note, some of these are not necessarily plausible, but are included to provide a full characterisation of the range of potential futures. Results are shown for all in Appendix C, Figs. C4-C8. I present here scenarios relating to land-sharing or -sparing practises attempting to find trade-offs between the extent and intensity of agricultural land.

Extensification had some mitigating effect on the negative impacts of agricultural expansion under the sharing scenario (Fig. 5.4A and 5.4B). However, at higher levels of expansion this was insufficient to prevent widespread declines in richness in hectads converted from other land uses to extensive agriculture. This was true despite some increases in hectads which were already agricultural but became less intensive (Fig. 5.5C and 5.5G). RaoQ generally increased under land-sharing, whilst F_{Eve} showed strong decreases. Community-weighted mean body size increased for both insect groups, contrasting with their opposite responses to agricultural expansion scenario.

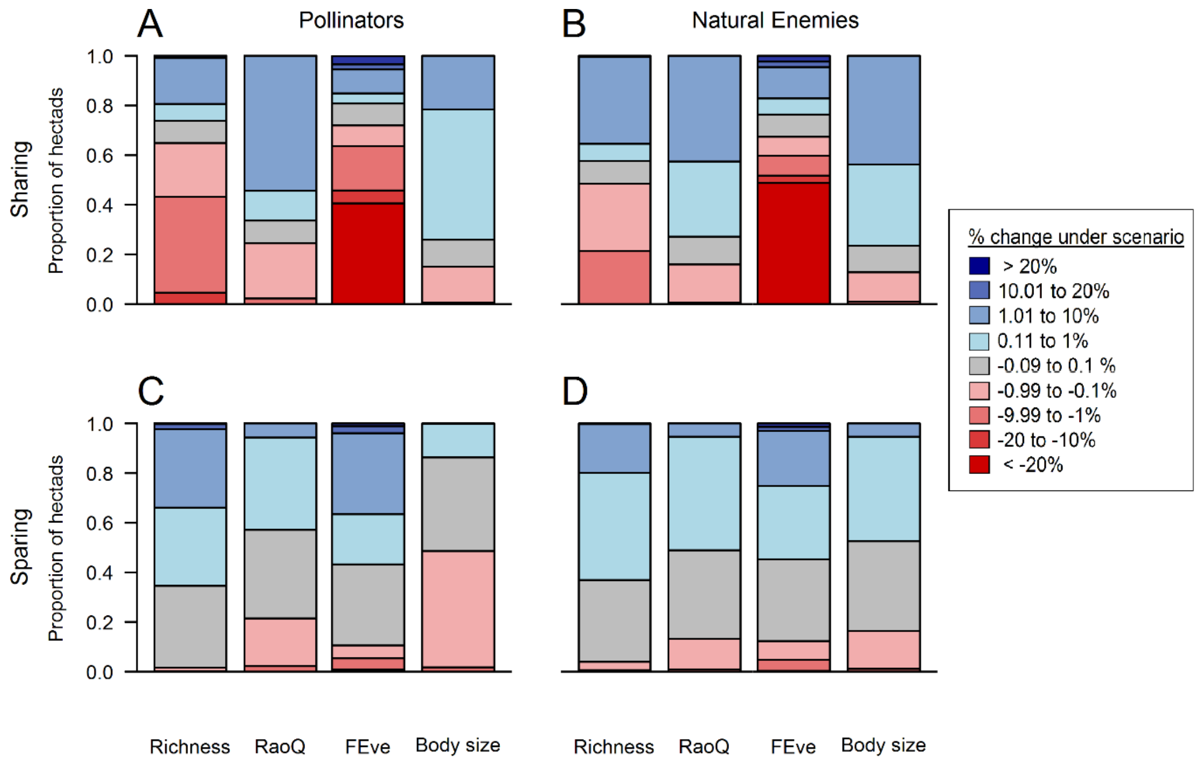

Figure 5.4. *Plots showing proportions of GB hectads with different levels of percentage change in species richness and functional diversity metrics under land-sharing (30% expansion of agricultural land and extensification of cropping, A, B) and land-sparing (30% restoration of grassland and extensification of cropping, C, D). Results are shown for pollinators (A, C) and natural enemies (B, D). Results for all possible scenario combinations are presented in Appendix C, Figs. C4-C7. RaoQ =Rao's quadratic entropy, FEve =functional evenness, Body size =community-weighted mean body size.*

The land-sparing example (Fig. 4C and 4D) showed more widespread increases in species richness. These were often less pronounced (<1%) than under the land-sharing scenario but were not countered by declines in other hectads (Fig. 5D and 5H). RaoQ showed a mixture of small increases and small decreases for pollinators and predominantly small increase for natural enemies. The effect on F_{Eve} was generally positive for both groups. Land-sparing retained the effect of grassland restoration on community-weighted mean body size, with shifts towards smaller-bodied pollinator and larger-bodied natural enemy communities.

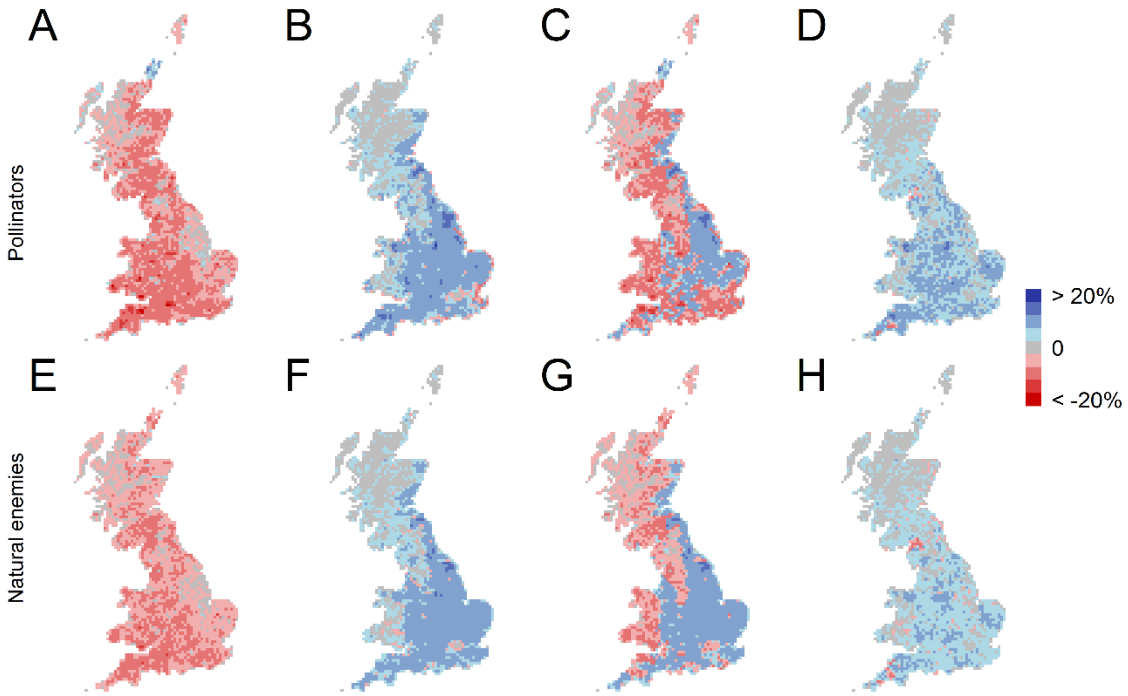

Figure 5.5. *Examples of percentage change in species richness for pollinators (A-D) and natural enemies (E-H) under different scenario combinations. Scenarios are: 30% expansion of agricultural land and intensification of cropping (A, E); 30% restoration of grasslands and extensification of cropping (B, F); 30% expansion of agricultural land and extensification of cropping (land-sharing, C, G); 30% restoration of grasslands and intensification of cropping (land-sparing, D, H).*

Individual species varied widely in their responses to each scenario (Appendix C, Fig C8), including species which appeared to benefit from generally detrimental scenarios such as high levels of agricultural expansion or intensification.

EXPLORING MODEL UNCERTAINTY AND PERFORMANCE

Exploring uncertainty by re-running scenarios 100 times showed a mean 76% agreement with the modal class across all scenarios, for cells which showed change in any scenario run (Appendix C, Table C1). Uncertainty was affected by spatial resolution, being relatively high in the assignment of some individual 1km whereas land cover patterns at coarser resolutions or regional scales were more conserved across scenario re-runs. SDM performance was generally better for pollinating bees than for natural enemies (Appendix C, Table C8). Performance for both groups was sufficient to imply confidence in their predicative ability under the scenarios.

5.5. Discussion

IMPACTS OF THE SCENARIOS ON BENEFICIAL INSECT SPECIES RICHNESS AND FUNCTIONAL DIVERSITY

Scenarios of land cover change

The results show that gains in agricultural production from increases in the area of agricultural land are likely to be accompanied by widespread detrimental impacts on beneficial insect species richness, in line with well-known detrimental impacts of conversion of semi-natural grasslands to agriculture on beneficial insect communities (Kremen et al. 2002, Kotze and O'Hara 2003, Ollerton et al. 2014, Senapathi et al. 2015). Whilst many areas of GB showed moderate decreases, the consequences for individual hectads may be more severe, with species richness losses of over 20%. Effects on functional diversity were rather more mixed, especially for pollinators. Where there are correlations between traits driving the response to land use change and those used to calculate functional diversity (Williams et al. 2010) it is probable that functional diversity will respond differently to species richness. In this case, traits such as body size, dispersal ability and diet breadth all mediate the responses of beneficial insects to landscape. Indeed, the results showed a shift in communities towards large-bodied pollinators (e.g. *Bombus spp.*) under agricultural expansion. This is in agreement with the findings of Bommarco et al. (2010) that small generalists are particularly sensitive to habitat loss. Larger pollinators tend to have longer foraging ranges (Greenleaf et al. 2007) and are thus better able to tolerate the fragmentation of resources imposed by highly agricultural landscapes (Woodcock et al. 2014), although they may be more susceptible to land use intensification in other contexts (Rader et al. 2014). There is ample evidence that certain pollinator communities occur preferentially in agriculturally dominated landscapes (e.g. Holzschuh et al. 2013, Redhead et al. 2018b, Powney et al. 2019). Expansion of these functionally-similar species can either increase functional diversity, when they arrive in landscapes where these functions were previously underrepresented, or reduce it where these communities replace or dominate one with greater functional diversity, hence the mixed results for pollinators. For natural enemies, functional diversity tended to decrease in line with species richness, suggesting either that natural enemies with a wider range of functions are reduced by agricultural expansion or that those species which do benefit from agricultural expansion are even more functionally homogenous than for pollinators. Compared to pollinators, many carabid and coccinellid natural enemies are less mobile and more closely linked to local habitat (Woodcock et al. 2010, Woodcock et al. 2014) so, although there are species which are more frequent in agricultural landscape, it is possible that the constraint of ability to survive in agricultural landscapes on function is even more severe. This reduction in functional diversity is important as a recent meta-analysis found functional diversity in predator communities to be a significant predictor of their capacity to provide natural pest control (Greenop et al. 2018). The decrease in community-weighted natural enemy body size is supported by observations that larger predatory carabids (e.g. *Carabus spp.*) are particularly vulnerable to agricultural land uses (Ribera et al. 2001, Cole et al. 2002) and observed declines linked to their reduced dispersal and lower reproductive rates (Kotze and O'Hara 2003).

Grassland restoration was generally beneficial for both pollinators and natural enemies. Expansions of 15-20%, corresponding to the targets of international (European Commission 2011) and national (Defra 2018a) biodiversity strategies, resulted in an average increase of 0.71-0.96% of pollinators and 0.33-0.45% natural enemies per hectad, with individual hectads showing up to 22% and 10% increases in pollinator and natural enemy richness, respectively. It is unsurprising that restoration of semi-natural grasslands has positive impacts on both groups, given the known importance of these habitats (Cole et al. 2002, Woodcock et al. 2014, Carrié et al. 2017, Holland et al. 2017). This scenario also had generally positive effects on all metrics of functional diversity, suggesting that grassland restoration benefits a functionally broad range of beneficial insects. The restoration of semi-natural grassland can be a very long-term process in terms of effective reconstruction of the target community (Walker et al. 2004, Redhead et al. 2014). That said, restored grassland can still show significant increases in biodiversity over much shorter timescales than those required to return to a pre-disturbance state (Török et al. 2010, Redhead et al. 2014) and the LCM2007 semi-natural grassland class does not consist solely of pristine examples. Therefore, the scenario does not assume full restoration, suggesting localised benefits for beneficial insect richness and functional diversity even at low to moderate levels of change.

Scenarios of cropping intensity

Scenarios of cropping intensity generally had less pronounced impacts than land cover change, when applied in isolation. This is as expected, given that these are effectively proxies for the crops and management regimes in the agricultural landscape and are therefore modifying the management intensity of a given land cover rather than changing it completely. The effect of the intensification scenario was particularly limited, perhaps because the species which have demonstrably survived in GB's already highly-modified agricultural landscapes are likely to be able to persist even if these landscapes are managed more intensively (Redhead et al. 2018b). The impact of the crop diversification scenario was similarly low. However, recent studies have found that habitat configuration or heterogeneity may be more important than crop diversity per se (Hass et al. 2018, Redlich et al. 2018) or that the effect of crop diversity has complex interactions with configurational diversity and the amount of semi-natural habitat in the landscape (Sirami et al. 2019). Because of the limited number of crops and uneven distribution of agricultural land quality in GB, cropping regimes identified as being ‘diverse’ under my rule base are mostly in parts of the country with relatively highly modified agricultural landscapes (e.g. root crop systems in the East of England). For many species, the association between occurrence and diverse cropping as modelled by the SDMs is thus likely to be biased towards negative.

The extensification scenario had more pronounced effects on species richness and functional diversity, reflecting a more profound change from the predominant agricultural systems of GB. For richness and RaoQ these were positive. Extensification was the only scenario to show an opposite effect for F_{Eve} to RaoQ, with a large proportion of hectads showing strong decreases in F_{Eve}. Unlike RaoQ, functional evenness is particularly sensitive to the presence of species present at low levels (Mason et al. 2005) and outlying trait values, especially where these appear in combination (Májeková et al. 2016). Extensification may thus promote a subset of species with relatively extreme trait values. Examining which species show the greatest expansions under extensification to shows these to include small, oligolectic bees with localised distributions (e.g. *Panurgus banksianus, Heriades truncorum*) and small, predatory beetles (e.g. *Notiophilus spp.*).

Scenario combinations

When scenarios were applied in combination it was clear that the differing responses to land cover and cropping intensity resulted in a wide range of possible outcomes. In some cases, there was a degree of trade-off between species richness and functional diversity. Attempting to mitigate against the detrimental impacts of agricultural expansion by decreasing the intensity of agriculture (i.e. land-sharing) appeared to help maintain or even increase RaoQ, but strong decreases in species richness and F_{Eve} were still widely evident. This scenario also created a strong polarisation between existing agricultural areas which showed increases in richness as they became less intensively used and areas which were converted to agriculture and thus experienced strong decreases.

Combining restoration of grassland with an intensification of remaining agriculture to maintain overall levels of food production (i.e. land-sparing) generally only slightly reduced the positive impacts of grassland restoration on species richness and functional diversity. Other studies have also found land-sparing is often determined to be preferable in terms of maximising biodiversity benefits, even when considered alongside delivery of crop yield (Kamp et al. 2015, Ekroos et al. 2016, Lamb et al.), but few of these have examined functional diversity. It should also be borne in mind that the delivery of ecosystem services from both pollinators and natural enemies is strongly driven by landscape composition (Bianchi et al. 2006, Chaplin-Kramer et al. 2011, Chaplin-Kramer et al. 2013, Martin et al. 2016, Holland et al. 2017), so landscapes which venture too far down the route of segregating habitats for biodiversity and crop production may end up undermining the delivery of these services to crops.

LIMITATIONS OF THE METHODS

The scenario approach has several limitations. The fate of individual 1km cells under any one scenario should be treated with caution due to the degree of uncertainty evident at this scale (Sharp et al. 2017), although predictions from SDMs should be less affected since these are made at the hectad scale. Because the scenarios explored a wide range of potential alternative futures, I did not include predications of climate change, which may potentially drive, exacerbate or mitigate against changes in land cover and land use intensity. Although the SDMs included climatic variables, and so could potentially take account of climate change, such scenarios would need to be timebound. This would require knowledge of the timescales over which changes in land cover and cropping systems occur. Since these can vary from gradual processes to step changes, as has been demonstrated by the complex history of agricultural land use change in GB (Best and Coppock 1962, Ridding et al. 2015), parametrising timebound scenarios is a complex task better suited to a narrower range of plausible futures driven by socioeconomic priorities (e.g. O’Neill et al. 2017). Whilst comparatively simplistic, the approach has the advantage of being transparent to the user. Because each individual scenario can be generated quickly, it becomes feasible to explore a wide range of scenarios focussed on plausible, near-future changes in agriculture at the national scale (Swinbank 2017, Defra 2018a) with multiple iterations to obtain estimates of uncertainty. The results thus are thus of particular relevance to policy makers in narrowing down land use policy targets and building stakeholder engagement and confidence (Holway et al. 2012). More complex approaches can then by deployed to further develop polices and determine how to incentivise transitions towards a desired target.

The use of SDMs also has its limitations. Whilst model performance was generally adequate, performance metrics suggest many factors driving insect distributions are unaccounted for (e.g. landscape configuration, vegetation communities, soils, local land management). Predictions from SDMs also assume that relationships with current land uses classes are representative of future ones. For example, the areas I currently classify as ‘diverse’ may not reflect the actual outcomes of future agricultural diversification, which might include crops not currently grown in GB or novel agricultural practices such as intercropping. Future 'intensive' agriculture might also look very different to current intensive landscapes, especially if 'ecological intensification' approaches succeed in creating agricultural landscapes which both promote biodiversity and enhance crop yields via enhanced ecosystem service delivery (Bommarco et al. 2013, Pywell et al. 2015, Landis 2017, Kleijn et al. 2019). Recent research has also identified that the extremes of land-sharing and land-sparing are both outperformed by combinations of spared land, high-intensity farmland and lower-intensity farmland (Lamb et al. 2019). Whilst such approaches cannot be explored with the current suite of scenarios, the methods could be adapted to simulate these and explore their effects.

CONCLUSIONS AND IMPLICATIONS FOR LAND USE POLICY AND ECOSYSTEM SERVICE DELIVERY

The results clearly show a range of possible consequences for beneficial insects depending on the future extent and intensity of agriculture. With declines in beneficial insects being and issue of global importance and GB at a pivotal time for determining future land use policy (Defra 2018a) it is particularly important to explore such potential futures explore the potential consequences of changes in land use and thus select and refine policy targets. Encouragingly, the results suggest that current policies aimed at increasing the area of semi-natural grassland should increase average richness and functional diversity of both pollinators and natural enemies. These increases are likely to occur even if agricultural practices are intensified, for species richness at least. In contrast, any expansion of arable land is likely to drive further declines in beneficial insect richness and functional diversity, even if agricultural practices become less intensive.

The relationships between species richness, functional diversity and ecosystem service delivery are complex (see overviews in Balvanera et al. 2006, Bianchi et al. 2006, Balvanera et al. 2013). Ecosystem service delivery at fine scales can depend more on the abundance of key species (Griffin et al. 2013, Kleijn et al. 2015, Winfree et al. 2015, Woodcock et al. 2019), a factor I did not directly consider in the current analysis (Woodcock et al. 2019) than richness or diversity. Despite this complexity, richness and functional diversity of beneficial insects are increasingly found to be important at broader spatiotemporal scales (Hoehn et al. 2008, Greenop et al. 2018, Dainese et al. 2019, Woodcock et al. 2019). It is thus difficult to predict exactly how the changes resulting from the scenarios might affect the ecosystem services delivered by beneficial insects across GB agricultural systems. Whilst it is hard to assess the relative merits of situations which show trade-offs between species richness and functional diversity, avoiding situations that lead to severe declines in either would seem advisable.

The methods used in this study demonstrate a valuable approach to the creation of scenarios for land use change and the exploration of their impacts on biodiversity at national scale. By using widely available spatial datasets (e.g. land cover maps) and occurrence data from biological records, modelled via open-source software (e.g. R and InVEST) the results demonstrate that scenario exploration can be performed in an intuitive, transparent and interoperable manner (Holway et al. 2012) and show the value of these data and methods for providing policy-relevant information.

5.6. Chapter acknowledgements

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Chapter 6: Discussion

6.1 Thesis overview

Here I briefly summarise the core aims, approaches and results contained in each chapter of this thesis.

In Chapter 1, I introduced the importance of insect delivered ecosystem services to the global food production system. I also explored some of the key knowledge gaps in our current understanding of insect-delivered ecosystem services which analysis of large-scale spatial datasets, the focus of this thesis, might help to address. In particular, my analytical chapters are relevant to current knowledge gaps on: i) the link between large-scale landscape structure and agricultural production, as mediated by the flows of ecosystem services (Chapter 3); ii) how beneficial insect communities and network structure varies across space and how this relates to landscape structure (Chapter 4); iii) how future changes in land management may affect populations of beneficial insects and their capacity to deliver ecosystem services (Chapter 5).

In Chapter 2, I reviewed the history of ecological resilience as a concept and explored its use in the context of food production systems and ecosystem services. It is clear that a identifying a standard definition of resilience in this context remains challenging (Béné et al. 2012, Myers-Smith et al. 2012, Standish et al. 2014, Tendall et al. 2015, Béné et al. 2016, Newton 2016, Quinlan et al. 2016, Ingrisch and Bahn 2018), and that resilience of a given system is multi-faceted and comprised of numerous sub-systems at a wide range of spatial scales and levels of ecological organisation (Bullock et al. 2017). Whilst working towards resilience in agricultural systems offers a potentially useful contrast to the technological and production-oriented paradigm that has led to the widespread environmental damage inflicted by agriculture over the twentieth century, we must be careful to acknowledge that building resilience is a means to an end (i.e. continued ability of GB landscapes to deliver multiple ecosystem goods and services, including food production). When analysing resilience of individual parts of the system it is important to define the limits of the system – i.e. “resilience of…” and “resilience to…” (Carpenter et al. 2001) - and to explore how resilience at one level is likely to affect or indicate resilience of the system as a whole (Bullock et al. 2017). If using metrics to quantify resilience, these should ideally be linked directly to system function and cover aspects of the resistance, recovery and response of the system (Béné et al. 2012, Béné et al. 2016, Ingrisch and Bahn 2018).

Chapter 3 applied some of these resilience concepts to temporal patterns of wheat yields and explored the relationship between yield resilience and landscape structure. Whilst the effect of landscape structure on beneficial insect communities is well-studied (Purtauf et al. 2005, Bianchi et al. 2006, Hendrickx et al. 2007, Chaplin-Kramer et al. 2011, Mitchell et al. 2014, Puech et al. 2015, Martin et al. 2016, Holland et al. 2017, Redlich et al. 2018, Sirami et al. 2019), this is seldom followed through to actual crop yields, and almost never to examination of yield variation over time (Holland et al. 2016, Martin et al. 2016, Karp et al. 2018, Martin et al. 2019). As a result, direct evidence for the benefits of managing landscapes for beneficial insects on crop yield or yield resilience is scarce, which acts as a barrier to uptake of such management by the farming industry (Kleijn et al. 2019). In Chapter 3 I used multiple metrics of crop yield resilience derived from a 10-year time series, relating to overall level of yield, interannual stability and resistance to a specific, extreme event. The relationship of these metrics to landscape structure was then explored at hectad resolution across England. The results showed that, the sensitivity of yield resilience to landscape context varied based on the metric of resilience chosen. Relative yield was maximised in landscapes with a high coverage of arable land, whilst stability was highest in landscapes with high coverage of arable land but in close proximity to semi-natural habitats and resistance was highest in landscapes with high coverage of semi-natural habitats, independently of the amount of arable land. This means that the general trend was of increasing importance of semi-natural habitat and decreasing importance of arable land as resilience metrics were derived from shorter portions of the time series. These findings demonstrate the value of several recommendations made in Chapter 2. Firstly, the additional knowledge that can be obtained by examining resilience of a given function, rather than focusing on absolute levels of delivery. Secondly, the importance of examining several metrics which relate to different facets of resilience in conjunction (Carpenter et al. 2001, Cabell and Oelofse 2012, Ingrisch and Bahn 2018). Thirdly, that attempting to capture too many aspects of resilience within a single metric may be misleading – this was particularly the case for relative yield across the entire time series, which although it conceptually captures multiple instances of resistance and recovery (Fig. 2.2 and 3.1) ends up, in this particular system, being strongly correlated with simple average yield. Such metrics also have the issue that, although we have adequately defined “resilience of…”, our definition of “resilience to…” (Carpenter et al. 2001) is broadened to any and all environmental perturbations occurring over the course of the time series. Whilst the exact biological mechanisms underpinning the relationships I describe in Chapter 3 can only be inferred, there are vast bodies of evidence linking: a) semi-natural habitats to reservoirs of natural enemy diversity (Woodcock et al. 2014, Holland et al. 2016, Tschumi et al. 2016a, Holland et al. 2017, Bengtsson et al. 2019); b) spillover of pest predation into crops (Tscharntke et al. 2005, Rand et al. 2006, Blitzer et al. 2012, Pywell et al. 2015, Woodcock et al. 2016a) and c); levels of pest control to richness, abundance and diversity (taxonomic and functional) of natural enemy communities (Griffin et al. 2013, Dainese et al. 2017, Greenop et al. 2018, Dainese et al. 2019). All this evidence is strongly supportive of ecosystem services mediating the observed relationships between crop yield and landscape. Crucially, these relationships may be masked under ordinary circumstances, potentially because agricultural management practices (including the application of agrochemicals) and the services arising from species resident in arable parts of the landscape are usually sufficient to ensure high average yields (Pywell et al. 2015, Gagic et al. 2017, Martin et al. 2019). It is only when yield resilience is examined over shorter timescales that we see the ability of environmental pressures to override the usual controls and show the benefit of semi-natural habitats. In a world where climatic extremes are predicted to become both more frequent and more severe (Rosenzweig et al. 2001, Rahmstorf and Coumou 2011, Trnka et al. 2014, GFS 2015, Iizumi and Ramankutty 2016, Harkness et al. 2020), and the reliance of agriculture on pesticides is being called into question in favour of integrated management approaches (Rusch et al. 2010, Hillocks 2012, Bommarco et al. 2013, Potts et al. 2016, Kleijn et al. 2019), relationships with landscape structure may become even clearer and more important. However, whether we can adapt from current practices sufficiently to build agricultural systems with increased resilience to climate change (Altieri et al. 2015) remains to be seen, given the degree of undesirable resilience of the current intensive agricultural paradigm (Wilson and Tisdell 2001, Gould et al. 2018, Kleijn et al. 2019).

Chapter 4 explored another set of relationships with landscapes, which have previously been difficult to quantify, those of network structure. Plant-pollinator networks offer valuable insights into how these ecological communities are structured and how they might respond to environmental change (Montoya et al. 2006, Vázquez et al. 2009, Burkle and Alarcón 2011, Pocock et al. 2012, Tixier et al. 2013, Gao et al. 2016, Tylianakis and Morris 2017, Bruder et al. 2019, Morrison et al. 2020). However, because they are time-consuming to construct experimentally for a given location, examining patterns across space (and thus relationships with landscape) has generally been limited to small numbers of sites along environmental gradients (Olesen and Jordano 2002, Trøjelsgaard et al. 2015, Welti and Joern 2015, Tylianakis and Morris 2017, Morrison et al. 2020). In Chapter 4, I used biological recording data to construct potential plant-pollinator networks for every hectad in GB. Metrics of network structure were calculated for every hectad, including robustness to simulated extinctions ordered by plant traits known to affect vulnerability to environmental pressures. The results showed a positive relationship between agricultural cover and robustness to a range of extinction scenarios. Increased robustness was attributable to changes in plant community composition (fewer extinction-prone species) and network structure (increased pollinator generality). This suggests an environmental filtering effect, whereby highly agricultural landscapes have already lost vulnerable species and retained those with traits enabling their survival under the pressures of intensive agriculture, such that further increases in these pressures have reduced effect. Crop-pollinator networks were especially robust, consisting almost entirely of unusually widespread, generalist species. Of course, these networks will only continue to be robust if ongoing pressures resemble historic ones, with different pressures potentially even inverting the relationship between agricultural cover and robustness (Morrison et al. 2020). Changes in the pressures associated with agricultural landscapes are highly likely, as such landscapes are prone to major upheavals over short timescales due to changes in cropping and management practices. For example, many pollinators which have shown increases over the past few decades are those associated with pollination of agricultural crops (Powney et al. 2019), by far the most extensive of which in GB is oilseed rape. In England alone this crop went from an area of 218000 Ha in 1982 to 742000 Ha in 2012, more than tripling over three decades (Defra 2019). Whilst the balance between provision of a superabundant but temporally limited resource (Westphal et al. 2003, Westphal et al. 2009, Holzschuh et al. 2013, Kovács-Hostyánszki et al. 2013, Shaw et al. 2020) and exposure to pesticides (Woodcock et al. 2016b, Woodcock et al. 2017) has had complex effects on pollinator communities, some species appear to have benefitted overall (Powney et al. 2019). But the moratorium on neonicotinoid seed treatments in 2013 and challenging climatic and market conditions have prompted reductions in the area of oilseed rape grown, to a recent low of 492000 Ha in 2019 (Defra 2019). Whether oilseed rape continues to decline, and which crops which replace it if so, is likely to have major impacts on the pollinator communities of intensive arable land quite independently of longer-term drivers such as climate change. It is also unknown whether the relatively limited communities which currently typify agricultural landscapes in GB can provide adequate pollination under all circumstances. If natural enemy communities are structured in similar ways this might also help to explain the findings of Chapter 3, where average levels of function may be maintained by a core community of species which can survive on agricultural land (with some supplementary effect of spillover from fragmented semi-natural habitats in the landscape) whilst under extreme circumstances these prove insufficient and the benefits of having other communities in the landscape are revealed.

The potential for future changes in agricultural landscapes was explored further in Chapter 5. Here I constructed a range of spatially explicit scenarios of change in GB land cover at 1km resolution (agricultural expansion vs. grassland restoration) and land use (intensification, extensification or diversification of cropping patterns). These scenarios used a range of historic and current spatial datasets to simulate where changes are likely to take place and validate the ability of the scenario approach to re-create historic change. Species distribution models (SDMs) were constructed based on biological records to determine the relationship between occurrence and current land cover and cropping patterns for pollinating bees and natural enemy beetles. These models were then used to predict occurrence under each scenario. Occurrence across species was then converted to indices of species richness and functional diversity under each scenario. The results showed a wide range of possible consequences for beneficial insect species richness and functional diversity in the context of GB land use change. Restoration of semi-natural grassland increased richness and functional diversity of both pollinators and natural enemies, even when agricultural practices were intensified on remaining cropped land. In contrast, any expansion of arable land is likely to be accompanied by further declines in richness and functional diversity of beneficial insects, even if cropping practices become less intensive in terms of cropping practices. It is clear from these results that large-scale improvements in beneficial insect populations require the restoration of semi-natural grasslands. Combining this with extensification of cropping brings most benefit. Whilst the requirement to maintain food production limits the extent to which agricultural land is likely to become less intensive, the concept of sustainable intensification suggests that the intensive arable landscapes of the future may not resemble those of the past, with greater integration of semi-natural habitats, more complex crop rotations and reduced reliance on agrochemicals (Pywell et al. 2015, Landis 2017, Kleijn et al. 2019).

6.2 Implications for the management of agricultural landscapes

At the spatial scales and resolutions analysed within this thesis (national coverage of 1-10km grid cells) it is clear that semi-natural habitat, and especially semi-natural grassland, plays an important role in both maintaining the richness and diversity of beneficial insects (Chapter 5) and in promoting the delivery of ecosystem services which maintain crop yields under environmental perturbations (Chapter 3). The importance of semi-natural grasslands as refuges for biodiversity are well known (Critchley et al. 2004, Öckinger and Smith 2007, Bullock et al. 2011, Woodcock et al. 2014, Holland et al. 2017, Bengtsson et al. 2019), as is their catastrophic decline in GB over the twentieth century (Fuller 1987, van Dijk 1991, Pedro Silva et al. 2008, Ridding et al. 2015). It also evident that the beneficial insects which thrive in these habitats are vulnerable to further degradation of their habitats, as evidenced by the reduced robustness of pollinator communities to plant extinctions ordered by fertility tolerance (Chapter 4) and the severe declines in species richness observed when semi-natural grasslands are replaced with agriculture, even when extensive cropping practices are used (Chapter 5). All of these findings suggest that conservation of remaining semi-natural grasslands, and the restoration or recreation of degraded ones, is likely to be beneficial for both insect communities and agricultural production. Current targets under the 25 Year Plan (Defra 2018a) include restoration of losses to nature suffered over the past 50 years and restoration of 500,000 hectares of wildlife-rich habitat (including semi-natural grassland) outside the current protected site network. However, there are important considerations of spatial scale and context. Although semi-natural habitats are generally beneficial to natural enemy and pollinator communities found on adjacent agricultural land (Bianchi et al. 2006, Chaplin-Kramer et al. 2011, Veres et al. 2013, Holland et al. 2016), this does not always translate to increased service delivery and ultimately, crop productivity (Veres et al. 2013, Martin et al. 2016, Tscharntke et al. 2016, Begg et al. 2017). So whilst land-sparing type scenarios often result in optimal outcomes for biodiversity and food production (Egan and Mortensen 2012, Kamp et al. 2015, Ekroos et al. 2016, Lamb et al. 2016, Lamb et al. 2019), giving the highest relative yields in Chapter 3 and the best outcome for insect species richness and functional diversity in Chapter 5, a degree of land-sharing has to take place if ecological intensification is to be successful. This must provide semi-natural habitats which are, on the one hand, of sufficient size and quality to support diverse insect communities and, on the other, sufficiently close to agricultural land to promote ecosystem service delivery. A variety of recent studies have effectively found that, in heavily modified and multi-functional landscapes such as those of GB, sharing vs. sparing is somewhat of a false dichotomy (Phalan 2018, Finch et al. 2019, Lamb et al. 2019). Even in interpreting my results from Chapter 3 there are subtleties around spatial scale here and exactly how we define ‘sharing’ and ‘sparing’ - sparing land such that patches of existing semi-natural habitat can appear within a hectad (so that at a hectad scale the landscape is in fact ‘shared’) is probably beneficial, whilst sparing to the extent that hectads become entirely arable or semi-natural is probably detrimental. It is thus probable that the most constructive approaches to enhancing landscapes for delivery of services provided by beneficial insects are those operating over multiple spatial scales (Bianchi et al. 2006, Begg et al. 2017, Landis 2017). These may consist of a variety of practices involving restoration of degraded semi-natural habitat, coupled with improvements to the general suitability of intensive agricultural land (supporting ecological intensification) and the introduction of novel agricultural practices intended to simultaneously improve or protect both agricultural production and biodiversity (e.g. agro-forestry, organic farming, cover cropping etc). Again, current GB policy is generally supportive of this approach, especially in terms of "developing and implementing policies that encourage and support sustainable crop protection with the minimum use of pesticides… supplementing them with improved crop husbandry and the use of natural predators" (Defra 2018a). Although the scenarios and SDMs developed under Chapter 5 cannot yet simulate the impact of such practices with confidence, they can help to understand the relative vulnerabilities of different areas of the GB landscape to a range of key drivers, which in turn helps target further research and refine the range of plausible policy and management options. Indeed, this is exactly what GB environmental policy bodies such as Defra are currently using such land use scenarios (including those ones described in Chapter 5) to do.

A further general conclusion from the results of this thesis is that protection of ecosystem services is not necessarily sufficient argument for the conservation of insect biodiversity (Kleijn et al. 2015). We have seen that landscapes dominated by arable land have higher average yields (Chapter 3) despite depauperate insect communities, that crop pollinators form communities which are unusually robust to plant extinctions (Chapter 4) and that functional diversity can increase even when species richness is reduced by agricultural expansion (Chapter 5). Whilst in all cases there are subtleties associated with these findings, if we focus solely on the transfer of ecosystem services to agricultural production, we run the risk of concentrating too much on a limited set of species which have already shown their ability to persist in agricultural landscapes despite the massive changes that these have undergone over the past century. The intrinsic value of insect biodiversity and its critical role in wider ecosystem functioning should not be forgotten (Yang and Gratton 2014, Forister et al. 2019, Saunders et al. 2019). A focus on agricultural resilience (Chapter 2) can help overcome this issue. Indeed, the direct measurements of resilience in Chapter 3 clearly help to show that a focus on production or assumptions about average levels of service delivery are misleading and potentially harmful to the livelihoods of farmers in the future. The farming industry in the UK is at pivotal time, with recent extreme weather events (e.g. Impey 2012, Kendon et al. 2019), pesticide resistance (Gould et al. 2018), the withdrawal of active ingredients (Hillocks 2012), public pressure (Myers et al. 2016) and the restructuring of agricultural subsidies (Rodgers 2019) all increasing the awareness that conventional approaches may be insufficient to maintain productive farming. But appreciation amongst farmers of the role that biodiversity can play in helping to buffer against these pressures is not yet widespread (Begg et al. 2017, Kleijn et al. 2019). Also, if increasing agricultural resilience remains a means to the sole end of continued or increased food production, the role of biodiversity remains implicit, with potential for increases in agricultural resilience at the cost of biodiversity. Perhaps a better goal is for 'resilience-enhancing landscapes', able to reliably provide multiple functions including food production, biodiversity and other ecosystem services under the environmental changes we are likely to see over the coming decades. Ultimately, our own willingness to adapt and modify our land use, expectations and lifestyles is an integral part of the ability of the landscape, and the ecological and agricultural systems it supports, to resist, recover from and reorganise in response to environmental change.

6.3 Advantages and limitations of the spatial modelling approach

The results described in this thesis show the potential benefits of combining existing spatial datasets via novel analyses in the field of insect-delivered ecosystem services. The methods used across the various analyses might be variously described as macroecological, landscape ecology (Böhm and Popescu 2016), or 'big data' (Hampton et al. 2013, Soranno and Schimel 2014) approaches, and combine elements from all of these fields. Essentially, they have in common the collation and integration of disparate datasets to form spatially explicit explanatory and response variables and model the statistical relationships between them.

Using spatial datasets from remote-sensing, biological records and surveys overcomes the challenge of replicating experimental approaches across sufficiently large areas to examine trends in space and time (Hampton et al. 2013, Soranno and Schimel 2014, Powney and Isaac 2015). Compared to experimental approaches, combining spatial datasets is relatively cheap and large volumes of data can be handled rapidly. However, some of the time saved in collecting the data is then expended in cleaning and handling it, and in designing sufficiently robust approaches to modelling the ecological patterns under investigation. There are, of course, other approaches to describing ecological patterns across larger spatial scales. Once such is to combine the findings of multiple experimental studies in meta-analyses (e.g. Chaplin-Kramer et al. 2011, Griffin et al. 2013, Shackelford et al. 2013, Greenop et al. 2018, Woodcock et al. 2019). This approach has the advantage of exploring whether common patterns are found across multiple systems. However, results are frequently very mixed, because each study has its own unique scale and context (Spake et al. 2019). Studies also use different methods to quantify all components of the system, from communities of beneficial insects (e.g. natural enemies), the functions they perform (e.g. predation of pests), the services these incur (e.g. control of pest populations) and the final good these deliver (e.g. crop yield). Meta-analytical approaches also have limited ability to detect potential trade-offs between different services (e.g. pollinator vs. natural pest control) or different taxonomic or functional groups of beneficial insects (Shackelford et al. 2013), without direct comparisons drawn in the same contexts. Whilst there is a growing field of attempting to improve the ability of meta-analyses to explore context-specific patterns (Gurevitch et al. 2018, Shackelford et al. 2019), the use of large-scale spatial data helps to provide valuable evidence of consistent patterns over space and time.

Some of the limitations of using spatial datasets have already been discussed in previous chapters. Several of these revolve around a fundamental trade-off between the generality of the predictions we can make, and the uncertainty associated with predictions at a given location (Hortal et al. 2015). In the case of Chapter 3, on the one hand, the direct linking of landscape and yield resilience allows predictions that are robust over relatively large spatial and temporal scales and avoids the complexities of meta-analyses covering the responses of multiple cropping systems and insect groups. One the other, we cannot predict exactly how yield will respond to environmental pressures at a given location. In Chapter 4 we can simulate the robustness of multiple networks and explore patterns over national extents, which would be impossible to do experimentally, but we do not know how well our networks reflect those of actual locations within the hectad-scale landscapes we examined. Chapter 5 explores a wide range of potential futures and their probable effects. However, uncertainty around future predictions for a given location are high, given the cumulative uncertainties from the input data, scenario generation and species distribution models. This latter example also highlights a general issue with the approach of combining existing datasets from disparate sources and disciplines, as is common in ecosystem service modelling (Hamel and Bryant 2017). Not only does each dataset have uncertainty associated with it, but every model used to process the dataset into a common, interoperable format will have a corresponding degree of uncertainty. This is even true of common geospatial operations such as reprojection between coordinate systems. Whilst such cumulative uncertainty does not necessarily undermine the general findings of large-scale spatial analyses, it should be described and quantified where possible as this a key part of building trust and credibility of between researchers, stakeholders and policymakers (Hamel and Bryant 2017). The methods used in the preceding chapters tend to account for the effect of uncertainty by randomised resampling or cross-validation approaches, but there are not necessarily transparent to those who wish to use research outputs in policy or to inform land management.

Unless data are available for a very wide range of variables, spatial modelling is often limited in its ability to explore mechanisms. For example, in Chapter 3, data were accessible on landscape structure and crop yields, but not on beneficial invertebrate or pest populations.

Whilst it would be possible to include natural enemy species richness or functional diversity (as modelled in Chapter 5) as a predictor of yield resilience, variations in the number of biological records in a given year would make it impossible to examine variation over time, and the SDM methods of modelling occurrence from raw data are unlikely to capture the subtle variations in natural enemy communities and their movements which are driven by landscape configuration. Indeed, when natural enemy richness was included in models in preliminary analyses, it showed no significant relationship whatsoever with yield or yield resilience. A further limitation is that the natural enemies analysed in Chapter 5 are only a small subset of total natural enemies – whilst they are useful as an indicator of scenario impacts on a functional group they are unlikely to be representative of the entire natural enemy population of a given landscape. Some other natural enemy groups are both relatively well represented in biological recording data and well-studied in terms of their impact on crop pests and thus form good candidate for further exploration (e.g. Syrphid flies Wotton et al. 2019). However, many potentially important groups are insufficiently well-recorded to obtain robust estimates of occurrence (e.g. parasitoid wasps and flies, aphidophagous Neuroptera). Still others are well recorded, but their role in pest-control is extremely context-dependent and limited to specific species, as is the case for birds (Rana et al. 2016, Benayas et al. 2017, Grass et al. 2017). There are other data gaps too - ideally, the plant-pollinator networks in Chapter 4 would be complemented by equivalent pest-natural enemy networks. Whilst DNA barcoding of natural enemy gut content has the potential to build robust potential networks (Barnes and Turner 2016, Bohan et al. 2017, Bush et al. 2017, Pornon et al. 2017), accurate, large-scale occurrence data on a suite of crops pests (e.g. aphids, slugs, Diptera) is difficult to obtain at the spatial and temporal resolution offered by biological recording schemes for pollinators or beetles. However, the potential network approach could still be applied for a limited number of well-sampled points, such as the Rothamsted network of suction traps.

A further fundamental trade-off which is apparent from the results in this thesis is thus that of spatial resolution versus spatial extent (Booth et al. 2014, Hortal et al. 2015, Di Marco et al. 2017). The finer the resolution, the more likely that there will be gaps in our ecological knowledge and the greater the effort required to overcome these, limiting the area that can feasibly be covered. This affects information on species occurrence, abundance, traits, tolerances and interactions – the Wallacean, Prestonian, Raunkieran, Hutchinsonian and Eltonian shortfalls, respectively (*sensu* Hortal et al. (2015)). Hence we can, for example, either construct abundance-weighted, multi-trophic networks for a single farm (Pocock et al. 2012) or unweighted, hectad-scale, plant-pollinator networks for the whole of GB (Chapter 4).

Although new developments and technologies in the fields of remote sensing (Zarnetske et al. 2019), image analysis (Zaks and Kucharik 2011), biological recording (Tulloch et al. 2013, Gray et al. 2014, August et al. 2015a, Powney and Isaac 2015) and molecular analyses (Kress et al. 2015, Barnes and Turner 2016, Bohan et al. 2017, Pornon et al. 2017) are likely to help increase the number of ecological datasets with extensive spatial coverage at fine spatial resolution, there will always be an upper limit to the number of sensors that can be deployed, sites visited, or samples analysed. It is therefore likely that experimental, meta-analytical and spatial modelling approaches are likely to continue to go hand-in-hand (Hampton et al. 2013, Hortal et al. 2015), although there may be increasing overlap between them. Ultimately, whilst the results of the spatial analysis presented in this thesis are only interpretable in the context of detailed experimental work examining mechanisms operating at finer resolution and more limited extent, demonstrating that these mechanisms operate with sufficient generality to show patterns and make predictions at regional or national scales provides compelling evidence to stakeholders and policymakers of their importance.

6.4 Future research

The methods and findings described in thesis offer several avenues for further research. Some progress in connecting the analyses made in the different chapters, to follow the linkage from landscape structure to beneficial insect communities to predicting crop yields under future change could be made even without additional data. For a given landscape it would be possible to map landscape structure (as in Chapter 3, Fig. 3.3), and create habitat specific potential networks (by subdividing occurring plants and pollinators by known or modelled habitat preferences, for example). Cross-habitat networks could also be constructed using known dispersal or foraging ranges to weight cross-habitat links. It could then be investigated how altering the configuration of the landscape alters the links to crop components of the networks. However, additional data to validate potential networks would greatly add to the value of such approaches. Data from well-characterised study landscapes are particularly valuable in this respect as they can help to both validate large-scale spatial modelling approaches and better determine the mechanisms behind the spatial patterns they uncover. For example, systematic, national-scale monitoring of pollinators via citizen science approaches (Birkin and Goulson 2015, Roy et al. 2016) offers the potential to link the kind of landscape structure variables analysed in Chapter 3 directly to pollinator occurrence and abundance. Patterns of crop yield at fine spatial scales are also becoming more readily available due to the widespread uptake of precision yield monitoring technology, which takes simultaneous readings of harvested yield and location from high-accuracy GPS. This enables estimation of yields not only at the field level, but also within the field (Muhammed et al. 2016, Hunt et al. 2019), leading to the potential to examine patterns of yield and their relation to proximity to non-crop habitats (Field et al. 2016) and landscape structure.

There is also an area for future research in constructing models for ecosystem service delivery. A number of models exist for predicting pollination and natural pest control from spatial data on land cover (e.g. Cresswell et al. 2000, Lonsdorf et al. 2009, Olsson et al. 2015, Groff et al. 2016). However, these depend on accurate parametrisation with data on the abundance, foraging range, diet and habitat requirements of beneficial insects. Improving these to ensure they have the capacity to replicate observed links between landscape and yield (such as those in Chapter 3) can be achieved by refining and improving parameterisation of existing models, or by simulation-based methods to see if simplified communities of natural enemies and pests in simulated landscapes give similar patterns of yield and yield resilience.

Our ability to determine spatial and temporal patterns in ecological data, and to offer optimal solutions for landscape management is often limited by the multiplicity of influences on ecological systems and the complexity of potential responses. This is easily seen in the preceding chapters, with multiple datasets and models required to construct response and predictor variables and control for confounding factors. Since many factors are also intercorrelated this makes it difficult to set up experiments to investigate the effects of multiple factors, since sites have to be selected to represent multiple factorial combinations of different environmental gradients (e.g. Staley et al. 2016). One approach to avoid having multiple contrasting gradients or subclasses is to employ the use of archetypes or syndromes (Václavík et al. 2013, Levers et al. 2018, Václavík et al. 2019, Alexandridis et al. 2020). These are multivariate classifications of landscapes by composition, configuration, soils, topography, climate and social factors which identify a limited number of characteristic landscape types. Archetypes can then be linked to the modelling approaches used here to make predictions or optimise the supply and demand of ecosystem services. Such approaches are best suited to large-scale exploratory work, since the assignment of a given landscape to a particular archetype creates its own source of uncertainty. The archetype approach is well suited to the development of scenarios (indeed the cropping intensity classes created for Chapter 5 are effectively crop-system archetypes) and can help refine the number of scenarios. Since archetypes have characteristic composition and configuration any modelling of scenario impacts can account for both.

6.5 Concluding remarks

We are at a time where there is great potential for major changes in global agricultural systems. The approaches to increasing food production which we have relied on for the past few decades are not sustainable. They have driven the destruction of biodiverse habitats and ecological communities and have ultimately undermined the ability of agricultural landscapes to provide the very ecosystem services required to support crop production. If agricultural systems are to continue to produce sufficient, nutritious food for a growing human population, especially under the increasing risk of major disturbances brought about by climate change, there need to be radical changes in our management of agricultural land. These need to take place at all spatial scales, from the management of fields to the way we arrange our agricultural landscapes. The widespread declines in the populations of insects that provide key ecosystem services to crops (and maintain ecosystem function) are one obvious facet of this problem. There is widespread recognition that these services are form a key part of the goals of sustainable or ecological intensification, where an increased synergy between the objectives of biodiversity conservation and agricultural production bring about benefits for both. However, if we are to reverse declines in these beneficial insects and ensure that they continue to support agricultural production we need to implement these changes rapidly. We thus urgently need evidence on what changes to make and how to target and incentivise them. The research presented in this thesis demonstrates the value of exploiting the rich array of data sources that we already have available, giving us the ability to explore relationships between agricultural landscapes, beneficial insects and crop production, and to explore patterns in the past, present and future. Whilst these approaches need to be supplemented with data from experimental and meta-analytical approaches, and are likely to be improved by new data from a wide range of sources, they remain key to providing the kind of large-scale evidence which is required by policy makers and convincing to agricultural land managers.

Appendices

A. Supplementary material for Chapter 3

A1. Cleaning data and selecting hectads for analysis

Data were initially cleaned to remove anomalous yield values, including zero values and those associated with whole crop silage harvests. This gave a total of around 22,000 yield samples. We then averaged these to mean yield per year per hectad, giving 1214 hectads with a yield sample in at least one year. Of course, in most cases it would be impossible to derive a meaningful metric of resilience from a hectad which only had data in a few years of the time series, so we further restricted this dataset to the 315 hectads with at least one sample in each year of the time series. This dataset required further refinement for analysis. This was because in hectads with low numbers of samples per year, variation across the time series may arise from selection of farms with varying management practices or local conditions rather than the temporal variation driven by climate and mediated by landscapes which is the focus of our analysis. In the initial dataset there was significant correlation between sample size and mean yield, suggesting that variation in yield over time was likely to be significantly driven by inadequate sampling of local spatial variation. To remove this, we filtered the full dataset by several criteria. Firstly, all hectads were required to have at least one sample of yield data in all years of the time series. Secondly, we explored thresholds for the minimum permissible number of samples per year and the number of years permitted to have this value, to determine which combination retained the maximum number of samples whilst removing the significant correlations between sample size and mean yield and between mean sample size and estimated mean yield over time (Fig. A1).

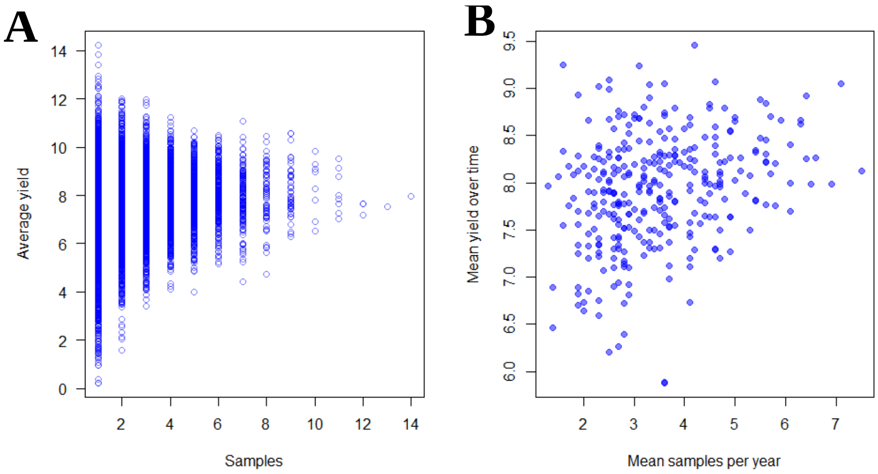


Figure A1. *Plots of effect of sample size on mean yield in the original dataset, both from individual years (A) and means across the time series per hectad (B).*

I identified threshold values of minimum number of samples per year and maximum permissible number of years with low sample values which rendered these correlations insignificant. These analyses suggested that threshold values of no more than one year with a single sample and no more than two years having less than three samples were sufficient to ensure that the per hectad averages were accounting for local spatial variation. A total of 137 hectads met these criteria.

I also checked that the method for selecting hectads with sufficient samples for calculating metrics of yield resilience did not bias the sample towards a particular kind of agricultural landscape in terms of cover of arable land and semi-natural habitats and the configuration of these land over types (see Appendix A4 for selection of metrics of landscape composition and configuration). Although it was clear that high mean numbers of samples per year were only found in landscapes with high coverage of arable land and correspondingly low coverage of semi-natural habitats (Fig. A2), the sampled hectads covered a wide range (40% - 100% coverage of arable land, 0- 25% coverage semi-natural habitats) with comparatively few hectads excluded from the sample having values outside these ranges. For configuration metrics, the selected hectads covered almost the full range of connectivity and proximity indices for both arable land and semi-natural habitats evident across all hectads (Fig. A2).

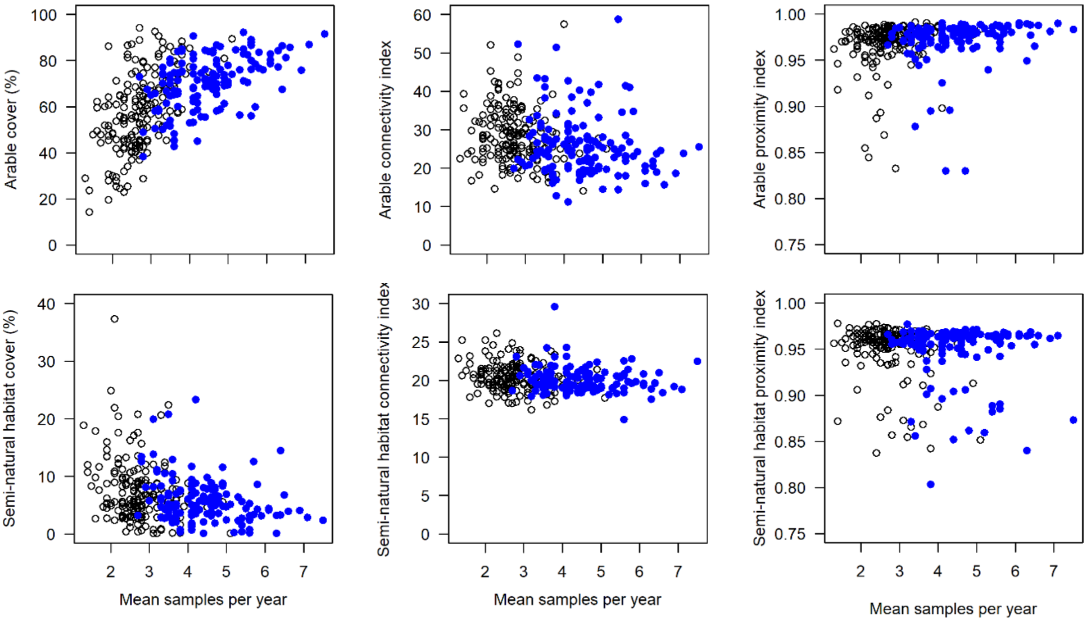


Figure A2. *Plots comparing mean sample size across the time series per hectad against landscape composition and configuration, to ensure the sampling approach did not bias towards a particular landscape type. Blue points are those hectads meeting the threshold values for analysis, black points are hectads with at least one sample per year (the minimum required to calculate resilience metrics) but not meeting the threshold values.*

A2. COMPARING METRICS OF RESILIENCE

The three metrics of resilience were 1) Relative yield 2) Yield stability around a moving average 3) Resistance to a specific extreme event. The three metrics cover different aspects of resilience and are calculated across different portions of the time series, but do show some degree of correlation with one another. Figure A3 shows the relationships between the metrics of resilience and with mean yield across the entire time series. Relative function showed a strong, positive correlation with mean yield (Pearson's correlation, r =0.99, p <0.001, n =137), whereas the other two metrics did not (r =-0.14, p =0.08 for yield stability; r =0.04, p =0.61 for resistance, n =137 in both cases).

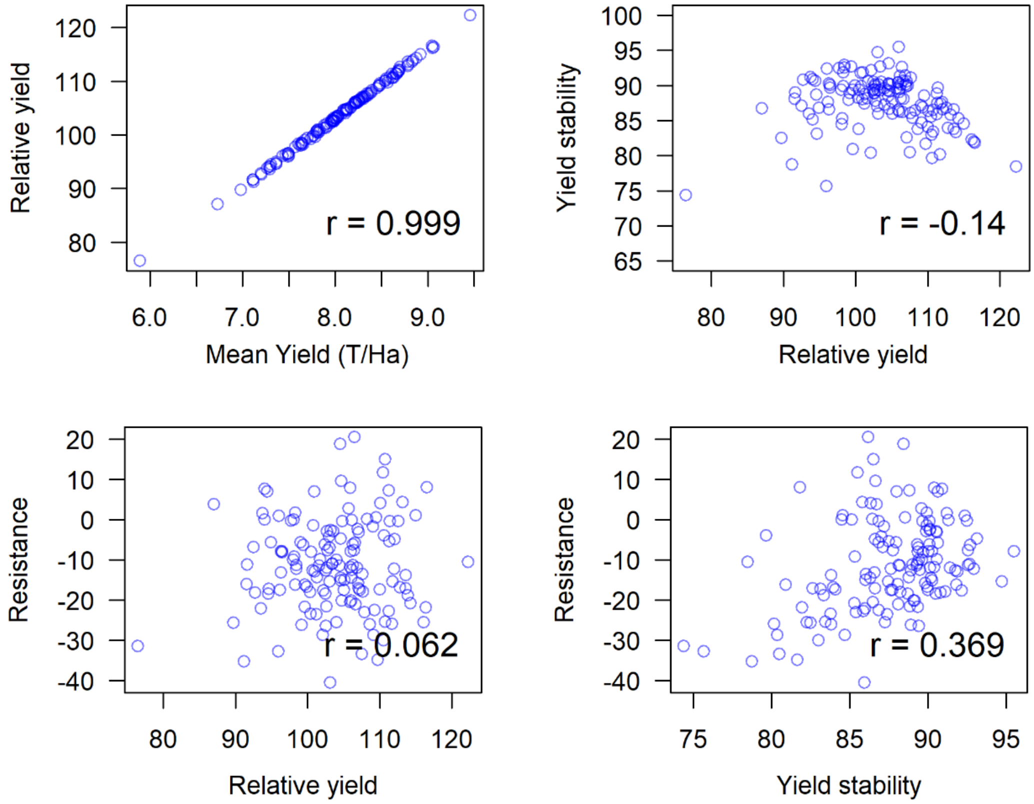


Figure A3. *Plots showing relationships between different variables quantifying wheat yield and its resilience (mean yield vs. relative yield, relative yield vs. yield stability, relative yield vs. resistance and yield stability vs. resistance). Pearson's correlations coefficients (r) for each pair of variables are superimposed on the plots.*

A3. CONSTRUCTING A POTENTIAL YIELD MODEL TO ACCOUNT FOR WEATHER AND SOIL EFFECTS

The potential yield model was based approaches developed by Sylvester-Bradley and Kindred (2014) and Lynch et al. (2017). The model has three main stages: 1) estimation of green area index (GAI) over the growing season as a function of accumulated growing degree days, 2) estimation of intercepted solar radiation and conversion to biomass, limited by soil plant available water content 3) apportioning of accumulated biomass to grain yield.

*1) **Estimation of green area index (GAI)***

The model assumed a sowing date of 1st of October, in line with the benchmark for winter wheat growth in the UK (Sylvester-Bradley et al. 2015). Following this date, the model accumulates GAI as a function of growing degree days above zero ˚C through the three key phases of wheat growth, further subdivided by growth stages (GS): foundation (Sowing-GS30 and GS30-GS31), construction (GS31-GS61) and production (GS61-GS69, GS69-GS87, GS87-senescense). GAI is accumulated at different rates over the different growth phases, following the benchmarks in Sylvester-Bradley et al. (2015). Required degree days to complete each growth phase and the associated progression in GAI are shown in table A1.

***Table A1.** Wheat growth periods used by the model to determine rate of GAI development as a function of thermal time (growing degree days).*

Growth phase	GAI at start	GAI at end	Thermal time
Sowing-GS30	0.0	1.6	1100
GS30-GS31	1.6	2.0	100
GS31-GS61	2.0	6.3	900
GS61-GS69	6.3	6.3	50
GS69-GS87	6.3	1.3	750
GS87-senescense	1.3	0	200

During each growth phase, GAI is estimated as the proportion of required degree days which have been accumulated in order to complete the phase, multiplied by the end GAI of that phase. Degree days accumulate as follows:

If T_{min} > 0˚C: degree days = $\frac{(T_{max}+ T_{min})}{2}$

If T_{min} < 0˚C: degree days = $\frac{(T_{max} - 0)}{2} - \frac{(0-T_{min})}{4}$

If T_{max} < 0˚C: degree days = 0

In order to account for vernalisation requirements, cumulative vernalisation days were also calculated as a function of mean daily temperature, following the equations in Spink et al. (2000) and Lynch et al. (2017). A crop requires 50 vernalisation days before progressing beyond GS31. When this does not occur, the estimated GAI remains constant until the crop is adequately vernalised and degree days accumulated over this period do not contribute to the following growth phases (Lynch et al. 2017). The effect of day length is accounted for by limiting progression beyond GS31 until day length has progressed beyond 14 hours. Day length was calculated from latitude and date using the *geosphere* package (Hijmans et al. 2017). Where accumulated degree days are sufficient to progress beyond GS31 before day length >14 hours, GAI remains constant until this threshold is met.

GAI development is stalled if the temperature falls below -5 ˚C once the crop has passed GS31 (Spink et al. 2000). Harvest was assumed to take place on the 31st of August. Where the GS87-senescense phase was not complete before this date, it was assumed that this phase progressed more rapidly, with GAI of zero by harvest.

2) *Estimation of intercepted solar radiation and conversion to biomass*

Once the GAI curve was constructed from temperate and day length data, the intercepted radiation was then calculated. Intercepted radiation assumed that approximately 50% of total solar radiation is photosynthetically active and that, of this, the proportion intercepted by the canopy is given by Beer's law, assuming a light extinction coefficient of 0.5 (Sylvester-Bradley and Kindred 2014):

Daily light interception (MJ) = $1 - e^{-0.5*GAI}$

This is then converted to biomass assuming a radiation use efficiency of 2.5 g of biomass per metre squared per MJ of intercepted light (Shearman et al. 2005). This is limited by the plant available water content (PAWC) of the soil. Rainfall from sowing to GS30 was summed to estimate the available water before the onset of rapid growth, with PAWC at this point being the lower of summed rainfall to date and estimated soil available water content (AWC) (Bell et al. 2018), as most soils being saturated prior to this date. After this date, daily PAWC is calculated following Lynch et al. (2017) as:

$$PAWC_d = (AWC_{d-1} + Rainfall_{d-1} - (Biomass_{d-1} \times 0.2)) \times 0.65$$

Where PAWC drops below the amount required for that day's biomass accumulation, no further biomass is accumulated until PAWC has increased from subsequent rainfall, to account for the effects of drought.

3) APPORTIONING OF ACCUMULATED BIOMASS TO GRAIN YIELD

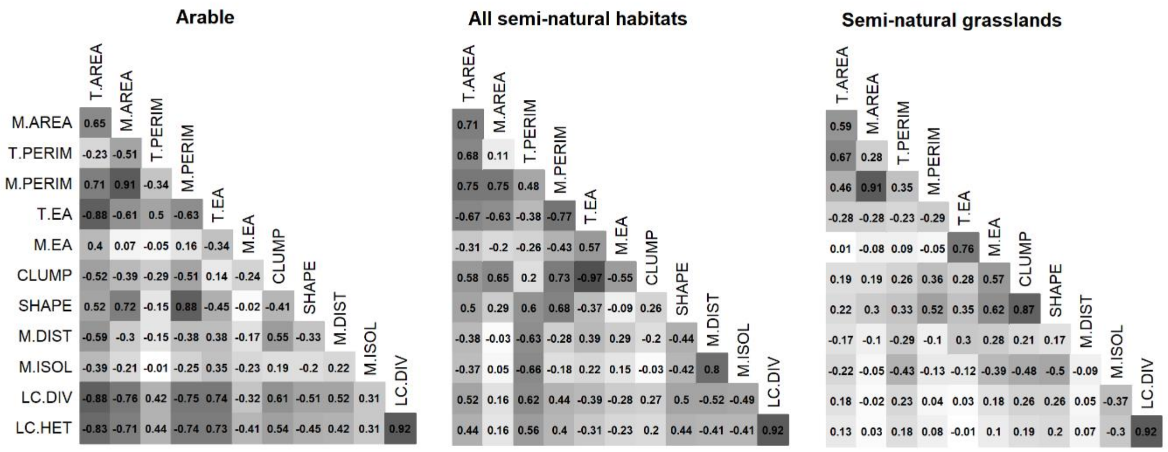
Yield was calculated as the sum of biomass accumulated after GS69 plus the sum of biomass accumulated between GS31 and GS61 multiplied by 0.3. The latter accounts for the redistribution of water soluble carbohydrates from the stem after flowering (Sylvester-Bradley et al. 2015, Lynch et al. 2017). Yield was penalised if waterlogging occurred after the onset of flowering (GS61). Although the effects of water logging on yield are complex, and depend on growth stage and context in general, excessive rainfall at late growth stages has a detrimental impact (Cannell et al. 1980, Belford 2009, de San Celedonio et al. 2014, Ploschuk et al. 2018). Waterlogging was identified if daily rainfall exceeded residual soil AWC. If this occurred for over 5 days, a yield penalty of 11.77 $g^{-1}m^{-1}d^{-1}$ was applied (Olgun et al. 2008) until such time as AWC_d returned to below the maximum.

A4. SELECTING METRICS OF LANDSCAPE COMPOSITION AND CONFIGURATION

Because there are a very large number of potential metrics for quantifying landscape configuration (McGarigal et al. 2012, Uuemaa et al. 2013, Gustafson 2019, Hesselbarth et al. 2019), I performed preliminary analyses to determine which metrics of configuration were least strongly correlated with landscape composition at the hectad scale (i.e. areas of different land cover types) and with one another. I calculated a number of metrics, chosen to sample from a range of metrics quantifying different key landscape structure components (Cushman et al. 2008). I avoided metrics which require making an assumption about threshold distances or distance decay functions (e.g. connectance indices, proximity indices) since I do not have empirical ecological data across a wide range of potentially influential organisms on which to base these. I calculated 10 class-level metrics, for each of arable land, all semi-natural habitats and semi-natural grasslands only (Table S2). I also calculated land cover diversity (inverse Simpson's index) across all land cover types within a hectad, and a measure of structural heterogeneity (inverse Simpson's diversity of individual land cover patches). I then examined intercorrelations between these metrics in order to select those for further analysis (Fig. A4). Correlations were calculated across the 315 hectads with at least one wheat yield sample in each of the ten years.

***Table A2**. Landscape composition and configuration metrics explored in preliminary analyses, as calculated from the 25m raster version of the CEH Land Cover Map 2015 (Rowland et al. 2017). Abbreviations are used in Figure A4.*

Metric	Description	Abbreviation
Total area	Total area of a given land cover	T.AREA
Mean patch area	Mean area of patches (a patch consisting of an area of adjacent cells of the same land cover type)	M.AREA
Perimeter density	Total length of patch perimeters per hectad	T.PERIM
Mean patch perimeter	Mean perimeter per patch	M.PERIM
Total edge area ratio	Total perimeter per hectad divided by total area per hectad	T.EA
Mean edge area ratio	Mean of perimeter divided by area per patch	M.EA
Clumpiness index	Proportional deviation of like adjacencies from that expected under a random distribution (McGarigal et al. 2012, Hesselbarth et al. 2019)	CLUMP
Shape index	Mean ratio of actual perimeter per patch to hypothetical minimum perimeter per patch (McGarigal et al. 2012, Hesselbarth et al. 2019)	SHAPE
Mean distance between patches	Mean nearest-neighbour distance between all possible pairs of patches	M.DIST
Mean distance to patches	Mean nearest neighbour distance from all non-patch cells to the nearest patch	M.ISOL
Landscape diversity	Inverse Simpsons index of diversity of ten aggregate land cover classes, Rowland et al. (2017)	LC.DIV
Structural heterogeneity	Inverse Simpsons index of patch diversity, calculated by defining patches as adjacent cells of the same aggregate land cover type	LC.HET



Arable

	T.AREA	M.AREA	T.PERIM	M.PERIM	T.EA	M.EA	CLUMP	SHAPE	M.DIST	M.ISOL	LC.DIV
M.AREA	0.65										
T.PERIM	-0.23	-0.51									
M.PERIM	0.71	0.91	-0.34								
T.EA	-0.88	-0.61	0.5	-0.63							
M.EA	0.4	0.07	-0.05	0.16	-0.34						
CLUMP	-0.52	-0.39	-0.29	-0.51	0.14	-0.24					
SHAPE	0.52	0.72	-0.15	0.88	-0.45	-0.02	-0.41				
M.DIST	-0.59	-0.3	-0.15	-0.38	0.38	-0.17	0.55	-0.33			
M.ISOL	-0.39	-0.21	-0.01	-0.25	0.35	-0.23	0.19	-0.2	0.22		
LC.DIV	-0.88	-0.76	0.42	-0.75	0.74	-0.32	0.61	-0.51	0.52	0.31	
LC.HET	-0.83	-0.71	0.44	-0.74	0.73	-0.41	0.54	-0.45	0.42	0.31	0.92

All semi-natural habitats

	T.AREA	M.AREA	T.PERIM	M.PERIM	T.EA	M.EA	CLUMP	SHAPE	M.DIST	M.ISOL	LC.DIV
M.AREA	0.71										
T.PERIM	0.68	0.11									
M.PERIM	0.75	0.75	0.48								
T.EA	-0.67	-0.63	-0.38	-0.77							
M.EA	-0.31	-0.2	-0.26	-0.43	0.57						
CLUMP	0.58	0.65	0.2	0.73	-0.97	-0.55					
SHAPE	0.5	0.29	0.6	0.68	-0.37	-0.09	0.26				
M.DIST	-0.38	-0.03	-0.63	-0.28	0.39	0.29	-0.2	-0.44			
M.ISOL	-0.37	0.05	-0.66	-0.18	0.22	0.15	-0.03	-0.42	0.8		
LC.DIV	0.52	0.16	0.62	0.44	-0.39	-0.28	0.27	0.5	-0.52	-0.49	
LC.HET	0.44	0.16	0.56	0.4	-0.31	-0.23	0.2	0.44	-0.41	-0.41	0.92

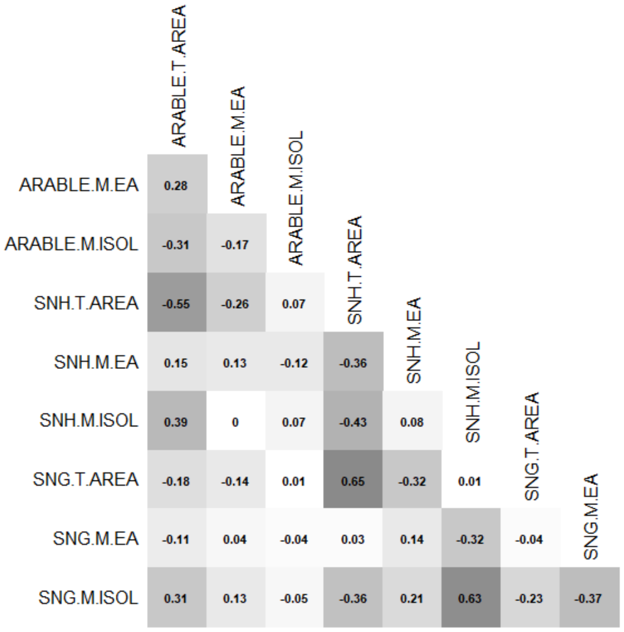
Semi-natural grasslands

	T.AREA	M.AREA	T.PERIM	M.PERIM	T.EA	M.EA	CLUMP	SHAPE	M.DIST	M.ISOL	LC.DIV
M.AREA	0.59										
T.PERIM	0.67	0.28									
M.PERIM	0.46	0.91	0.35								
T.EA	-0.28	-0.28	-0.23	-0.29							
M.EA	0.01	-0.08	0.09	-0.05	0.76						
CLUMP	0.19	0.19	0.26	0.36	0.28	0.57					
SHAPE	0.22	0.3	0.33	0.52	0.35	0.62	0.87				
M.DIST	-0.17	-0.1	-0.29	-0.1	0.3	0.28	0.21	0.17			
M.ISOL	-0.22	-0.05	-0.43	-0.13	-0.12	-0.39	-0.48	-0.5	-0.09		
LC.DIV	0.18	-0.02	0.23	0.04	0.03	0.18	0.26	0.26	0.05	-0.37	
LC.HET	0.13	0.03	0.18	0.08	-0.01	0.1	0.19	0.2	0.07	-0.3	0.92

Figure A4. *Pairwise Pearson's correlation coefficients for landscape and class-level metrics of composition and configuration, for each of arable, all semi-natural habitats and semi-natural grasslands only. Cells in the correlation matrices are shaded according to absolute value of the correlation coefficient, from white =0 to dark grey =1. Plots created using the corrplot package (Wei and Simko 2017). See table 1 for full variable names and descriptions.*

From Fig. A4, it can be seen that many metrics correlate strongly with total area, for at least one of the three land cover groups. In many cases, this might be expected at national scale and hectad resolution. For example, because the total area of semi-natural habitats within hectads tends to be relatively small, high edge densities are only encountered in hectads with correspondingly large areas. The clumpiness and shape indices were relatively strongly correlated with area for arable and all semi-natural habitats. Landscape diversity and structural heterogeneity were both strongly negatively correlated with area of arable land and positively correlated with area of semi-natural habitats. The metrics with lowest average correlation with total area were mean edge area ratio (M.EA on Fig. A4) and mean distance to patches (M.ISOL on Fig. A4). These also showed relatively low correlations with one another (0.23, 0.15 and 0.39 for each land cover group). I therefore used these, along with total area, in further analyses.

When hectads were restricted to the 137 meeting the thresholds identified in Appendix A1 some correlations between landscape structure variables relating to different land cover types were evident (Figure A5). I therefore constrained candidate models to exclude highly correlated (r > 0.6) pairs of variables which are likely to contribute to were higher variance inflation factors were observed in the global models (Table A3). In general, high correlations and correspondingly high variance inflation factors arose from the fact that semi-natural grasslands are a subset of semi-natural habitats and are therefore highly likely to be positively intercorrelated, especially in terms of total area.



	ARABLE.T.AREA	ARABLE.M.EA	ARABLE.M.ISOL	SNH.T.AREA	SNH.M.EA	SNH.M.ISOL	SNG.T.AREA	SNG.M.EA
ARABLE.M.EA	0.28							
ARABLE.M.ISOL	-0.31	-0.17						
SNH.T.AREA	-0.55	-0.26	0.07					
SNH.M.EA	0.15	0.13	-0.12	-0.36				
SNH.M.ISOL	0.39	0	0.07	-0.43	0.08			
SNG.T.AREA	-0.18	-0.14	0.01	0.65	-0.32	0.01		
SNG.M.EA	-0.11	0.04	-0.04	0.03	0.14	-0.32	-0.04	
SNG.M.ISOL	0.31	0.13	-0.05	-0.36	0.21	0.63	-0.23	-0.37

Figure A5. *Pairwise Pearson's correlation coefficients for predictor variables in the global model, for the 137 hectads meeting criteria for analysis. SNH = semi-natural habitat, SNG = semi-natural grassland, T.AREA = total area, M.EA = Mean edge area ratio, M.ISOL = Mean distance to patches). Cells in the correlation matrices are shaded according to absolute value of the correlation coefficient, from white =0 to dark grey =1. Plot created using the corrplot package (Wei and Simko 2017)*

Table A3. *Variance inflation factors for all predictor variables in the global models for each response variable*

	Arable			Semi-natural habitat			Semi-natural grassland		
Response	**Cover**	**Connectivity**	**Proximity**	**Cover**	**Connectivity**	**Proximity**	**Cover**	**Connectivity**	**Proximity**
Relative yield	1.37	1.11	1.11	3.03	1.26	1.98	2.12	1.12	1.52
Yield stability	1.50	1.13	1.12	3.21	1.26	2.34	2.30	1.14	1.96
Resistance	1.54	1.12	1.15	3.31	1.24	2.13	2.17	1.15	1.57

Note that for further analyses Edge area ratio was transformed to an index of land cover connectivity (1/M.EA, such that units are squared unit area of land cover per unit length of perimeter) and mean isolation was transformed to an index of proximity ((10^4 – M.ISOL /) 10^4, such that a value of 1 indicates all cells adjacent to the target land cover and a value of zero indicates that cells are on average 10km distance from the nearest patch of target land cover).

This was done to aid interpretation of regression coefficients, such that positive coefficients always indicate an increase in resilience with increasing area, connectivity or proximity to the land cover in question.

B. Supplementary material for Chapter 4

B1. EXTRACTING AND CLEANING PLANT-POLLINATOR INTERACTIONS FROM BIOLOGICAL RECORD ANNOTATIONS

Pollinator biological records with associated metadata were algorithmically screened for text matching a valid scientific or vernacular plant name (or a widely used synonym or abbreviation of either). In most cases, such matches record the visitation to a flower by a pollinating insect. However, there are other reasons for a valid match in the comments field, including descriptions of local habitat (e.g. “English oak woodland”), pollinator behaviour (e.g. “flying near blackthorn hedge”) or sampling methods (e.g. “swept from *Arrhenathrum eliatus* sward”). In order to exclude these, all plant species producing a match were screened according whether they produce flowers which are known to be visited by insects and whether such visits are likely to result in beneficial pollen transfer (i.e. the plant is primarily entomophilic). These criteria excluded the majority of trees and grasses, which are likely to derive from habitat descriptions or interactions other than flower visits (e.g. honeydew feeding). Even though some primarily wind-pollinated grass flowers are known to be visited by certain pollinators, their impact on pollen transfer is likely to be very slight in temperate climates (Clifford 1964, Adams et al. 1981). Some records could also be spurious if species were misidentified, albeit the volunteers recording interactions were mostly expert naturalists from specialist recording societies (see Acknowledgements in manuscript). It is recognised that, without manual checking of every record, some records will always remain spurious. However, these were likely to be only a very minor proportion of the dataset and are therefore unlikely to have a substantial influence on the resulting networks.

I ignored all interactions that were not resolved to at least genus level. Some records produced a match to plant genus level but not to species. For genera where there were no other records in the dataset of species from that genus this was considered to be insufficient data to infer a valid interaction and ignored. For records where a single species is the only GB representative of the genus (e.g. *Bartsia, Bellis, Calluna, Convolvulus, Daucus, Hedera, Onobrychis*) I assumed all such genus-level records to refer to this species. I also made this assumption for the few other genera where occurrence in GB is dominated by one species (e,g. *Pyrus, Erysimum, Sambucus*) or where all species in the genus form an aggregate (*Taraxacum*). There were 79 plant genera for which at least one unique interaction was recorded to genus level only and valid interactions were recorded to at least two plant species within the genus (Table B1). These included genera which were described by a vernacular name (e.g. *Salix* from willow, *Rosa* from rose) or those which contain species complexes for which the recorder is unlikely to be able to make a clear identification to species level (e.g. *Euphrasia, Leontodon*). In such cases, an interaction with the genus was assumed to imply an interaction with all recorded species within it. Similarly, an interaction with a single species from these 79 genera was assumed to imply an interaction with all other species present in the interactions database within the genus in question. These assumptions were justified by the fact that monolectic or even narrowly oligolectic pollinators are comparatively rare (Waser et al. 1996, Minckley and Roulston 2006, Petanidou and Potts 2006), especially in the UK pollinator fauna. It is also highly likely that many networks based on plant observations, from single or multiple sites, commonly *over*estimate the degree of specialisation of many pollinators, partly as a result of limited sampling effort resulting in missed observations of existing interactions (Bosch et al. 2009, Pornon et al. 2017). In total, extrapolating species-level interactions from genus-only data according to the assumptions above added 6487 unique interactions to the database (39% of total interactions in the database).

I also removed species defined as “casuals” in PLANTATT (“a casual is a plant that is present only as populations which fail to persist in the wild for periods of more than approximately five years” Hill et al. 2004). This was because their range of occurrence cannot be effectively modelled due to a lack of reliable occurrence data and patchy distributions determined by the presence of gardens or agricultural cultivation. The database thus retained some crop (e.g. *Brassica napus*, *Vicia faba*) and garden species which have persistent naturalised populations. Plant status in the final database was divided between natives (67.9%), archaeophytes (12.0%), neophytes (17.6%) and those with uncertain native status (2.2%). It should be noted that the interactions in the database describe flower visitation rather than pollination in the strict sense, where actual pollen transfer relies on a variety of factors, including pollinator behaviour, physiology (Ballantyne et al. 2015) and species’ relative abundance, for which I had no available information.

Table B1. *Plant genera for which interactions were assumed from genus-only records. These genera had at least one unique interaction recorded only to genus level as well as valid interactions recorded to at least two plant species within the genus. For each genus, the table gives the number of unique interactions recorded to genus level only (table sorted in descending order), the percentage that such interactions comprise of total number of unique interactions with plants of that genus and the number of plant species within the genus in the interactions database, to which interactions were assumed from genus-only records.*

Genus	**Unique interactions recorded to genus level only**	**% of total unique interactions for plants in genus**	**Plant species recorded within genus**
Salix	143	71.1%	8
Ranunculus	63	28.6%	6
Leontodon	61	52.1%	2
Cirsium	58	26.9%	8
Myosotis	41	82.0%	2
Centaurea	37	21.9%	3
Matricaria	33	71.7%	2
Veronica	33	45.2%	5
Mentha	31	33.7%	4
Thymus	30	40.0%	3
Acer	29	38.2%	3
Silene	28	45.9%	3
Rumex	25	92.6%	2
Geranium	24	38.1%	9
Rosa	22	51.2%	5
Ligustrum	21	36.2%	2
Vicia	20	33.3%	7
Stellaria	20	25.0%	4
Cotoneaster	19	57.6%	3
Trifolium	19	19.6%	7
Potentilla	19	17.0%	4
Campanula	18	47.4%	5
Viburnum	17	54.8%	2
Inula	15	44.1%	3
Crepis	15	23.8%	3
Sorbus	14	45.2%	2
Viola	14	36.8%	5
Euphorbia	14	18.9%	4
Euphrasia	13	56.5%	2
Sonchus	13	24.1%	3
Erica	13	22.4%	3
Prunus	13	12.5%	7
Senecio	13	5.9%	6
Dipsacus	12	22.6%	2
Malus	12	20.7%	2
Hypericum	10	37.0%	6

Sinapis	10	30.3%	2
Rubus	10	4.4%	4
Limonium	9	50.0%	2
Symphytum	9	36.0%	2
Vaccinium	9	29.0%	3
Ulex	9	18.4%	3
Scrophularia	8	61.5%	2
Lamium	8	18.6%	3
Sedum	8	17.0%	4
Solidago	8	11.1%	2
Linaria	7	25.9%	3
Galium	6	20.7%	6
Epilobium	6	18.2%	4
Arctium	6	12.0%	2
Achillea	6	9.0%	2
Allium	6	7.5%	4
Leucanthemum	6	6.1%	2
Dactylorhiza	5	38.5%	3
Anthemis	4	26.7%	2
Ribes	4	25.0%	3
Melilotus	4	16.7%	3
Persicaria	4	13.3%	5
Medicago	4	10.3%	2
Carduus	4	9.5%	3
Aster	4	7.5%	3
Brassica	4	7.1%	4
Vinca	3	50.0%	2
Papaver	3	30.0%	2
Pilosella	3	17.6%	2
Stachys	3	8.3%	4
Oenanthe	3	4.5%	3
Spergularia	2	50.0%	2
Pedicularis	2	22.2%	2
Cerastium	1	14.3%	2
Peucedanum	1	12.5%	2
Valeriana	1	10.0%	2
Calystegia	1	7.1%	2
Geum	1	5.0%	2
Ononis	1	4.5%	2
Primula	1	3.7%	3
Reseda	1	2.3%	2
Hyacinthoides	1	1.4%	2
Heracleum	1	0.5%	2

B2. ASSESSING SAMPLING COMPLETENESS OF PLANT-POLLINATOR INTERACTIONS

To assess the completeness of the plant-pollinator interactions database, I constructed interaction accumulation curves for all records used to construct the database (i.e. pollinator occurrence records from which I were able to extract a valid plant interaction and which were not removed by data cleaning). These included both raw species-level and genus-level records, but not the species-level records generated by extrapolation from genus-level data (see Appendix 1), which would inflate estimates of completeness. Interaction curves were created by sequentially selecting random records and assessing the cumulative number of unique interactions represented in the selection (Fig. B1). Randomisations were performed 1000 times and the mean value used to define the accumulation curve. I then used the *estimateR* function in the *vegan* R package (v2.4-5, Oksanen et al. 2017) to estimate asymptotic interaction richness, using the bias-corrected Chao estimator (Chiu et al. 2014). The proportion of estimated interaction richness represented by observed interactions was then calculated. I also repeated this process independently for each plant and pollinator species with >10 records to obtain an estimate of average interaction richness per plant and pollinator species.

Results suggested that the plant-pollinator interactions database captured around 60% of estimated total interactions (mean 60% for pollinators, mean 57% for plants). This is comparable to other studies performing high-effort, multi-temporal field sampling of individual networks (Chacoff et al. 2012, Falcão et al. 2016). Apparent underrepresentation may derive from two main sources. Firstly, the data have a comparatively limited representation of the total species richness of insect-pollinated plants in GB (around 55%), so all interactions associated with these missing species will be likewise absent. In the majority of cases these are likely to represent rare or localised plant species which have a low probability of being recorded in an interaction with a pollinator via the pollinator-focussed biological recording schemes from which all interaction records were derived. Secondly, the data may miss interactions between plant and pollinator species which are present in the dataset. Where tested, interactions based on field observation (and the data were ultimately drawn from a large number of field observations) tend to underestimate total interaction richness (Nielsen and Bascompte 2007, Pornon et al. 2017), even where sampling effort is intensive (Chacoff et al. 2012) and where a large proportion of species from both levels of the network are sampled (Chacoff et al. 2012, Falcão et al. 2016). Whilst there are indications that poor sampling can bias network metrics, there is evidence that this has a low impact on emergent network properties, such as robustness (Falcão et al. 2016) and metrics constrained by species traits (Vizentin-Bugoni et al. 2016).

However, there is also the possibility that interaction accumulation curves overestimate the total number of potential interactions. Interactions may be rarely recorded because either or both of the plant or pollinator species involved are rare, or because they represent atypical interactions (e.g. occasional visits made by highly generalist pollinators). In either case, such interactions may inflate the estimated interaction richness but are not necessarily indicative of large numbers of unsampled interactions (Chacoff et al. 2012).

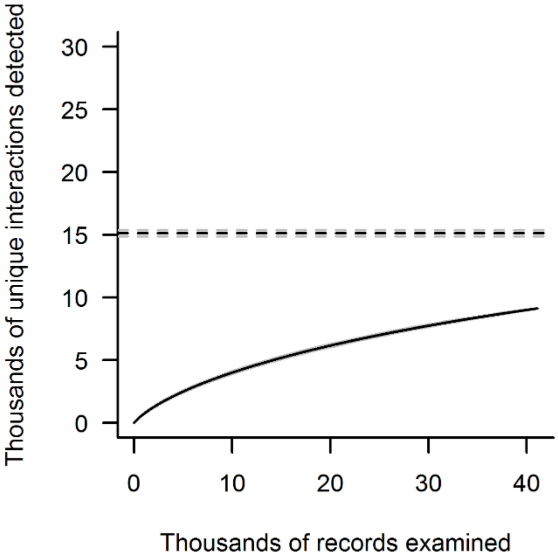


Figure B1. *Accumulation curve of plant-pollinator interaction richness across all records used to construct the database (black line = mean of 1000 randomised accumulations). Horizontal, dashed lines indicate estimated asymptotic interaction richness (black) ± standard error (grey).*

B3. SETTING THRESHOLDS FOR ESTIMATING OCCURRENCE FROM FRESCALO DATA

For each species of plant and pollinator, FRESCALO produces a probability of occurrence in each hectad. To transform this to presence/absence, I assigned a species as present in a hectad if its probability of occurrence was greater than a set threshold. To define this threshold, hectads with observed presence records were ranked by their modelled probability of occurrence and any hectad with a probability of occurrence greater than the 95th percentile was treated as an estimated presence. This approach performed well in terms of filling in gaps in species distributions due to under-recording (i.e. false negatives or ’omission errors’) without adding new areas to the currently-known range (i.e. presumed false positives, ‘commission errors’). However, this threshold resulted in ‘infilling’ of peninsulas for coastal species (Fig. B2), so for species classified as ‘coastal’ in PLANTATT (Hill et al. 2004), the threshold was set at 75% probability of occurrence regardless of the values at observed presence records (set by visual examination of output FRESCALO probability of occurrence maps). Under both thresholds, all hectads with observed presence records were assumed to have the species present, regardless of their FRESCALO probability of occurrence.

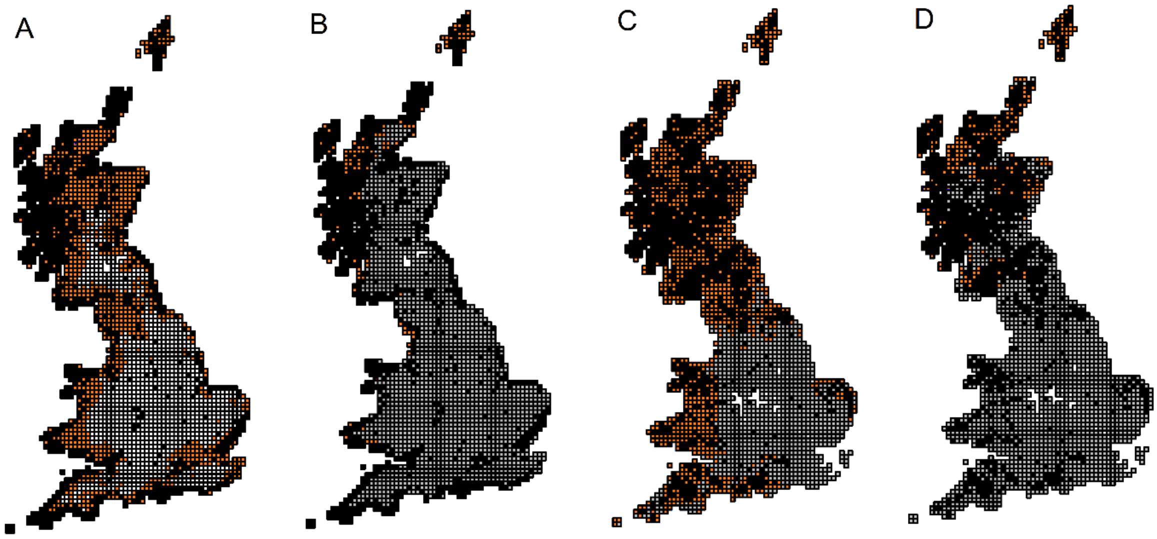


***Figure B2**. Examples of estimating occurrence per hectad from FRESCALO output for two species: A & B) a coastal species,* Armeria maritima*; C & D) a species with an inland, upland and northerly distribution and therefore likely to be under-recorded* Pedicularis palustris*. Black filled cells across all panels indicate recorded presence from raw biological records. A) Orange filled cells indicate that the species was not recorded but with a FRESCALO probability of occurrence greater than or equal to the 95th centile of values from cells with recorded presences for* Armeria maritima*. B) Orange filled cells indicate that the species was not recorded but with FRESCALO probability of occurrence greater than 75% for* Armeria maritima*. C) As A, for* Pedicularis palustris*. D) As B, for* Pedicularis palustris*.*

B4. EXPLORING NETWORK REWIRING SCENARIOS

Unlike many network studies, the networks were constructed from multi-temporal, multi-habitat data which can be assumed to capture the majority of extant interactions in GB. Therefore each of the per hectad potential networks includes information on interactions observed anywhere in GB over the 30 year time period from which I drew biological records and so already implicitly includes some potential rewiring. I did not have data on other interactions occurring at different spatial or temporal locations by which to construct potential rewiring scenarios (e.g. Kaiser-Bunbury et al. 2010). Nor did I have detailed information on energetics (e.g. Thierry et al. 2011) or large-scale variation in dependency on nectar feeding across the pollinator groups (e.g. Vanbergen et al. 2017) that could provide the basis for rewiring scenarios. Therefore, any potential further rewiring scenario has to contain assumptions regarding the likelihood of forming novel interactions inferred from existing data on, for example, plant and pollinator traits (Stang et al. 2006). The large number of assumptions involved makes it debatable whether such trait-based rewiring scenarios are more ecologically meaningful than only using the previously observed interactions.

Nevertheless, to check the sensitivity of the observed spatial patterns in the plant-pollinator networks I assessed the probable impact of rewiring on the metric of robustness to global simulated extinction (R_g) by constructing trait-based rewiring scenarios. The first scenario assumed that, following extinction of a plant, any pollinator with no remaining resources could rewire to other plants of the same genus present in the hectad (in addition to the assumptions regarding genera already made, see Appendix 1). This scenario increased the total potential interactions by 36%. A second, more extreme, rewiring scenario, allowed pollinators to rewire to any plant species of the same family, flower morphology and flower colour and overlapping in flowering period (flower traits taken from Fitter and Peat (1994)). This scenario increased the total potential interactions by 70%.

Under both rewiring scenarios, all measures of R_g increased slightly (Table B2), as expected given that networks were inevitably more generalised. The increase was relatively consistent across hectads, such that there were very strong correlations with R_g from networks from only observed interactions (Table B2). By comparing values derived from the rewiring scenarios in generalised linear models testing the relationship of *Rg* with proportion of agricultural land, it was clear that there was very little difference in the model coefficients or their significance when rewiring scenarios were applied (Table B2). This suggests that the observed spatial patterns in relative network robustness are robust to rewiring.

Table B2. *The impact of two rewiring scenarios (based on plant genus or flower traits) on robustness to global simulated extinction (R_g) and its relationship with agricultural cover. Results are the mean and standard deviation of R_g across hectads, correlations with R_g derived from observed interactions only and the slope of the relationship with agricultural cover as derived from linear mixed models.*

				Correlation with values from observed interactions		Relationship with agricultural cover	
R_g measure	Rewiring scenario	Mean	SD	Pearson's R	p value	Slope	p value
$R_{g\ Trend}$	Observed	0.84	0.05			0.38	<0.001
	Genus	0.88	0.05	0.98	<0.001	0.41	<0.001
	Trait	0.89	0.05	0.97	<0.001	0.44	<0.001
$R_{g\ N}$	Observed	0.92	0.03			0.49	<0.001
	Genus	0.94	0.03	0.97	<0.001	0.48	<0.001
	Trait	0.95	0.03	0.98	<0.001	0.47	<0.001
$R_{g\ F}$	Observed	0.85	0.04			0.36	<0.001
	Genus	0.88	0.04	0.97	<0.001	0.36	<0.001
	Trait	0.89	0.03	0.95	<0.001	0.33	<0.001
$R_{g\ R}$	Observed	0.93	0.01			0.45	<0.001
	Genus	0.96	0.01	0.95	<0.001	0.39	<0.001
	Trait	0.96	0.01	0.95	<0.001	0.42	<0.001

B5. EXPLORING THE IMPACT OF UNCERTAINTY ON NETWORK METRICS

In order to obtain an estimate of uncertainty in the network metrics, and its probable impact on the results, I performed randomisations of the hectad-level potential networks. Uncertainty in these networks arises from two major sources: the data and methods used to model the occurrence of plant and pollinator species and the interactions database used to construct potential networks. I therefore assessed these sources of uncertainty both independently and in combination.

First, for each hectad-level network, I reselected species at random as determined by their FRESCALO probability of occurrence. For each species, a random number was drawn from a uniform distribution. If this number was greater than its FRESCALO probability of occurrence, the species was removed from the resampled network. Thus a species with a FRESCALO probability of occurrence of 0.95 in a single hectad has a 95% chance of remaining in the hectad-level network. Once this had been done for all plant and pollinator species, I calculated all network metrics from these resampled networks.

Second, from the full, hectad-level network I reselected plant-pollinator interactions based on a log transform of the number of times they were recorded. This was set so that interactions with >10 records had a probability of 1, to account for the highly skewed distribution of numbers of records, the scarcity of interactions with larger numbers of records, and the fact that levels of recording were not even across insect groups. For each interaction, a random number was drawn from a uniform distribution. If this number was greater than its log transformed number of records divided by log of 10, the interaction was removed from the resampled network. Once this had been done for all interactions, I calculated all network metrics from this resampled network.

Third, I combined the two resampled networks, only retaining interactions present in both, and recalculated metrics once more. This three-stage randomisation process was repeated 100 times for each hectad. I then calculated the mean, standard deviation and range for network metrics derived from networks resampled according to each source of uncertainty across randomisations.

Results showed that, for all metrics, uncertainty arising from occurrence data had a greater impact that uncertainty from interactions (Figs B3 and B4). This is unsurprising, as adding or removing a species obviously affects all the interactions with which it is associated, whereas individual interactions may have little impact on the properties of the network as a whole. For connectance, resampling by occurrence tended to increase connectance (because of the strong relationship between connectance and network species richness), whilst resampling interactions reduced it (because removing interactions without altering species richness will decrease connectance by definition). When sources of uncertainly were combined, these two effects tended to cancel one another out, such that mean resampled connectance for resampled networks combing both sources of uncertainty was virtually identical to connectance as calculated from the full network (Fig. B3A and Fig B4). Smaller networks in the North of GB showed slightly higher variability in connectance from resampled networks, suggesting a correspondingly increased impact of uncertainty on connectance in these areas (Fig. B4).

For generality of both plants and pollinators, resampling by either occurrence or interactions reduced values in comparison to those from full networks, but in a very consistent fashion (Fig. B3B & C and Fig. B4), such that estimates of generality from full and resampled networks were all significantly intercorrelated (Pearson’s r, $r > 0.98$, $p < 0.001$). This was also evident in the limited spatial variability in uncertainty of generality scores, with standard deviations in generality from resampled networks showing no clear spatial pattern (Fig. B4).

For *Rg*, resampling by occurrence introduced variation around the value from the full dataset, but did not consistently reduce or increase the value (as shown for $R_{g\ Trend}$ in Fig. B3D). In contrast, resampling interactions slightly reduced *Rg* but very uniformly across hectads (Fig. B3D). When the two sources were combined, $R_{g\ Trend}$ was thus on average slightly lower than that observed from full networks, but with substantial variation, especially for network with lower $R_{g\ Trend}$ (Fig. B3D). Uncertainty did appear to vary spatially in its impact on $R_{g\ Trend}$, with areas of particularly high or low $R_{g\ Trend}$ showing correspondingly higher uncertainty. In spite of this variation, the correlation across hectads between full and resampled $R_{g\ Trend}$ was still high ($r = 0.92$, $p < 0.001$) and mapped $R_{g\ Trend}$ from both full and mean resampled networks showed very similar spatial patterns (Fig. B4).

When general linear mixed models were fitted using the mean values from resampled networks, in no case did the relationship with agricultural land change in qualitative terms (i.e. significance and direction of effect). This suggests that, whilst the impact of uncertainty around the estimates of occurrence and interactions is highly likely to affect the degree to which a per-hectad potential network reflects the real-world equivalent pollination network (along with the values of individual hectad-level metrics), they are much less likely to bias the observed spatial patterns across hectads and the relationships with agricultural land.

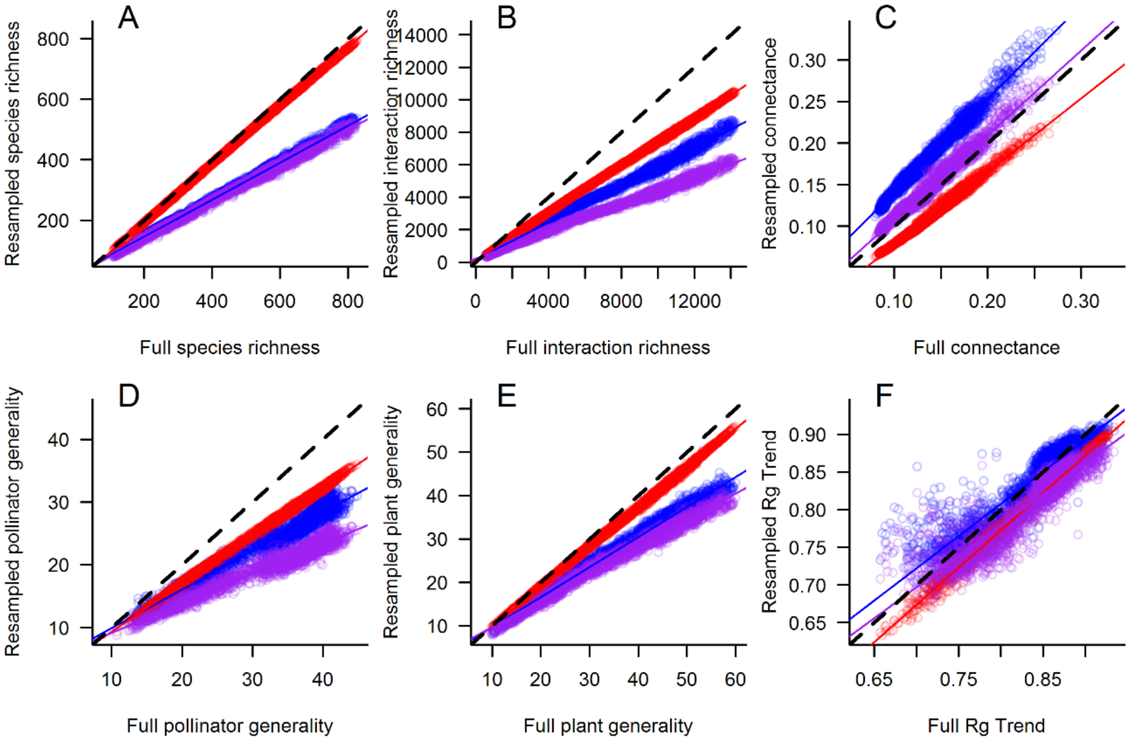


Figure B3. *Scatterplots of network metrics from full networks versus networks resampled according to different sources of uncertainty. A) Total network species richness (plants + pollinators) B) network interaction richness C) connectance, D) pollinator generality E) plant generality F) robustness to global extinction ordered by plant historic distribution trend ($R_{g\ trend}$). For all panels, blue circles and lines indicate resampling of occurence data, red circles and lines indicate resampling of species interaction data, and purple circles resampling of both occurrence and interaction data. Coloured lines indicate trend from linear regression, black, dashed lines indicates a slope of one and intercept of zero.*

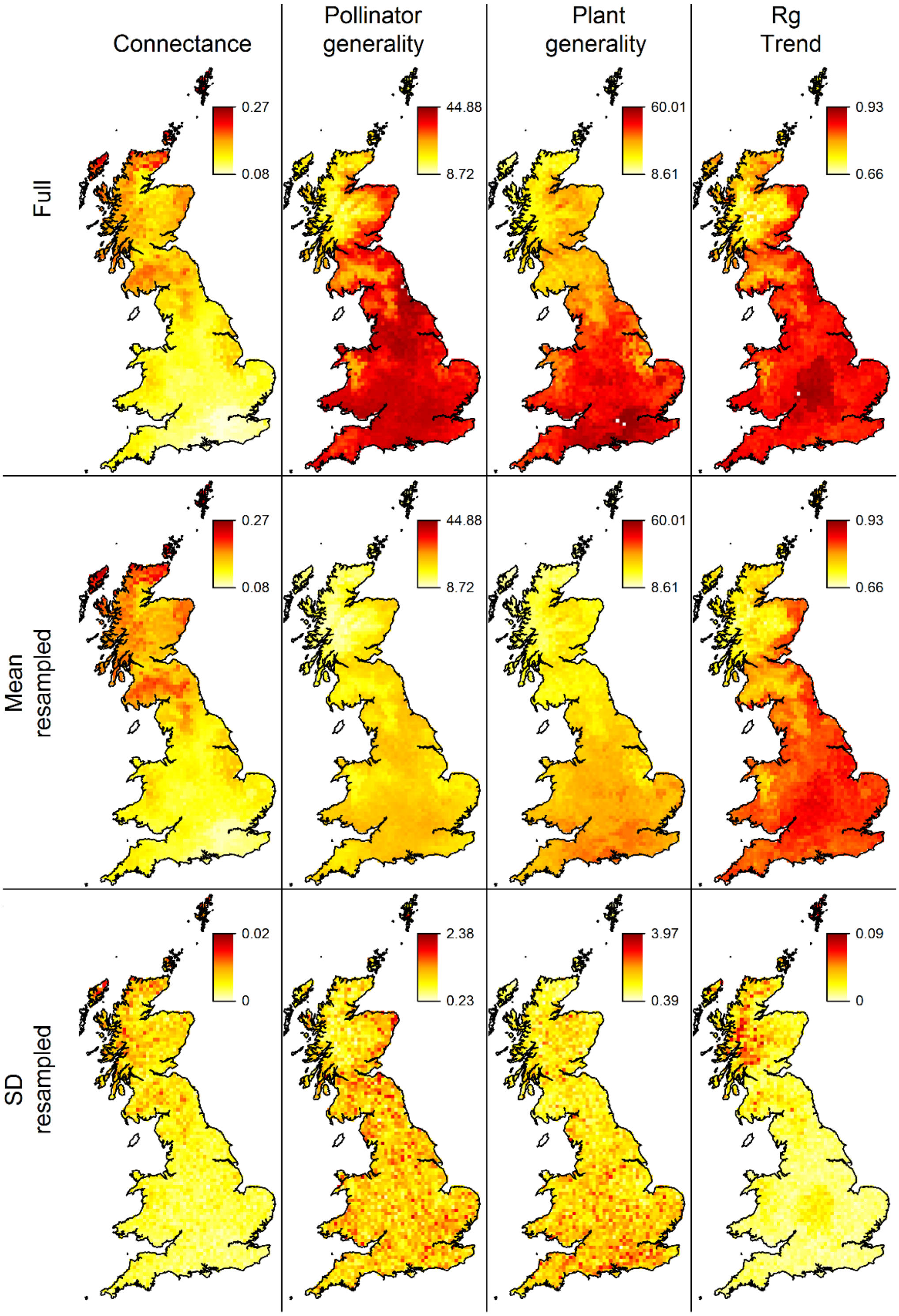


Figure B4. *Comparison of maps of hectad-level network metrics from full dataset (top row), mean value from 100 random resamples of occurrence and interaction data combined (centre row) and standard deviation of the latter (bottom row). Four network metrics are shown (left to right columns: connectance, pollinator generality, plant generality and robustness to global extinction ordered by plant trend* $R_{g\ trend}$*). Colour stretches for each metric are consistent between full and resampled networks to facilitate comparison.*

B6. ACCOUNTING FOR SPATIAL AUTOCORRELATION

Preliminary analyses identified that an exponential spatial autocorrelation (SAC) structure gave significant increases in model fit over a null model (χ^2 =2647.37, d.f. =1, $p < 0.001$). However, the null model also had significantly poorer model fit than the model with a random effect of environmental zone (χ^2 =126.25, d.f. =1, $p < 0.001$), and there was no additional improvement in model fit when the random effect was modelled in combination with SAC (χ^2 =0.10, d.f. =1, $p > 0.999$). This suggested that using environmental zones as a random factor was sufficient to account for SAC effects resulting from inherent spatial patterns of species occurrence. However, FRESCALO defines neighbourhoods based on both spatial proximity and biological similarity, so there is the potential for complex autocorrelation patterns to occur which may not be captured by assuming a predetermined SAC structure. I therefore used a randomisation approach (Fortin and Jacquez 2000) to account for SAC. Response variables were randomised across hectads 1000 times within environmental zones, and distribution of resultant model statistics compared to those from the full model. Only where the relevant statistics lay above or below 95% of those derived from randomisations (i.e. $p < 0.05$) were significant model results interpreted as being not attributable to autocorrelation.

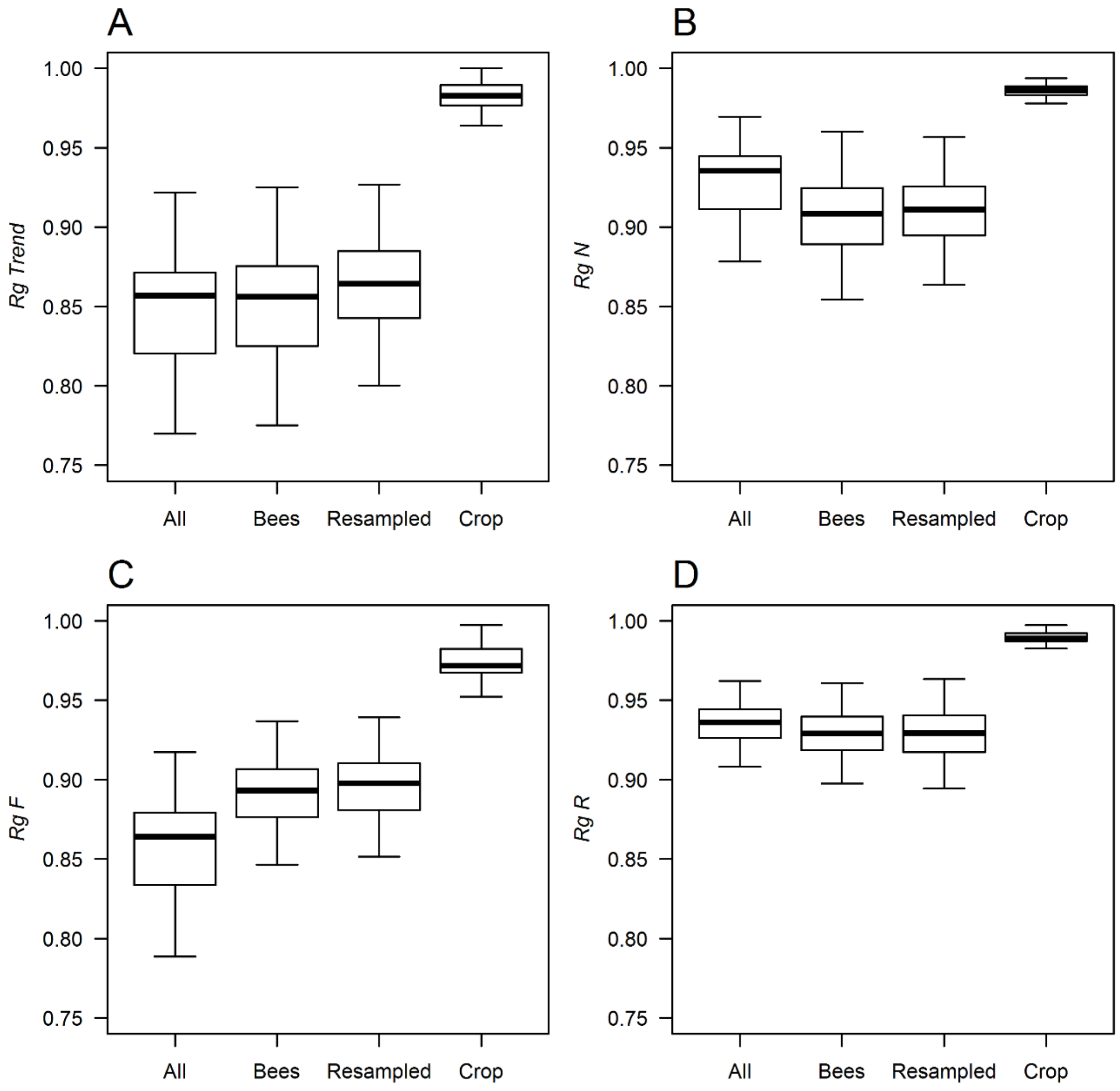


Figure B5*. Box plots comparing robustness to simulated extinction (Rg) across hectads for networks of all pollinators ('All'), bee-only networks ('Bee'), resampled networks of equivalent bee species richness to local crop-pollinating bee networks ('Resampled') and crop-pollinating bees only ('Crop'). The four panels A-D show extinctions ordered by trend (Rg trend), Ellenberg fertility (Rg N), Ellenberg moisture tolerance (Rg F) and randomised extinctions (Rg R), respectively. Crop-pollinating bees were:* Andrena carantonica, A. chrysosceles, A. cineraria, A. dorsata, A. flavipes, A. fulva, A. haemorrhoa, A. minutula, A. nitida, Bombus hortorum, B. hypnorum, B. lapidarius, B. lucorum s.l., B. pascuorum, B. pratorum, B. terrestris, Halictus confusus, H. rubicundus, Lasioglossum calceatum, L. leucozonium, L. malachurum, L. morio, O. bicornis.

C. Supplementary material for Chapter 5

C1. CLASSIFYING BASELINE LAND USE INTENSITY FROM CROPPING PATTERNS

Table C1. *Simple rules governing classification of crop type on currently arable dominated 1km cells, based on average cover per cell across three years (2015-2017).*

Class	Description	Rules	Potential drivers of expansion scenario
Intensive	Cropping systems dominated by simple rotations of winter cereals and break crops, typically oilseed rape	Winter cereals + oilseeds > all other crops	Widespread uptake of genetic modification permitting continuous wheat cropping Increased concerns over food security due to a growing population and increased trade tariffs Land-sparing practices leading to more intensive use of remaining arable land
Diverse	Cropping systems typified by multiple crops, including horticultural crops and vegetables	Average number of crops > 6 OR Root crops + maize + field beans > cereals + oilseeds	Desire to decrease reliance on a few crop types Increased concerns over food security for non-cereal crops due to dietary health issues
Extensive	Cropping systems dominated by spring cereals and temporary grass	Spring cereals > winter cereals OR Grass > any other crop	Increased societal desire to minimise environmental impacts of agriculture Rotational control of major crop pests (e.g. blackgrass) Land-sharing practices leading to less intensive use of arable land

C2. EXPLORING SCENARIO UNCERTAINTY

Exploring uncertainty by re-running scenarios 100 times showed a mean of 76% agreement with the modal class across all scenarios, for cells which showed change in any scenario run (see Table C1). Values across all cells were higher (>90%), because cells which did not change show, by definition, complete agreement across all 100 runs. Uncertainty in the results of the scenarios was affected by spatial resolution. Although uncertainty in the assignment of individual 1km cells could be relatively high, general trends in regional LULC patterns at coarser resolutions or at regional scales were much more conserved across scenario re-runs. Although it is necessary to use a spatial grid of sufficiently fine scale to incorporate processes such as proximity effects, the fate of individual cells under any one scenario should be treated with caution (Sharp et al. 2017). Results at broader scales (e.g. summaries by administrative or environmental units) are much more likely to be robust. In turn, the results of the pollinator SDMs should be less affected by uncertainties at the individual 1km cell level, since scenario results were transformed to percentage LULC at hectad scale.

Table C2. *Results of uncertainty analysis obtained be re-running each scenario 100 times. Values are mean % agreement with modal class for all 1km cells/cells which showed change under at least one scenario re-run.*

	Expansion step (% from baseline)					
Scenario	**5**	**10**	**15**	**20**	**25**	**30**
i) Agricultural expansion (SSSIs protected)	98/87	96/76	95/69	94/62	94/64	95/74
ii) Agricultural expansion (SSSIs unprotected)	98/88	96/76	95/68	94/61	93/63	95/76
iii) Grassland expansion	99/90	98/82	98/81	98/81	97/82	95/83

C3. VALIDATING SCENARIOS OF FUTURE AGRICULTURAL LAND USE/LAND COVER

Attempting to recreate the configuration of LCM2007 from the Dudley-Stamp map using the scenario generator tool gave a result which was at best 73% accurate (Kappa =0.54) in terms of correctly assigning 1km cells to improved grassland, arable land or semi-natural grassland/heathland (I disregard other LULC classes as these did not change under the scenarios). This was achieved using all parameters and an equal weighting between transition likelihoods and suitability factors (Table C2). Although this figure derived from per-1km cell classification suggest only moderate agreement between observed and predicted land covers, broader patterns in terms of dominant habitat per 10km cell (Table C2) and which regions showed change were generally more accurate. This suggests that the tool is fit-for-purpose in terms of creating plausible scenarios, especially when these are broad in scope and exploratory in nature.

Table C3. *Comparison of LCM2007 with results from using the scenario generator tool to reconstruct historic change from the Dudley-Stamp map, under different combinations and weightings of parameters. Accuracy refers only to LULC classes which changed under the scenarios. ALC refers to the use of the agricultural land classification as a suitability factor. Results are given for individual 1km cells (i.e. resolution of the scenario outputs) and dominant habitat per 10km cell (i.e. resolution of the beneficial invertebrate species distribution models).*

		1km resolution		**10km resolution**	
Parameters used in tool	**Factor weighting**	**% Accuracy**	**Kappa**	**% Accuracy**	**Kappa**
Transition matrix only	-	61.0	0.34	59.1	0.30
Transition matrix + proximity	-	61.2	0.35	59.4	0.31
Transition matrix + proximity + ALC	0.3	69.9	0.49	72.4	0.52
Transition matrix + proximity + ALC	0.4	70.1	0.50	72.3	0.52
Transition matrix + proximity + ALC	0.5	72.7	0.54	77.8	0.61
Transition matrix + proximity + ALC	0.6	70.6	0.51	73.2	0.53
Transition matrix + proximity + ALC	0.7	69.6	0.49	70.5	0.49

C4. CLEANING DATA AND SELECTING SPECIES DISTRIBUTION MODELS AND PARAMETERS

Data on were filtered to remove non-pollinating bees (e.g. “cuckoo” bees) and any species with taxonomic issues (e.g. species aggregations or synonyms that affect reliability of long-term records). All data were limited to records from 2000-2012 to avoid records from prior to the major changes in agricultural extent and practice which occurred over the 20th century (Robinson and Sutherland 2002, Ollerton et al. 2014) and the lag between the current year and records being submitted to the recording schemes. I also removed species with less than 25 records, as suggested by preliminary analyses which assessed the impact of number of records on model performance (Fig. C2).

Table C4 *Model performance metrics for different species distribution models and bias rasters (i.e. methods of limiting selection of pseudoabsences) for pollinator and natural enemy species. Metrics are given as means across all species within the group (± 1 standard error). Thresholds refer to limiting pseudoabsences to cells with at least a given number of other species from the group in question (Hickling et al. 2006, Redhead et al. 2015), effort-weighted approaches use modelled recorder effort estimated from the density of all records (Hill 2012).*

					Bias raster		
Group	**Metric**	**Model**	**None**	**Threshold =1**	**Threshold =5**	**Threshold =10**	**Effort weighted**
Pollinating bees	AUC	Null Model	0.57 (0)	0.57 (<0.01)	0.57 (<0.01)	0.57 (<0.01)	0.57 (<0.01)
		Logistic Regression	0.86 (0.01)	0.73 (0.01)	0.69 (0.01)	0.69 (0.01)	0.72 (0.01)
		Random Forest	0.89 (0.01)	0.78 (0.01)	0.70 (0.01)	0.70 (0.01)	0.76 (0.01)
		MaxNet	0.87 (0.01)	0.74 (0.02)	0.70 (0.02)	0.69 (0.02)	0.73 (0.01)
	Kappa	Null Model	-0.01 (0)	-0.01 (<0.01)	-0.01 (<0.01)	-0.01 (<0.01)	-0.01 (<0.01)
		Logistic Regression	0.55 (0.02)	0.34 (0.02)	0.25 (0.02)	0.25 (0.02)	0.32 (0.02)
		Random Forest	0.59 (0.01)	0.39 (0.02)	0.28 (0.02)	0.25 (0.02)	0.37 (0.02)
		MaxNet	0.56 (0.02)	0.36 (0.03)	0.29 (0.03)	0.26 (0.03)	0.33 (0.02)
Natural enemies	AUC	Null Model	0.58 (0)	0.58 (<0.01)	0.58 (<0.01)	0.58 (<0.01)	0.58 (<0.01)
		Logistic Regression	0.8 (0.01)	0.68 (0.01)	0.66 (0.01)	0.66 (0.01)	0.67 (0.01)
		Random Forest	0.83 (0.01)	0.69 (0.01)	0.65 (0.01)	0.64 (0.01)	0.69 (0.01)
		Max Net	0.81 (0.01)	0.70 (0.02)	0.67 (0.02)	0.64 (0.02)	0.67 (0.02)
	Kappa	Null Model	0.00 (<0.01)	0.00 (<0.01)	0.00 (<0.01)	0.00 (<0.01)	0.00 (<0.01)
		Logistic Regression	0.46 (0.01)	0.24 (0.02)	0.20 (0.02)	0.21 (0.02)	0.23 (0.02)
		Random Forest	0.46 (0.02)	0.24 (0.02)	0.18 (0.02)	0.16 (0.02)	0.24 (0.02)
		MaxNet	0.42 (0.02)	0.28 (0.03)	0.23 (0.03)	0.19 (0.03)	0.24 (0.03)

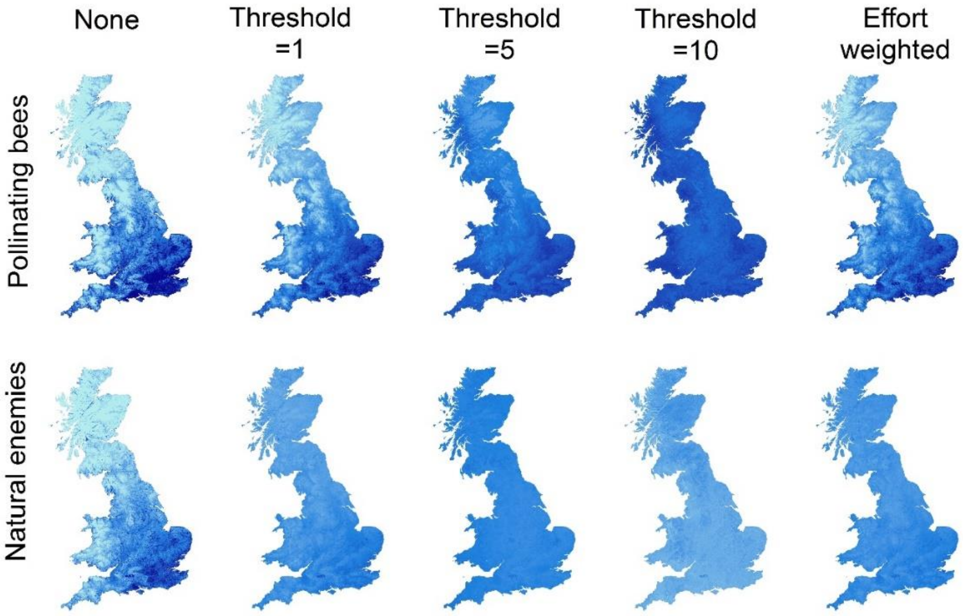


Figure C1. *Maps of species richness under baseline conditions modelled using logistic regression models and the different bias rasters (i.e. methods of limiting selection of pseudoabsences). Darkest shades correspond to >=100 species, lightest shades to <=20 species, with a linear colour stretch between these extremes. It can be seen that having no bias raster underestimates the number of species in the north of the country by allowing pesudoabsences where species occur but are under-recorded, whilst overly restrictive bias thresholds underestimate richness in the south, by permitting pseudoabsences only in very well recorded areas, and thus limiting the sampled range of habitats and climatic variables.*

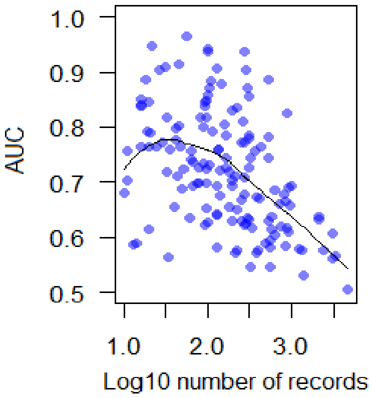


Figure C2. *Effect of number of occurrence records (i.e. unique 1km squares in which the species was recorded) on model performance as measured by AUC for logistic regression models. Black line indicates the locally smoothed trend (generated by the loess R function). AUC increases with number of records up to around 25 records, then decreases due to increasing generalisation of the species, suggesting a threshold of around 25 records for inclusion in scenario analysis.*

C5. BENEFICIAL INVERTEBRATE TRAITS AND DATA SOURCES

Trait data for 116 bee species and 81 natural enemies were obtained from the literature and online resources. Full lists of trait values for the species are given in Tables C5 and C6

Table C5. *Trait data for 116 bee species. Traits are intertegular distance (ITD, mm), diet breadth (O = oligolectic vs. P = polylectic), sociality (Sol = solitary vs. Soc = social), voltinism (U = univoltine, B = bivoltine, C = continuous) and flight season (number of months for which a species is usually found as a flying adult).*

Species	ITD	Diet Breadth	Sociality	Voltinism	Flight Season	Species	ITD	Diet Breadth	Sociality	Voltinism	Flight Season
Andrena angustior	1.88	P	Sol	U	3	*Bombus ruderatus*	4	P	Soc	C	7
Andrena apicata	NA	O	Sol	U	2	*Bombus soroeensis*	4.91	P	Soc	C	3
Andrena argentata	NA	P	Sol	U	2	*Bombus sylvarum*	4.44	P	Soc	C	5
Andrena barbilabris	2.1	P	Sol	U	2	*Bombus terrestris*	5.66	P	Soc	C	12
Andrena bicolor	2.13	P	Sol	B	6	*Ceratina cyanea*	1.39	P	Sol	U	5
Andrena bimaculata	2.72	P	Sol	B	6	*Chelostoma campanularum*	0.93	O	Sol	U	3
Andrena bucephala	2.15	P	Sol	U	2	*Chelostoma florisomne*	1.79	O	Sol	U	5
Andrena chrysosceles	2.14	P	Sol	U	4	*Colletes daviesanus*	2.44	O	Sol	U	4
Andrena cineraria	2.83	P	Sol	U	2	*Colletes fodiens*	2.6	O	Sol	U	3
Andrena clarkella	3.1	O	Sol	U	4	*Colletes hederae*	3.23	O	Sol	U	4
Andrena denticulata	2.12	O	Sol	U	2	*Colletes similis*	2.5	O	Sol	U	3
Andrena dorsata	2.11	P	Sol	B	4	*Colletes succinctus*	2.9	O	Sol	U	3
Andrena flavipes	2.34	P	Sol	B	8	*Dasypoda hirtipes*	5.7	O	Sol	U	4
Andrena florea	2.43	O	Sol	U	3	*Eucera longicornis*	3.29	O	Sol	U	3
Andrena fucata	2.45	P	Sol	U	2	*Halictus rubicundus*	2.18	P	Soc	C	6
Andrena fulva	2.26	P	Sol	U	2	*Halictus tumulorum*	1.49	P	Soc	C	6
Andrena fulvago	2	O	Sol	U	3	*Heriades truncorum*	1.55	O	Sol	U	3
Andrena fuscipes	2.02	O	Sol	U	5	*Hoplitis claviventris*	1.93	P	Sol	U	4
Andrena haemorrhoa	2.65	P	Sol	U	5	*Lasioglossum albipes*	1.64	P	Soc	U	8
Andrena hattorfiana	2.74	O	Sol	U	3	*Lasioglossum calceatum*	1.82	P	Soc	C	8
Andrena helvola	1.89	P	Sol	U	2	*Lasioglossum cupromicans*	NA	P	Sol	U	7
Andrena humilis	2.68	O	Sol	U	4	*Lasioglossum fratellum*	1.51	P	Soc	U	6
Andrena labialis	2.7	O	Sol	U	3	*Lasioglossum fulvicorne*	1.31	P	Soc	C	8
Andrena labiata	1.76	P	Sol	U	2	*Lasioglossum laevigatum*	1.84	P	Sol	U	6
Andrena lapponica	2.58	O	Sol	U	3	*Lasioglossum lativentre*	1.56	P	Sol	U	7
Andrena marginata	1.95	P	Sol	U	3	*Lasioglossum leucopus*	1.21	P	Sol	U	6
Andrena minutula	1.43	P	Sol	B	6	*Lasioglossum leucozonium*	1.91	P	Sol	U	9
Andrena minutuloides	1.39	P	Sol	B	3	*Lasioglossum malachurum*	1.79	P	Soc	C	7
Andrena nigroaenea	2.84	P	Sol	B	4	*Lasioglossum minutissimum*	0.86	P	Sol	NA	7
Andrena nitida	2.97	P	Sol	U	5	*Lasioglossum morio*	1.1	P	Soc	C	8
Andrena ovatula	2.04	P	Sol	B	6	*Lasioglossum parvulum*	1.25	P	Sol	U	5
Andrena pilipes.s.s.	NA	P	Sol	B	5	*Lasioglossum pauxillum*	1.24	P	Soc	C	17

Andrena praecox	2.26	O	Sol	U	3	*Lasioglossum prasinum*	1.72	P	Sol	U	5
Andrena scotica	2.73	P	Sol	U	4	*Lasioglossum punctatissimum*	1.23	P	Sol	U	7
Andrena semilaevis	1.47	P	Sol	U	3	*Lasioglossum puncticolle*	1.49	O	Sol	U	7
Andrena similis	2.34	O	Sol	U	3	*Lasioglossum rufitarse*	1.44	P	Sol	U	5
Andrena subopaca	1.49	P	Sol	U	3	*Lasioglossum smeathmanellum*	NA	P	Sol	U	7
Andrena synadelpha	NA	P	Sol	U	3	*Lasioglossum villosulum*	1.33	P	Soc	U	8
Andrena tarsata	1.76	O	Sol	U	3	*Lasioglossum xanthopus*	2.37	P	Sol	U	5
Andrena thoracica	NA	P	Sol	B	6	*Lasioglossum zonulum*	1.95	P	Sol	U	7
Andrena tibialis	2.85	NA	Sol	U	4	*Macropis europaea*	2.52	O	Sol	U	3
Andrena trimmerana	2.25	P	Sol	B	7	*Megachile centuncularis*	2.72	P	Sol	U	5
Andrena wilkella	2.32	O	Sol	U	3	*Megachile leachella*	NA	P	Sol	U	3
Anthidium manicatum	3.59	P	Sol	U	4	*Megachile ligniseca*	3.9	P	Sol	U	5
Anthophora bimaculata	5.64	P	Sol	U	4	*Megachile maritima*	NA	P	Sol	U	3
Anthophora furcata	3.24	O	Sol	U	5	*Megachile versicolor*	3.35	P	Sol	U	4
Anthophora plumipes	4.43	P	Sol	C	4	*Megachile willughbiella*	3.55	P	Sol	U	3
Bombus hortorum	5.31	P	Soc	C	7	*Melitta haemorrhoidalis*	2.74	O	Sol	U	2
Bombus humilis	4.77	P	Soc	C	4	*Melitta leporina*	2.39	O	Sol	U	3
Bombus hypnorum	4.7	P	Soc	C	7	*Melitta tricincta*	NA	O	Sol	U	3
Bombus jonellus	4.62	P	Soc	C	7	*Osmia aurulenta*	2.88	P	Sol	U	3
Bombus lapidarius	4.9	P	Soc	C	7	*Osmia bicolor*	2.7	P	Sol	U	3
Bombus lucorum.s.l.	4.49	P	Soc	C	7	*Osmia bicornis*	3.14	P	Sol	U	4
Bombus magnus	5.66	P	Soc	C	12	*Osmia caerulescens*	2.35	P	Sol	U	5
Bombus muscorum	3.1	P	Soc	C	5	*Osmia leaiana*	2.67	O	Sol	U	5
Bombus pascuorum	4.45	P	Soc	C	7	*Osmia spinulosa*	2.03	O	Sol	U	5
Bombus pratorum	4.61	P	Soc	C	7	*Panurgus banksianus*	2.2	O	Sol	U	3
Bombus ruderarius	4.73	P	Soc	C	5	*Panurgus calcaratus*	1.8	O	Sol	U	4

Table C6 *Trait data for 81 natural enemy species (65 carabids and 16 ladybirds). Traits are body size (mm), diet breadth (O = omnivore, GP = generalist predator or SP = specialist predator), wing length (BA = brachypterous/apterous, M = macropterous or D = dimorphic).*

Species	**Body Size**	**Diet**	**Wing**	**Species**	**Body Size**	**Diet**	**Wing**
Carabids				*Notiophilus aquaticus*	5.12	SP	D
Acupalpus meridianus	3.35	GP	M	*Notiophilus biguttatus*	5.12	SP	D
Agonum fuliginosum	6.46	SP	D	*Notiophilus germinyi*	5.00	SP	D
Agonum gracile	6.00	SP	M	*Notiophilus palustris*	5.22	SP	D
Agonum marginatum	9.47	SP	M	*Notiophilus rufipes*	5.34	SP	M
Agonum muelleri	8.11	O	M	*Notiophilus substriatus*	4.74	SP	B
Agonum viduum	8.09	SP	M	*Olisthopus rotundatus*	6.88	SP	D
Anchomenus dorsalis	6.70	GP	M	*Paradromius linearis*	5.11	GP	D
Anisodactylus binotatus	11.17	SP	M	*Philorhizus melanocephalus*	3.10	GP	D
Badister bullatus	5.56	GP	M	*Platynus assimilis*	11.50	SP	M
Bembidion aeneum	3.93	GP	D	*Poecilus cupreus*	10.82	GP	M
Bembidion biguttatum	4.02	GP	M	*Poecilus versicolor*	9.80	GP	M
Bembidion guttula	3.12	GP	D	*Pterostichus diligens*	5.69	SP	D
Bembidion lampros	3.60	GP	D	*Pterostichus madidus*	15.83	O	BA
Bembidion lunulatum	3.69	GP	M	*Pterostichus melanarius*	15.03	GP	D
Bembidion mannerheimii	3.09	SP	B	*Pterostichus niger*	17.52	GP	M
Bembidion obtusum	3.19	GP	D	*Pterostichus strenuus*	6.13	GP	D
Bembidion properans	3.77	GP	D	*Pterostichus vernalis*	6.65	GP	D
Bembidion quadrimaculatum	4.09	GP	M	*Stomis pumicatus*	7.51	GP	B
Bembidion tetracolum	5.48	GP	D	*Syntomus foveatus*	3.47	GP	D
Calathus fuscipes	11.68	GP	B	*Syntomus obscuroguttatus*	3.40	GP	B
Calathus melanocephalus	7.30	SP	D	*Trechus obtusus*	3.86	SP	D
Calathus rotundicollis	9.63	GP	D	*Trechus quadristriatus*	3.83	SP	M
Carabus granulatus	19.39	GP	B	*Trichocellus placidus*	4.66	SP	M
Carabus nemoralis	23.41	GP	B	**Ladybirds**			
Carabus problematicus	23.66	GP	B	*Adalia bipunctata*	4.50	GP	M
Carabus violaceus	25.83	GP	B	*Adalia decempunctata*	3.80	SP	M
Cicindela campestris	13.72	SP	M	*Anatis ocellata*	7.80	SP	M
Clivina fossor	5.89	GP	D	*Anisosticta novemdecimpunctata*	4.00	SP	M
Cychrus caraboides	16.33	SP	B	*Aphidecta obliterata*	4.50	GP	M
Demetrias atricapillus	5.06	GP	M	*Chilocorus bipustulatus*	3.50	SP	M
Dyschirius globosus	2.47	SP	D	*Chilocorus renipustulatus*	4.50	SP	M
Elaphrus cupreus	8.45	SP	M	*Coccinella hieroglyphica*	4.00	SP	M
Elaphrus riparius	6.87	SP	M	*Coccinella septempunctata*	6.50	GP	M
Harpalus rufipes	13.15	O	M	*Coccinella undecimpunctata*	4.50	SP	M
Leistus ferrugineus	6.87	SP	D	*Exochomus quadripustulatus*	3.80	SP	M
Leistus fulvibarbis	7.04	SP	D	*Harmonia axyridis*	7.00	GP	M
Leistus spinibarbis	8.77	SP	D	*Harmonia quadripunctata*	5.50	SP	M
Leistus terminatus	6.62	SP	D	*Hippodamia variegata*	4.50	GP	M
Loricera pilicornis	7.06	SP	M	*Myrrha octodecimguttata*	4.50	SP	M
Nebria brevicollis	11.69	GP	M	*Myzia oblongoguttata*	7.00	SP	M
Nebria salina	11.35	GP	M				

Table C7 *Bibliography of trait data sources*

Reference	**Traits**
Bees	
Bommarco R., Biesmeijer J.C., Meyer B., Potts S.G., Pöyry J., Roberts S.P., Steffan-Dewenter I. & Öckinger E. (2010). Dispersal capacity and diet breadth modify the response of wild bees to habitat loss. Proceedings of the Royal Society of London B: Biological Sciences, 277, 2075-82	ITD, diet breadth, sociality
Carrié R., Andrieu E., Cunningham S.A., Lentini P.E., Loreau M. & Ouin A. (2017). Relationships among ecological traits of wild bee communities along gradients of habitat amount and fragmentation. Ecography, 40, 85-97.	ITD, diet breadth, sociality, flight season
Fortel L., Henry M., Guilbaud L., Guirao A.L., Kuhlmann M., Mouret H., Rollin O. & Vaissière B.E. (2014). Decreasing Abundance, Increasing Diversity and Changing Structure of the Wild Bee Community (Hymenoptera: Anthophila) along an Urbanization Gradient. *PLOS ONE*, 9, e104679.	ITD, sociality
Greenleaf S.S., Williams N.M., Winfree R. & Kremen C. (2007). Bee foraging ranges and their relationship to body size. *Oecologia*, 153, 589-596.	ITD
Bees, Wasps & Ants Recording Society (2018). Species Gallery & Accounts. URL: http://www.bwars.com/category/taxonomic-hierarchy/bee	Diet breadth, sociality, flight season
Carabids	
Purtauf T., Dauber J. & Wolters V. (2005). The response of carabids to landscape simplification differs between trophic groups. *Oecologia*, 142, 458-464.	Diet breadth
Ribera I., Foster G.N., Downie I.S., McCracken D.I. & Abernethy V.J. (1999). A comparative study of the morphology and life traits of Scottish ground beetles (Coleoptera, Carabidae). In: *Annales Zoologici Fennici*. JSTOR, pp. 21-37.	Body size, diet breadth, wing length
Kotze D.J. & O'Hara R.B. (2003). Species decline—but why? Explanations of carabid beetle (Coleoptera, Carabidae) declines in Europe. *Oecologia*, 135, 138-148.	Body size, diet breadth, wing length
Homburg K., Homburg N., Schäfer F., Schuldt A. & Assmann T. (2014). Carabids.org – a dynamic online database of ground beetle species traits (Coleoptera, Carabidae). *Insect Conservation and Diversity*, 7, 195-205.	Body size, diet breadth, wing length
Lindroth C.H. & Bangsholt F. (1985). *The Carabidae-Coleoptera-Of Fennoscandia and Denmark*. Brill Archive.	Body size, wing length
Ladybirds	
Comont R.F., Roy H.E., Lewis O.T., Harrington R., Shortall C.R. & Purse B.V. (2012). Using biological traits to explain ladybird distribution patterns. *Journal of Biogeography*, 39, 1772-1781.	Body size, diet breadth
Comont R.F., Roy H.E., Harrington R., Shortall C.R. & Purse B.V. (2014). Ecological correlates of local extinction and colonisation in the British ladybird beetles (Coleoptera: Coccinellidae). *Biological Invasions*, 16, 1805-1817.	Body size, diet breadth

C6. Exploring SDM performance

***Table C8**. Model performance metrics averaged across all species for each of the two functional groups. Values are means with standard errors in parentheses. Kappa = Cohens kappa as calculated from observed and expected frequencies (Cohen 1960), proportion correct = proportion of presences and absences correctly identified, specificity = probability of correctly predicting a known absence, sensitivity = probability of correctly predicting a known presence, area under curve = area under the receiver operating curve (Fielding and Bell 1997).*

Group	Kappa	Proportion correct	Specificity	Sensitivity	Area Under Curve
Pollinators	0.34 (0.02)	0.79 (0.01)	0.47 (0.03)	0.84 (0.02)	0.73 (0.01)
Natural enemies	0.22 (0.02)	0.74 (0.01)	0.43 (0.03)	0.78 (0.02)	0.66 (0.01)

C7. RESULTS PLOTS FOR ALL SCENARIO COMBINATIONS

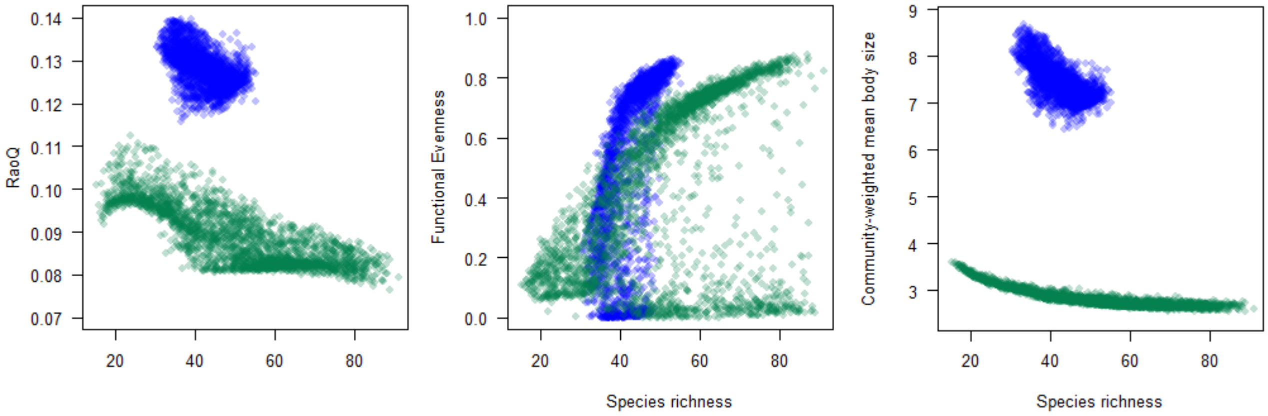


Figure C3. *Scatterplots showing pairwise relationships between species richness and functional diversity metrics (RaoQ, functional evenness and community-weighted mean body size) under the baseline scenario for pollinators (green) and natural enemies (blue)*

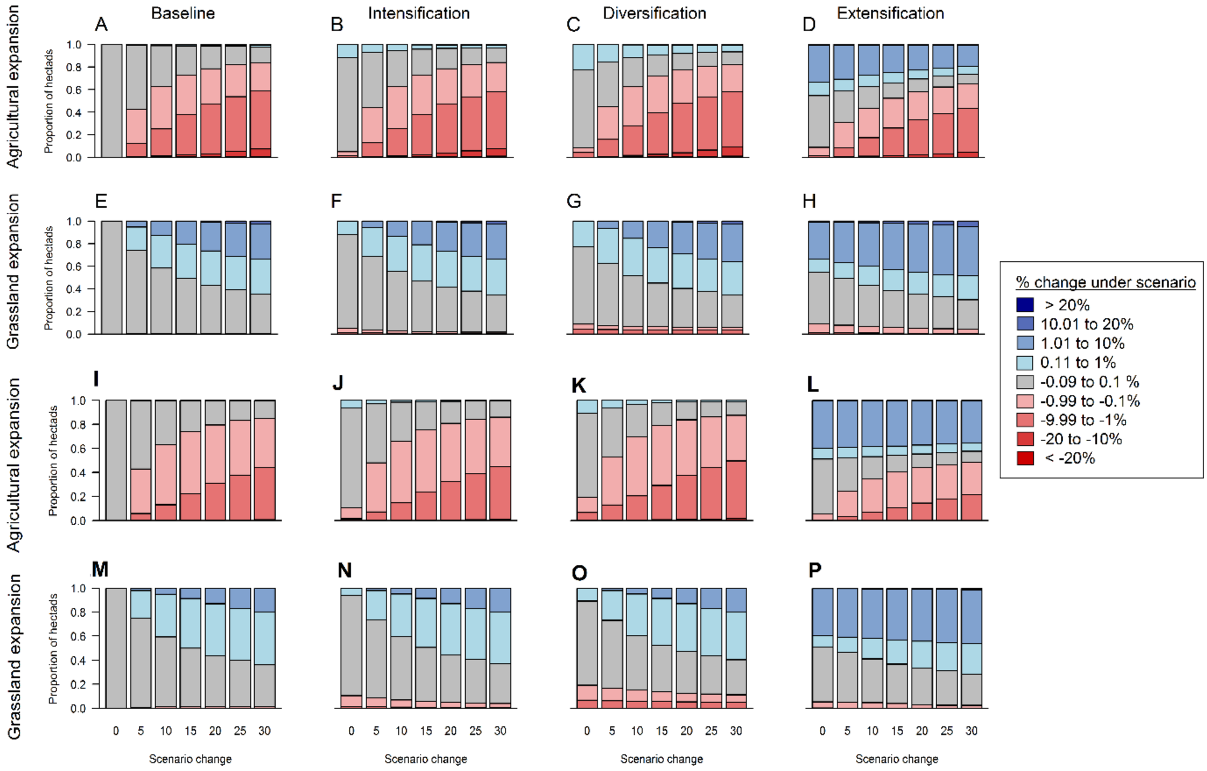


Figure C4. *Plots showing proportions of GB hectads with different levels of percentage change in pollinator (A-H) and natural enemy (I-P) species richness under different combinations of land cover (rows) and cropping intensity change (columns) scenarios.*

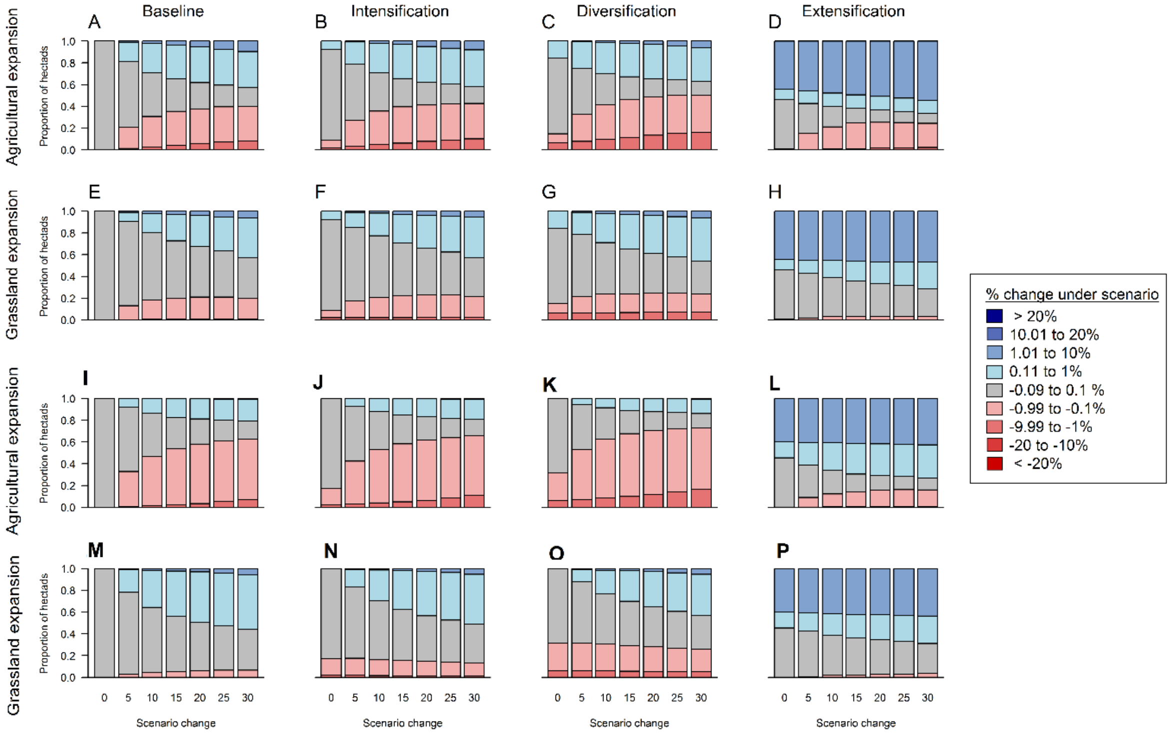


Figure C5. *Plots showing proportions of GB hectads with different levels of percentage change in pollinator (A-H) and natural enemy (I-P) RaoQ under different combinations of land cover (rows) and cropping intensity change (columns) scenarios.*

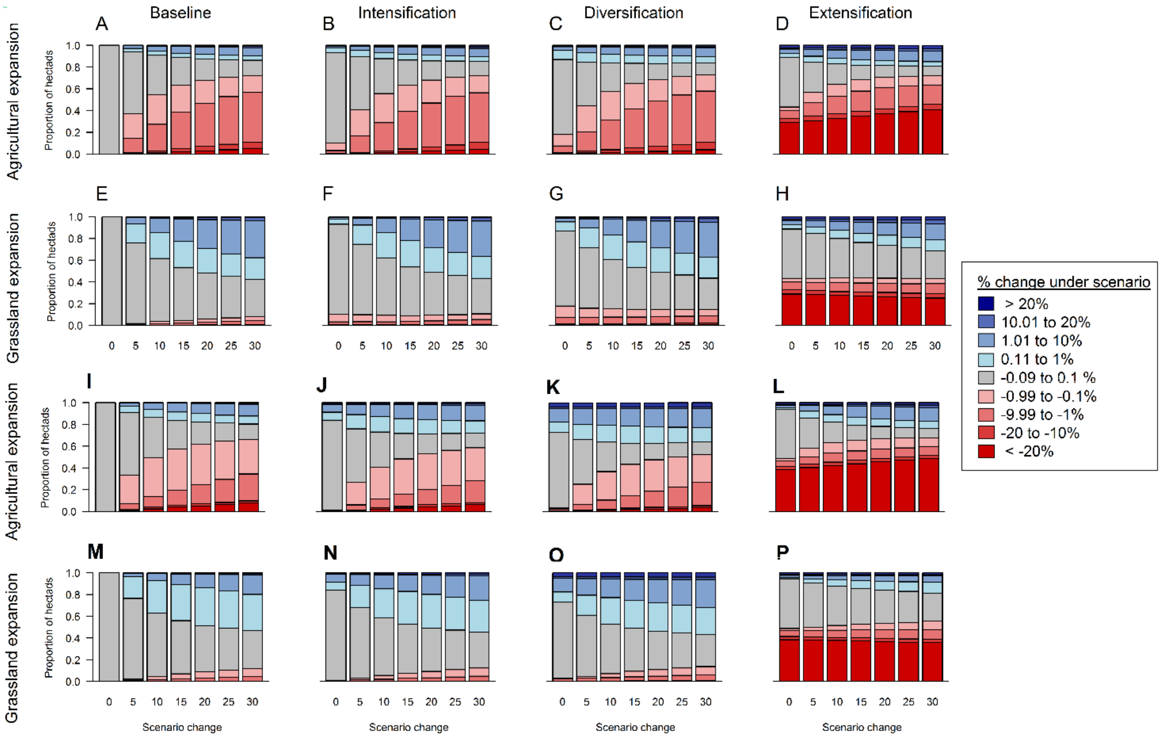


Figure C6. *Plots showing proportions of GB hectads with different levels of percentage change in pollinator (A-H) and natural enemy (I-P) functional evenness under different combinations of land cover (rows) and cropping intensity change (columns) scenarios.*

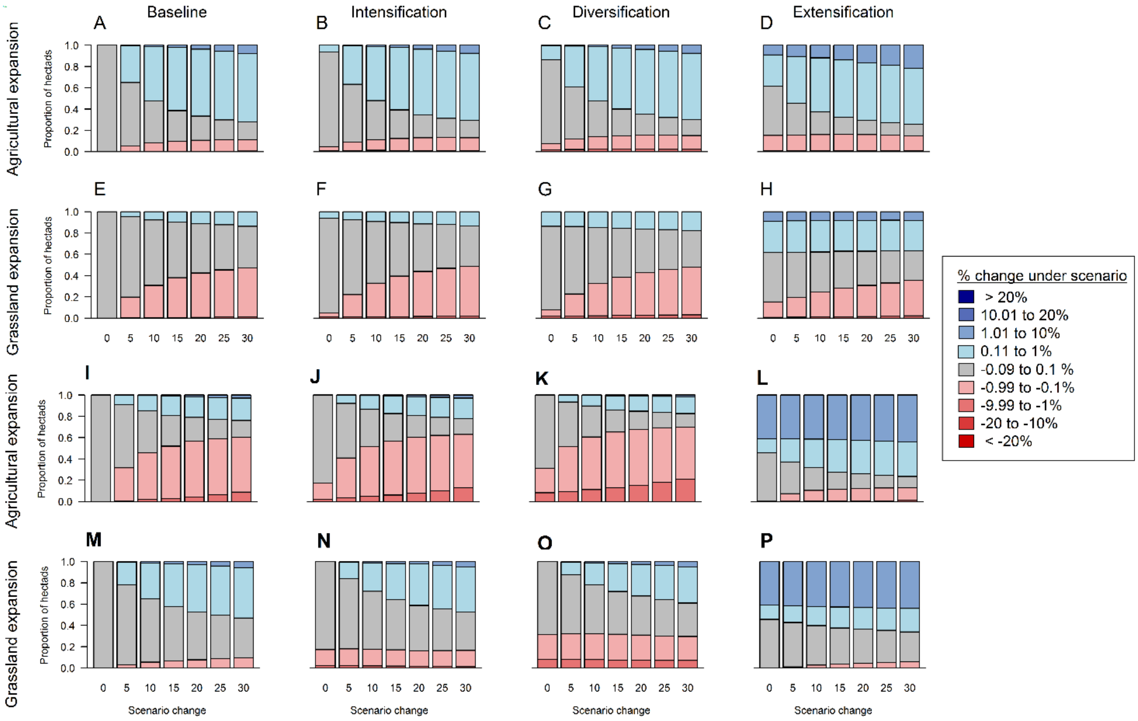


Figure C7. *Plots showing proportions of GB hectads with different levels of percentage change in pollinator (A-H) and natural enemy (I-P) community weighted mean body size under different combinations of land cover (rows) and cropping intensity change (columns) scenarios.*

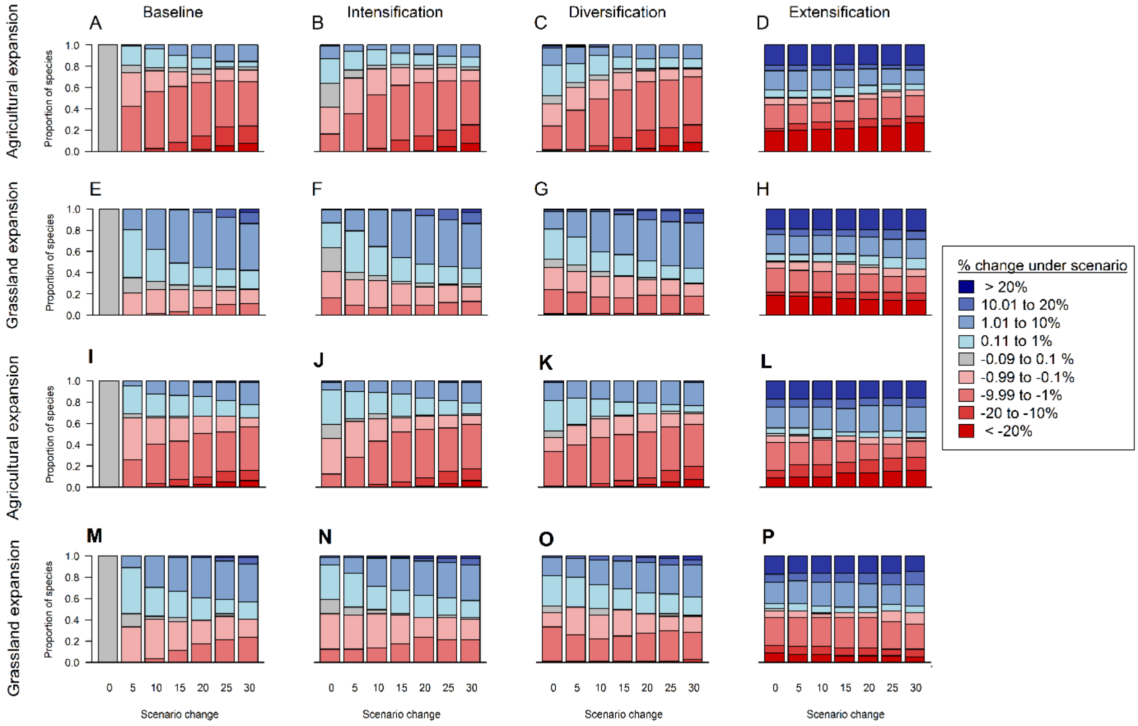


Figure C8. *Plots showing proportions of species with different levels of percentage change in total probability of occurrence (a measure of whether GB landscape suitability has increased or decreased for a given species), for pollinators (A-H) and natural enemies (I-P), under different combinations of land cover (rows) and cropping intensity change (columns) scenarios.*

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