UNRAVELLING ABIOTIC AND BIOTIC DRIVERS OF BIODIVERSITY CHANGE IN LOCAL PLANT AND INVERTEBRATE COMMUNITIES AFTER 80 YEARS - A RE-VISITATION STUDY ON THE STUDLAND PENINSULA

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Abstract

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How ecological communities respond to long-term environmental change via changes in species richness and composition is an urgent question in the 21st century as anthropogenic forces drive biodiversity declines across taxa and regions. As environmental conditions change over time, effects may cascade through co-occurring taxa, directly disturbing some species and altering the structure of ecological networks to disturb others However, a paucity of data has meant that studies investigating abiotic and biotic drivers of biodiversity change over periods of decades are rare, particularly those spanning multiple co-occurring taxa. The aim of this thesis is to investigate how effects of long-term (*ca.* 80 years) environmental change propagate through co-occurring plant and insect communities, driving changes in species richness and composition across taxa.

To achieve this aim I utilised a uniquely rich re-visitation study of species occurrence data on the Studland peninsula in the south of England. Data collection was led in the 1930s by the naturalist Cyril Diver, and in the 2010s by the National Trust in collaboration with a team of citizen scientists. I asked: 1) How have vascular plant assemblages of Studland changed in response to a changing abiotic environment between the 1930s and the present day?; 2) Have plant and insect taxa undergone congruent biodiversity changes under shifting environmental conditions?; 3) What abiotic and biotic factors relating to adult and larval ecological requirements have influenced long-term biodiversity change in Studland's hoverflies?; 4) How are the plant and insect communities of Studland likely to change in coming decades under proposed management interventions?

1) Using multilevel models of differences in Ellenberg indicator values (EIVs) between assemblages of vascular plant species occurring in each time-period, I found that the most prominent driver of plant species compositional change was changing hydrological conditions, followed by successional processes. 2) Using hierarchical modelling of species loss/gains and a range of multivariate techniques, I found that species richness and compositional changes in plant and insect communities displayed cross-taxon congruence – correlated patterns of biodiversity change – over the *ca.* 80 year time-period, likely driven by a combination of abiotic and biotic change. 3) Hierarchical modelling of species loss/gains in the hoverfly community suggested that species richness in adult assemblages is limited by adult resource availability (plants) at highly localised scales, while compositional change is strongly affected by the availability of suitable larval microhabitat at the wider scale of a few kilometres. As with the plants, hydrological change was the main abiotic driver of change in the hoverfly community. 4) Bayesian Belief Network (BBN) models predicted that local management interventions to increase drainage and control ecological succession could benefit the taxa and habitats of Studland through increased species richness. However, BBN models also predicted that the health of the regional metacommunity is of utmost importance in maintaining a healthy local system.

I have shown that congruent biodiversity change occurs across diverse plant and insect taxa, and is driven by changes in both abiotic and biotic conditions. These drivers do not act independently from one another, as demonstrated by effects of wetter winter conditions on hoverfly composition, coupled with effects of species richness change in the plant community, while the plant community was itself also responding to hydrological change via changing species composition. Crucially, my results suggest that the health of the regional metacommunity is of the utmost importance in

maintaining a healthy local system when faced with environmental changes as seen at Studland; a reservoir of species available to take advantage of new conditions is vital. Therefore this work suggest a joint emphasis placed on local and regional conservation practices to mitigate effects of the anticipated acceleration in environmental change.

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Author's Declaration

I confirm that all aspects of the work presented in this thesis are my own, with the following exceptions:

Chapter 2 has been published in collaboration with Diaz, A., Gillingham, P. K., Stafford, R. and Bullock, J. M. as:

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Table of Contents

List of Figures

List of Tables

List of Appendices

Abbreviations

CDP	Cyril Diver Project
EIV	Ellenberg Indicator Value
GLMM	Generalized Linear Mixed Model
CTC	Cross-taxon congruence
RDA	Redundancy Analysis
BBN	Bayesian Belief Network

1. Introduction

Two limiting factors constraining community ecological research are *i)* the number of species which can simultaneously be studied (Vellend 2016), and *ii)* the time-scale over which environmental and ecological processes are investigated (Dornelas et al. 2012). The ecological literature is replete with studies of either wide temporal scope (e.g. Prach 1993; Keith *et al.* 2011; McGovern *et al.* 2011; Diaz *et al.* 2013) or taxonomic coverage (e.g. Van Veen *et al.* 2008; Peters *et al.* 2016). However, there are few notable exceptions with depth along both temporal and taxonomic axes (Biesmeijer 2006, Magurran and Dornelas 2010, Ewald et al. 2015, Storkey et al. 2016). As environmental conditions change over time, effects can cascade through co-occurring taxa, directly disturbing some species and altering the structure of ecological networks to disturb others (e.g. Trophic cascades (Paine 1974, Pace et al. 1999)). For instance, changing precipitation levels in desert ecosystems directly affect the of types grass species which occur, in turn affecting the relative abundances of granivorous rodents (Ernest et al. 2008). Anthropogenically induced environmental change is forecast to accelerate deep into the 21st century (Masson-Delmotte et al. 2018), amplifying pressures on communities which are already under duress. It follows that long-term studies on processes affecting multiple co-occurring taxa over periods of decades are needed in order to better anticipate community responses. Such research should serve to inform management for conservation as we embark on a period of potentially unprecedented environmental change.

In the following chapters I utilise a uniquely rich re-visitation dataset of species occurrences to investigate how long-term environmental change (*ca.* 80 years) propagates through plant and insect communities, culminating in species richness and compositional change across taxa. Throughout, I aim to determine how abiotic and biotic factors combine to drive local biodiversity change, and what the implications are for ecological communities in the coming decades.

1.1 Background – Temporal Trends in Biodiversity

Despite the importance of temporal biodiversity trends (Chapin III et al. 2000, Dornelas et al. 2012, Lindenmayer et al. 2012), they are much less well studied and understood than spatial patterns and processes (Magurran and Dornelas 2010). This is not due to a misunderstanding of their importance, but rather to a combination of the rarity of datasets of sufficient temporal scope, and difficulty in obtaining funding for long-term projects under typical funding cycles (Dornelas et al. 2012). As more species are included in a study, logistical limitations increase due to the associated increase in person/hours required. As such, long-term studies in community ecology tend to be limited in taxonomic breadth, covering for example plant species (e.g. Diaz *et al.* 2013), or bird species (e.g. Harrison *et al.* 2014), but rarely plant and bird species. To overcome such logistical limitations, ecologists sometimes use workaround methods such as space for time substitutions (Blois et al. 2013), or study compact modules or functional groups of interacting species embedded within wider food webs (Holt 1997). However, laudable efforts of recording schemes in some countries for taxa including a number of insect groups, birds and plants (e.g. Thomas *et al.* 2004), have allowed for considerable advances in this area in recent decades through studies of long-term biodiversity trends across these groups (Thomas et al. 2004, Biesmeijer 2006, Baker et al. 2012, Sánchez-Bayo and Wyckhuys 2019). Some notable long-term experimental studies have also coincided with and added to advances achieved via recording scheme data (Silvertown et al. 2006, Pérez-Rodríguez et al. 2015). Despite these advances, literature on effects of long-term processes acting across multiple co-occurring taxa is still relatively scant (Ernest et al. 2008, Özkan et al. 2014, Ewald et al. 2015).

Both the spatial scale of analysis and specific biodiversity metrics used must be made explicit when investigating temporal biodiversity trends, though not all studies have been sufficiently careful in doing so (McGill et al. 2015). At global scales we are in the midst of a major extinction crisis (Barnosky et al. 2011), as land use change (Baker et al. 2012, Hooftman and Bullock 2012, Senapathi et al. 2017) and anthropogenic climate change (Parmesan 2006) push many communities to rely on sparsely distributed protected areas for their survival (Thomas and Gillingham 2015). However, despite the prevalence of global declines, the ubiquity of such downward trends in local communities is not at all clear where major anthropogenic disturbances have not occurred – a topic subject to recent controversy in the ecological literature (Cardinale et al. 2018). Furthermore, we should expect temporal rates of species turnover to decrease as communities examined move upwards in scale from local to regional – local communities contain only a subset of the regional species pool and thus have more scope to fluctuate in composition than more saturated regional areas (Adler and Lauenroth 2003). To further complicate the issue, species compositional changes at regional scales are accelerating under effects of climate change (Parmesan 2006). Such complexity highlights the need for clarity on scales of analyses.

Another complexity to consider is that metrics of temporal biodiversity change come in many forms (Legendre and Gauthier 2014, McGill et al. 2015). This is an important point to remember when comparing results. However, most of these metrics focus on changes in the number of species present (species richness differences), or the identities or relative abundances of species present (compositional differences). Throughout this thesis I will be focusing primarily on species losses and gains over an approximately 80 year period, as well as how aggregated species-level traits are associated with such losses and gains. As such, my analyses will concentrate mostly on changes in species richness and changes in the identities of species present in either time-period (compositional change) rather than on changing abundances.

The phenomenon of biotic homogenisation across ecological communities highlights the aforementioned importance of clarity in the spatial scale of analysis and the biodiversity metrics used. In 2003, Sax & Gaines highlighted the seemingly paradoxical phenomenon of local and regional gains in species richness occurring in many areas, while richness at wider scales – continentally and globally – continued to decline (Sax and Gaines 2003). This phenomenon can be explained, at least in part, by the process of biotic homogenisation, where more common species – both indigenous and invasive – extend their ranges, while rarer species are lost, leading to reductions in β-diversity (spatial variation in composition) and greater similarity across communities, but leaving limited changes in the overall numbers of species present (Olden 2006, Smart et al. 2006).

Variable trends in local species richness change over time, coincident with declines at wider scales, may be a widespread pattern of biodiversity change over the last 100 years or more, though the validity of this claim has been questioned (Cardinale et al. 2018). Two wide ranging meta-analyses found that species richness was equally likely to increase or decrease in terrestrial plant communities (Vellend et al. 2013), and across a range of marine and terrestrial communities globally (Dornelas et al. 2014). Dornelas *et al.* (2014) also highlighted compositional changes of as much as 10% turnover in species composition per decade while species richness remained stable on average. These studies have been criticised on the grounds that the time-series data used were not entirely fit for purpose, and that claims of "global" trends were inappropriately broad given the scope of analyses (Gonzalez et al. 2016). However, the authors have in turn defended their conclusions, and point out that though their analyses are not perfect, they are of the highest standard possible given the current data available, and thus comprise the best available evidence (Vellend, Dornelas, et al. 2017). Regardless of global average trends, the variability found across the wide range of communities included in these meta-analyses underscores the need for research into the plethora of specific processes underlying such trends in local communities.

The need to understand both the context in which a community is embedded, and the underlying processes at play, when investigating biodiversity trends in local communities thus seems clear. Biodiversity change does not necessarily correlate across scales, and it is possible for patterns of local, regional and global change to differ substantially (McGill et al. 2015). Indeed, it should be no surprise to find variable patterns in biodiversity change across communities in differing environments, particularly those composed of different groups of species, as the contingent nature of processes underlying community dynamics has been a longstanding finding in community ecology (Lawton 1999). Asking how diverse co-occurring taxa collectively react to environmental change is a pressing issue for the practical purposes of management and conservation – particularly when potentially isolated protected local areas are the spatial units of conservation for collectives of taxa, as is often the case under current practices (Gillingham et al. 2015).

1.1.1 The role of abiotic environmental change

Surprisingly few studies have documented how compositional change tracks temporally changing abiotic environments over periods of decades (Leibold and Chase 2018). This is despite the well-documented influence of the abiotic environment on species composition across spatial extents (Chase and Leibold 2003, Austin 2007). Again, this is almost certainly due to logistical limitations and a lack of appropriate long-term datasets. As usual however, some excellent exceptions do exist; for instance in studies of ecological succession (Connell and Slatyer 1977), experimental manipulations of soil nutrients (Crawley et al. 2005), and range adaptations to climate change (Parmesan 2006).

The impact of abiotic environmental change on species richness and composition has generally been an important underlying factor in cases where data have been available to investigate it effects. Species richness often remains stable even where large compositional change occurs, and there is evidence to suggest that this may be due to suitably adapted species tracking environmental fluctuations (Brown et al. 2001). Environmental stochasticity was also a major driver of compositional change in temporal studies spanning microbes, plants and animals (Mutshinda et al. 2009, Hatosy et al. 2013, Kalyuzhny et al. 2014).

Studies illustrating long-term effects of abiotic drivers on richness and composition spanning multiple *co-occurring* taxa are rarer still than single taxon studies. However, Özkan et al. (2014) found limited effects of environmental factors underlying 20 years of biodiversity change in co-occurring phyto- and zoo-plankton data. Contrastingly, Ewald et al. (2015) found that extreme hot or cold weather events had short-term effects on abundances in 11 out of 26 insect taxa in a 42 year time-series of co-occurring insects recorded at genus, family and class level in cereal fields in Southern England. They also found correlations in abundance trends with temperature and precipitation, and detrimental effects of pesticide use on temporal abundance trends across taxa. Ernest et al. (2008) found that changes in precipitation patterns altered the composition of grass species which had knock-on effects on types of rodents present due to trophic dependencies. It remains unclear however, how co-occurring taxa respond in tandem to direct effects of abiotic environmental change in most ecosystems. This is clearly an important area of research for conservation biology in the decades to come under expected climate scenarios (Masson-Delmotte et al. 2018).

Where species composition does change due to changes in the abiotic environment, this is because species with relevant physiological or behavioural traits to exploit new conditions arrive, while unsuited species are excluded (e.g. Silvertown *et al.*2015). Thus when studying biodiversity responses to abiotic change, analyses focusing on trait composition of species present are valuable and informative (Mcgill et al. 2006, Violle et al. 2007). Throughout this thesis, I will place a large emphasis on functional traits explicitly defined in terms of how species perform along environmental gradients. I will use such traits in models to predict whether species have been lost or gained between time-periods, thus indirectly inferring abiotic environmental factors which have driven biodiversity change across the study area.

1.1.2 The role of interactions between taxa

That interactions between co-occurring taxa can have important effects on temporal biodiversity patterns within those taxa is almost a tautological statement; one need just imagine the effects of removing all plant species on a co-occurring assemblage of herbivores. However, effects of such group level interactions may be less obvious – while still being of utmost importance (Kiers et al. 2010) – in cases of less extreme temporal change in one or another group of co-occurring species. For example, long-term species richness differences in co-occurring plants and pollinators are closely correlated (Biesmeijer 2006), and while the direction of causation is unclear, the importance of each of these taxa for one another for pollination suggests it is a strong underlying driver. Similarly, a study out of the Rothamsted monitoring scheme found correlated migration patterns between aphids and their parasitoids (Pérez-Rodríguez *et al.* 2015). Hunting and habitat destruction of large seed dispersers have also had detrimental effects on plant biodiversity in tropical forest ecosystems (Dirzo and Miranda 1990).

Correlated patterns of biodiversity change between taxa are not always due to biotic interactions however; shared responses to environmental change can also underlie correlations (Ranta et al. 2008a). It is thus important to partition abiotic and biotic drivers of biodiversity change where possible, in order to fully understand temporal patterns of change (Mutshinda *et al.* 2009). Throughout this thesis, I attempt to identify such correlated changes in biodiversity among co-occurring plant and insect taxa, and where possible, attribute such correlations to shared responses to the abiotic environment or biotic interactions between taxa.

1.1.3 Biodiversity trends in plants and insects

The sedentary nature of plants, and their direct dependence on the abiotic environment, make them ideal for study in permanent plots analysing factors affecting community dynamics (e.g. Crawley *et al.* 2005). Numerous studies have assessed biodiversity change in plant communities over the time-period of this doctoral research (1930s-2010s), finding a range of drivers including species dispersal mode (Lavergne *et al.* 2006), effects of topography on soils and microclimate (Bennie et al. 2006) and stress tolerance of plant species (Newton et al. 2012). However, the majority of studies of local-scale temporal vegetation change deal with 50 year intervals or less (Vellend, Baeten, et al. 2017), and trends display a large degree of variation depending on the environmental context within which a community is embedded (Vellend et al. 2013). Nonetheless, specific changes in species richness and composition of plant communities are likely to be ubiquitously important for co-occurring taxa, as trophic and structural dependencies make plants a vital cornerstone of wider ecological communities (Scherber *et al.* 2010*;* Rzanny *et al.* 2013).

Insects comprise a large Class of taxa likely to experience effects of biodiversity change in plants both directly and indirectly (Kagata and Ohgushi 2006). Insects provide vital ecosystem services (e.g. pollination and decomposition), and like plants, form a foundational component of terrestrial ecological networks. Furthermore, habitat specificity and environmental filtering due to narrow physiological constraints for many insect species also allow them to serve as useful ecological indicators of wider environmental change (Thomas 2005). Despite a relative lack of information on global biodiversity change in insects (Diniz-Filho *et al.* 2010; Cardoso *et al.* 2011), there are reasons to believe that they may be experiencing an even more extreme extinction crisis than plants and macrofauna (Thomas et al. 2004, Dunn 2005, Dunn et al. 2009, Dirzo et al. 2014, Sánchez-Bayo and Wyckhuys 2019).

Spatiotemporal trends in select insect taxa in the UK – including Bees, Wasps, Ants, Hoverflies and Butterflies – have been documented in more detail in recent decades than in any comparable region (Thomas et al. 1994, 2015). These taxa are also well documented in some other north-western European countries over this period (e.g. Biesmeijer 2006; Carvalheiro *et al.* 2013). Monitoring schemes have revealed general declines in species richness throughout the 20th century, though trends have varied across spatial scales (Keil et al. 2011). Declines have also proceeded at differing rates during distinct time-periods, with extensive richness declines and biotic homogenisation occurring before 1990 in an era of intense landscape modification, and a slowing of declines post 1990 coinciding with increased investment in conservation efforts (Carvalheiro et al. 2013a, Thomas et al. 2015).

Modern declines in insect biodiversity have likely been driven by a combination of abiotic and biotic factors (Sánchez-Bayo and Wyckhuys 2019). Widespread land use change for agricultural intensification, along with use of pesticides which are physiologically damaging to insects were likely important causal factors (Potts et al. 2010). Correlated biodiversity trends in pollinators and outcrossing plant species dependent on insects for pollination also suggest a causal pathway via trophic dependencies as previously discussed, although the direction of causality is uncertain (Biesmeijer 2006). Climate change is another important factor, though it may be more likely to increase species richness in insects in more northerly areas such as the UK, as many species have thermophilus life-history stages preferring warmer conditions (Thomas et al. 2015).

In order to aid the development of effective conservation management strategies for insects, a better understanding is needed of detailed drivers of community change, and in particular, how species specific traits mediate community responses (Thomas 2005, Carvalheiro et al. 2013a). While broad trends in biodiversity change may be described in relation to external causal factors (eg. climate warming (Parmesan et al. 1999)), different species can respond to environmental change in diametrically opposing ways. Responses of generalist and specialist species within closely related groups are a prime example of such conflicting trends (Dennis et al. 2011, Eskildsen et al. 2015, Aguirre-Gutiérrez et al. 2016). Data on insect communities documented within the Studland case study presented herein – particularly the hoverfly community – provide a valuable opportunity to make a contribution to the understanding of mechanisms underlying long-term biodiversity change in insects relating to the abiotic and biotic environment.

1.2 The Cyril Diver Project: A re-visitation study 80 years on

The empirical basis of the research presented in this thesis is a historical resurvey study of the Studland peninsula in Dorset on the south coast of England (*figure 1.1*). Species occurrences and distributions of a wide range of plants and insects were recorded by Cyril Diver and contemporaries in the 1930s (Diver and Diver 1933, Good 1935, Diver 1938), and resurveyed in a citizen science innovative led by the National Trust between 2013 and 2015 (“The Cyril Diver Project”).

Diver was strongly active in debates concerning the direction of ecological research when the field was still relatively young, arguing in 1944 that increasing trends towards theoretical modelling introduced a danger of misrepresenting “Biological Reality” (Cooper 2003). These empirical principals are clearly apparent in his meticulous approach towards data collection on Studland, aimed at building an understanding of plant and insect communities from the ground up as outlined in his 1938 publication entitled “The Plant-Carpet in relation to Animal Distribution” (Diver 1938).

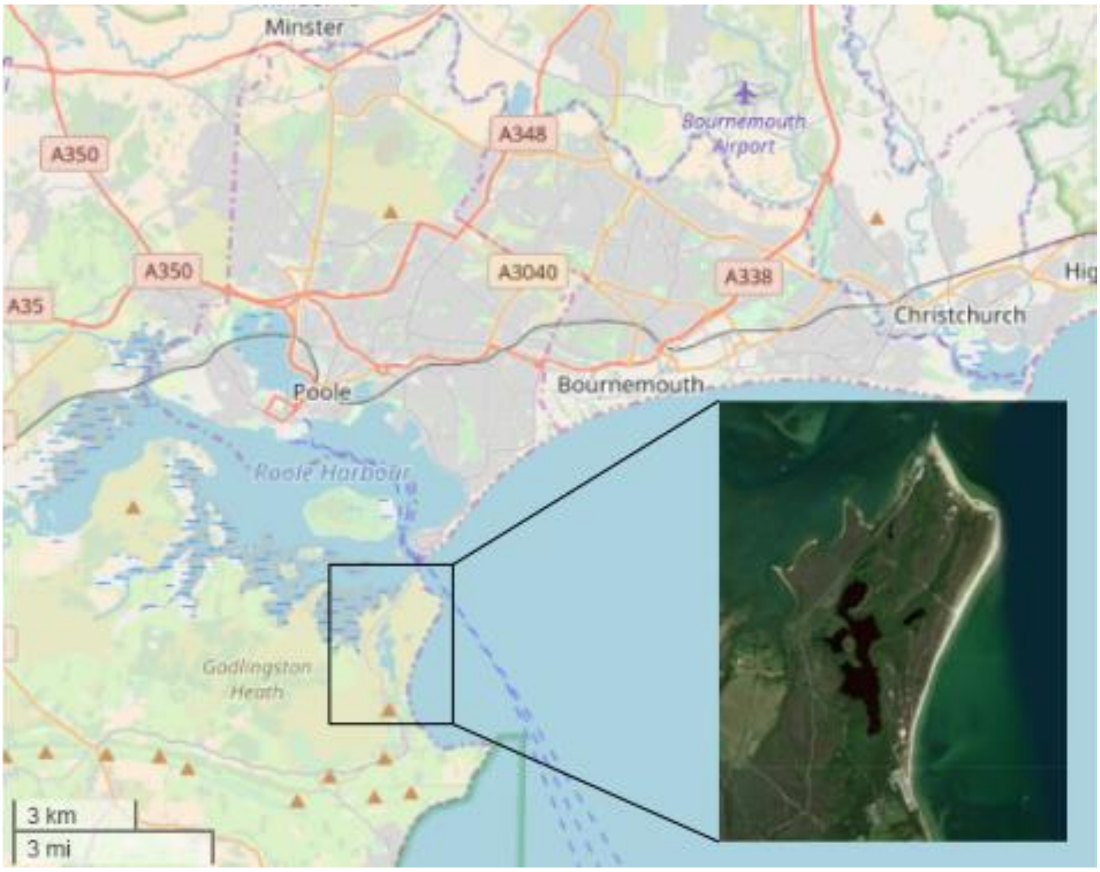

Figure 1.1 The Studland peninsula (inset) is situated in Poole harbour in the county of Dorset on the south coast of England.

1.2.1 The Studland study system: Habitats and “Sampling compartments”

Diver went to great pains to reconstruct the physiography of Studland and its development over hundreds of years as dune ridges gradually formed (Diver 1933). He described the peninsula in terms of both underlying abiotic conditions and the resulting vegetative communities that developed. The Studland peninsula is composed of several broad habitat types, described by Diver as follows:

> *“…though it may be loosely described as a heath, several distinct types of country are recognizable: sandy beach, marram dunes, dry and damp heaths, the harbour shore and various saltings, freshwater marshes and swamps, Little sea and smaller freshwater pools, scrub and woodland, grass and turf, and recently disturbed areas. These general types considered in reference to their physiography, history, and geological basis, form the natural major units or loci.”* (Diver 1938)

These habitat types remain a useful category for analysis of the ecological communities of Studland, and for comparisons between the communities of the 1930s and the present day. Diver’s original habitats have been adapted into seven broad categories for analyses presented in this thesis, namely: Lowland Heath (Wet and Dry), Dune heath, Dune, Woodland, Marsh (Saline), Shoreline, and Aquatic (edge) (*figure 1.2*). Habitat type will be a key factor of analyses in the following chapters.

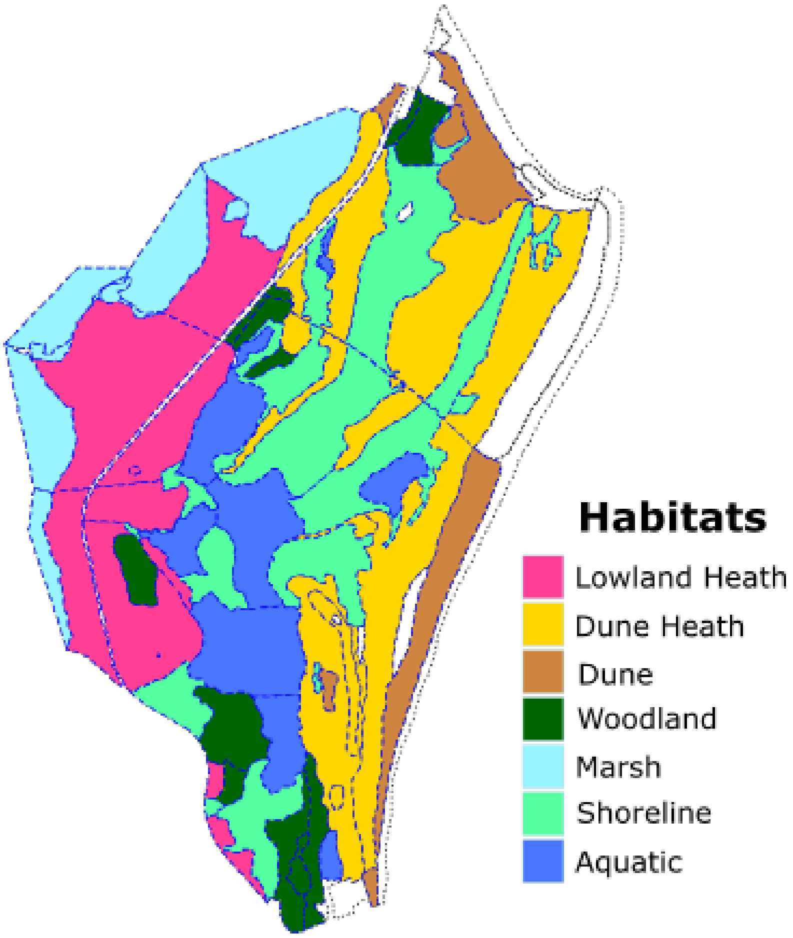

Figure 1.2 Habitats and sampling compartments of Studland. Habitats are colour coded, while sampling compartments are demarcated by dashed lines.

Analyses of biodiversity change on Studland will be primarily based on complimentary lists of species occurrences from the 1930s and 2010s. The sampling units for species lists (hereafter 'sampling compartments') were established by Diver in the 1930s from sets of what he called 'locus-habitats' (*figure 1.3*). He offered the following description of these locus habitats in 1938:

> *"The term 'locus-habitat' is here used to denote a place characterized by a more or less uniform set of conditions. Within such a unit several separable sets of conditions are usually represented, but they are only treated as a biotic complex if they are so distributed as to form a relatively fine mosaic throughout which they freely interact"* (Diver 1938).

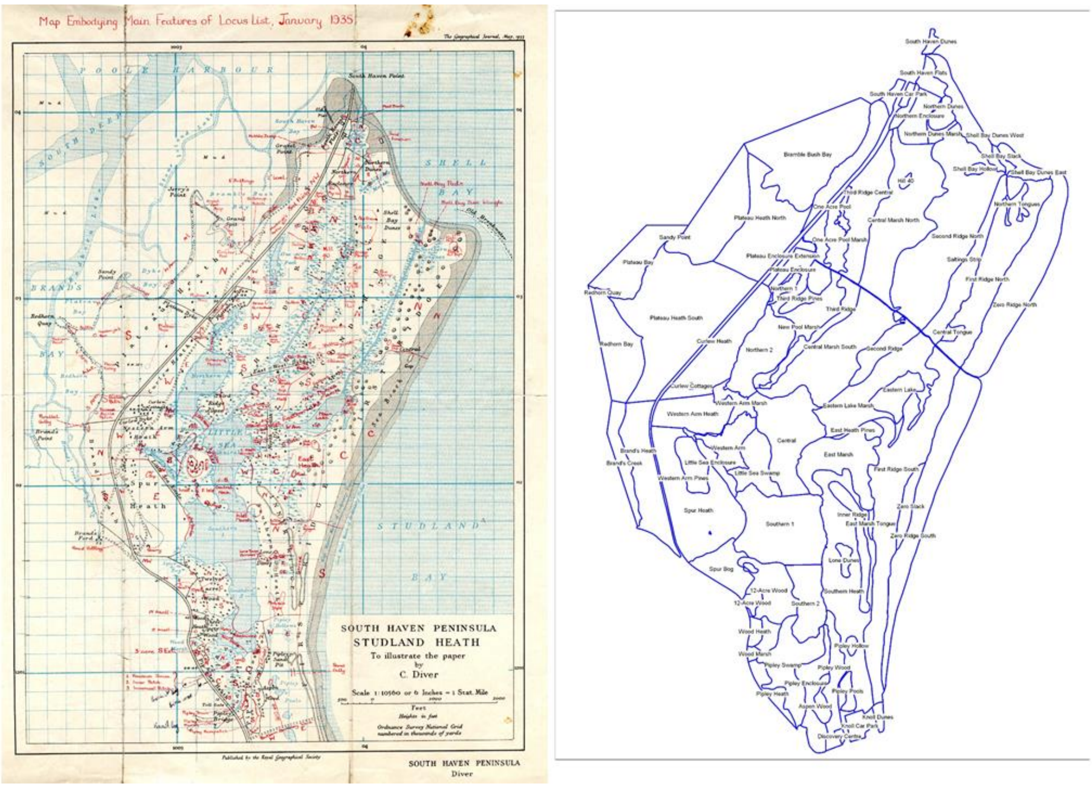

Figure 1.3 Diver's original 'locus-habitats' (left) and the reconstructed contemporary sampling compartments (right).

Diver's sampling compartments were reconstructed in a GIS in the 2010s as part of the CDP by Dorset Environmental Records Centre (DERC) using his original ordinance survey maps for guidance (*figure 1.3*). In this way project members could collect contemporary data that was directly comparable with data from the 1930s. It is worth noting the great efforts that went into relocating compartment boundaries, particularly by Robin Walls of the CDP plant resurvey group, and David Brown of the National Trust, but also with inputs from many others contributors to the project.

Resurveys of historical vegetation plots can be quite robust to approximate errors in relocation of plots (Kopecký and Macek 2015), and the effort and expertise underlying the relocation of the Studland compartment boundaries allows for great confidence on analyses bases upon them. As part of a special feature on vegetation resurvey in the journal *Applied Vegetation Science*, Kapfer *et al.* 2017 suggested that sample plots for resurvey of historical vegetation data should be divided into three categories: Permanent, Quasi-permanent, and Non-traceable. Permanent plots are physically marked in the field, Quasi-permanent plots can be relocated using a plot-specific geographic position, and Non-traceable plots are those for which plot-specific location information is not available and plots can only be relocated to a physically and environmentally relatively homogenous area. I consider the sampling compartments of Studland to fall somewhere between the Permanent and Quasi-permanent categories, as though they were be relocated using various physical indicators and detailed ordinance survey maps and notes, the precise boundaries between them may not always be in the exact same positions for historical and contemporary sampling.

1.2.2 Dorset's changing plant communities: Spatiotemporal metacommunity context

Long-term biodiversity change is unusually well documented in plant communities across the English county of Dorset – the wider setting of the Studland case study presented in this thesis. From 1931 to 1936 Ronald Good surveyed plant communities in 7575 local plots distributed widely throughout Dorset, and a series of studies over the past decade resurveying many of Good's plots have investigated biodiversity change in the intervening years (Keith *et al.* 2009, 2011; Hooftman & Bullock 2012; Newton *et al.* 2012; Jiang *et al.* 2013; Diaz *et al.* 2013). When extrapolated across the county, Dorset has seen a significant decline in α-diversity (local richness) of plants on average due to widespread habitat loss and agricultural intensification (Jiang *et al.* 2013), while patch size and connectivity of remaining semi-natural habitat fragments have also seen large reductions (Hooftman and Bullock 2012). Furthermore, there remains only one biodiversity hotspot for plants in Dorset presently, located in the southeast of the county – surrounding the study area of this thesis – yet such hotspots were widespread across the county in the 1930s (Jiang *et al.* 2013).

Biodiversity change in Dorset's plant communities is further complicated when broken down into remaining fragments of differing ecological habitat types. Woodland, lowland heath and calcareous grasslands have seen variable patterns of richness and compositional change at the county level and within intact local patches, with each habitat experiencing idiosyncratic drivers of change between sampling periods (Keith *et al.* 2009, 2011; Newton *et al.* 2012; Diaz *et al.* 2013: *table 1.1*). Despite detailed documentation of biodiversity change in Dorset's plant communities, it remains unknown in most cases whether higher taxa co-occurring with the plants have undergone analogous changes, either through expressing shared responses to environmental change, or through direct biotic interactions with the plants (but see eg,: Senapathi *et al.* 2015 for analyses of changes in hymenoptera in a subset of contemporaneous plots). Identifying such linkages in Dorset, which is unusually rich in historical data, should provide clues as to how long-term biodiversity changes transverse taxa in communities more generally which have seen, or will see, similar changes in environmental conditions.

Table 1.1 Summary of published findings on biodiversity change in Dorset's plant communities between the 1930s and 2000s based on resurveys of Good's sample plots across the county. Each resurvey concerned a specific ecological habitat type. Results highlight the variable manner in which biodiversity change can occur across a landscape and how specific ecological or environmental contexts can affect changes driven in part by shared drivers.

Paper	Habitat	Diversity metric	Increase/Decrease
Newton *et al.* 2012	**Calcareous Grasslands**	**α**	29.31 +/- 7.65 *to* 40.18 +/- 16.41 ~ *Increase*
		β	*No change detected*
		γ	219 *to* 280 ~ *Increase*
	Notes: Decrease in "stress-tolerant" species. Increase in mesotrophic grassland species. Increase in Ellenberg N indicator on average.		
Diaz *et al.* 2013	**Lowland Heath** (All patches = **AP**, intact patches = **IP**)	**α**	17.5 *to* 16 (µ), P = 0.023 ~ **AP** *Marginal decrease* 18 *to* 11 (µ), P = 0.023 ~ I**P** *Decrease*
		β	*No change detected ~* ***AP*** *Significant decrease ~* ***IP***
		γ	380 *to* 263 ~ ***AP*** *Decrease* 291 *to* 173 ~ **IP** *Decrease*
	Notes: Overall **AP's** shifted somewhat towards grasslands and **IP's** shifted towards woodlands. **IP's** became more homogenised.		
Keith *et al.* 2009, 2011	**Woodlands**	**α**	57 +/- 2.8 *to* 53 +/- 1.6 ~ *Small Decrease (not significant)*
		β	*Not reported. However taxonomic homogenisation headline finding.*
		γ	*117 species lost, 47 species gained, net loss of 70 species ~ Decrease*
	Notes: Invasive species not responsible for biotic homogenisation. Rather, it was due to reorganisation of remaining species.		

1.2.3 Data collection

The first of two broad periods of data collection took place in the 1930s largely between 1931 and 1938, and the second between 2013 and 2015. Though the duration of sampling periods differed by approximately four years, Diver and his colleagues did not live permanently close to Studland and thus their sampling was restricted to weekends and holidays, whereas the naturalists performing the resurvey effort sampled weekly throughout the year for the three years from 2013 to 2015. The resurvey effort in the 2010s also had more people involved in sampling comprising a range of experts and amateurs, and had Diver's lists to perform targeted searches for species present in the 1930s. Though the differing sampling regimes in each time-period are clearly not ideal, the discrepancies just described go some way to evening out the differences in sampling effort. As each sampling effort aimed at recording the full biota of taxa subject to analysis in this thesis through extensive within time-period resurveys, it can be considered that comparative analyses of biodiversity change between time-periods are both reasonable and meaningful.

Sampling efforts in each time-period recorded occurrences and distributions of a wide range of plant and insect species across the peninsula. However, analyses of biodiversity change for the purposes of this thesis are focused on six broadly defined taxa; vascular plants, non-vascular plants, grasshoppers and crickets (Orthoptera), ants (Hymenoptera, Formicidae), hoverflies (Dipteral, Syrphidae), and dragonflies and damselflies (Odonata). These groups were selected primarily on the basis that sampling efforts were explicitly focused on them as taxonomic units, and were sufficient in each time-period to compile close to full or full species lists at the sampling compartment level, although minor omissions due to sampling error are of course possible, and even likely. These taxa also span a range of broad taxon level differences desirable for comparative analyses to address the research questions of this thesis. These include differing trophic levels, mobility and life-history characteristics, and inter-taxa trophic interactions.

Analyses of biodiversity change for these six focal taxa were based on slightly differing subsets of compartments for each taxon depending on the availability of data. The baseline set of sampling compartments used for analyses of biodiversity change included the 74 compartments for which reliable vascular plant species lists were available for both sampling periods (depicted in *figure 1.2*). Species lists for each of the other 5 taxa were available for differing subsets of the baseline sampling compartments, as reliable lists were not available for all taxa in all compartments (*table A1.1*). In some instances, species lists were unavailable because the focal taxon was unlikely to inhabit the compartment, this is particularly true for compartments in the aquatic habitat. In other cases, historical lists were missing, or the compartment was not heavily targeted for sampling under the more recent survey, and thus meaningful biodiversity comparisons could not be made.

1.3 Hierarchical Regression and Bayesian Inference

Throughout this thesis I heavily utilise hierarchical regression models applied in a Bayesian statistical framework. Here I lay out some of the key concepts underlying these methods. Hierarchical Bayes has been widely used in ecology for some time (e.g. Kéry 2010), so I focus primarily on the manner in which these approaches help overcome some of the shortfalls of an observational dataset such as that produced by the Cyril Diver Project.

A common feature of naturally occurring ecosystems subject to observational studies is hierarchical structures of organisation – individuals within populations, populations within species, species within genera, and so on. Similarly, hierarchical organisation can be identified in the spatial and temporal structuring of populations and communities. On the Studland peninsula for example, we have sampling compartments within broad habitat types, and habitats nested within the peninsula as a whole (*figure 1.2*). Within a hierarchical regression modelling framework, such structures can be identified, and estimates of how response variables (eg. proportions of species gains vs losses) vary at distinct levels of the hierarchy can be computed (eg. compartment and habitat level) (Gelman and Hill 2006). This type of analysis offers several benefits, including improved estimates at each level of the model by sharing information across levels (Gelman and Pardoe 2006). Further, one can easily combine separate hierarchies within a single model; for instance allowing a response variable to vary by species ID and sampling compartment simultaneously. Explanatory variables can thus be added within models at any level of the hierarchy pertinent to the scientific question being explored (eg. compartment, species or data level predictors) (Kéry and Royle 2016).

While hierarchical regression models can be fitted in a frequentist statistical framework (Bolker et al. 2009), fitting such models the Bayesian way using software packages such as jags (Denwood 2016) or stan (Stan Development Team 2018a) offers a number of benefits. These models can become complex, with many parameter estimates based on sparse data, and in such cases Bayesian methods will often fit models that are not computationally viable for frequentist methods (Kéry and Schaub 2012). Prior information on parameter values can be incorporated in a Bayesian framework where such information is available. Derived parameters can be easily computed from posterior distributions of Bayesian models, a feature I make use of while estimating congruence in biodiversity changes between taxa in chapter 3. Bayesian methods also offer a number of benefits for model fitting and validation, discussed in detail in the following section. Finally, philosophical interpretations of Bayesian model outputs and inferences are preferred by many, myself included, who do not care for the hypothetical reruns of reality encountered in frequentist statistics (Gelman and Shalizi 2013).

1.3.1 Posterior predictive checks, Regularisation and Information Criteria

Bayesian models fitted using Markov Chain Monte Carlo (MCMC) offer a number of specific benefits for model fitting, validation, and evaluation, some of which I will briefly outline here.

MCMC produces a posterior distribution for each parameter of a fitted model comprising a chain of plausible estimates for parameter values, usually at least 1000 iterations in length.

With posterior predictive checks, we can use posterior distributions to examine whether parameter estimates obtained from fitted models are reasonable given the real world ecological data we have collected (Gelman et al. 1996). This approach works as a means of testing model adequacy, and is analogous to a form of reverse engineering. It works by taking posterior distributions of parameter estimates from fitted models and using them to simulate fake datasets – one for each iteration of the model output – which are compared with the real world data used to fit the model (Kéry 2010). Comparisons with real world data can be performed using test statistics computed to test specific aspects of fitted models, or with simple comparisons of raw data (Gelman et al. 2004). Essentially, if there is a large divergence between the distribution of the ecological data used to fit the models and the simulated datasets derived from parameter estimates, we can conclude that the fitted model does not fit the data well (Kéry 2010). We must then go back to the drawing board to specify a new model, or attempt to figure out why the model is not working as expected.

Overfitting of a model to a dataset is a danger present when conducting most types of statistical analyses. The use of regularizing priors in Bayesian analyses is one good means of minimising this risk. In practice, models fitted in a Bayesian framework often use prior distributions that are as uninformative as possible, in essence saying that we know nothing about value of a parameter before the model estimates it (Gelman and Hill 2006, Kéry 2010). However, it is often the case that a large range of "possible" parameter values are extremely unlikely. For example, in looking for an average height difference between men and women, values above 1 meter in difference may be deemed unreasonable. This also tends to be particularly true in instances where standardised predicters are used (McElreath 2016a). Regularizing priors allow us to make more conservative estimates of parameter values where appropriate.

Bayesian models also have an explicit set of information criteria for use in out of sample predictive assessment, analogous to the AIC of frequentist statistics (McElreath 2016a). These include DIC, BIC, WAIC and LOOIC – LOOIC being an approximation of leave one out cross validation. Of these, WIAC and LOOIC have the advantage of being computed as an entire posterior distribution of their own, thus allowing for uncertainty in the information criteria themselves to be computed (Vehtari *et al.* 2017).

1.4 Research Aims and Thesis Structure

The aim of this thesis is to investigate how effects of long-term environmental change propagate through co-occurring plant and insect communities, driving changes in species richness and composition across taxa. Throughout, I attempt to partition the roles of direct abiotic disturbances and biotic interactions among broad taxa which underlie such changes. To achieve my aim, I use historical and contemporary data on the plants and insects of Studland collated through the Cyril Diver Project. As historical CDP data were not accompanied by coincidental data on environmental conditions, a subtheme of this research involved inferring environmental change, and effects thereof, from data derived from aggregated traits of occurring species. I will also attempt to synthesise my results in terms of future implications for biodiversity at Studland and beyond in order to aid conservation management.

The specific questions I address to achieve the overall thesis aims are:

i) How have the vascular plant assemblages of Studland changed in response to a changing abiotic environment between the 1930s and the present day?

ii) Have plant and insect taxa with differing evolutionary histories, ecological requirements, and phenotypic characteristics undergone congruent richness and compositional changes under shifting environmental conditions after an 80 year period?

iii) What biotic and abiotic factors relating to adult and larval ecological requirements have influenced long-term biodiversity change in a community of insects which undergo complete metamorphosis?

iv) How are the plant and insect communities of Studland likely to change in the coming decades under proposed management interventions?

I address these questions through chapters 1 to 6 of this thesis in the following manner:

1. **Thesis introduction and background.**
2. **How have the plant assemblages of Studland changed in response to changing environmental conditions between the 1930s and the present day?**

   In chapter 2, I use Hierarchical Logistic Regression modelling on Ellenberg Indicator Values of the plant species occurring across Studland to reveal the manner in which the plant community has adapted to a changing environment via changes in species composition. In addition to revealing factors influencing the functional composition of the plant community, this chapter also provides a quantitative metric of abiotic change across the peninsula between time-periods which I use in later chapters to assess the effects of these changes on other taxa.
3. **Have plant and insect taxa with differing evolutionary histories, ecological requirements, and phenotypic characteristics undergone congruent richness and compositional changes under shifting environmental conditions after an 80 year period?**

   Cross-taxon congruence (CTC) is a measure of correlated patterns of change or turnover across taxa. Here I assess temporal CTC in biodiversity change (species richness and composition) across six plant and insect taxa, and attempt to partition observed congruencies resulting from shared responses to environmental change vs other causes (eg. biotic interactions). In contemporary communities CTC is sometimes used as an ecological indicator to infer the state of taxa which are difficult to sample from knowledge of more cryptic taxa. I also discuss the potential of temporal CTC for use as an ecological indicator using historical resurvey data of plants and insects.

4. **What biotic and abiotic factors relating to adult and larval ecological requirements influence long-term biodiversity change in a community of insects which undergo complete metamorphosis?**

   In this chapter I uncover abiotic and biotic drivers of change in species richness and composition in the hoverfly community of Studland, testing hypotheses relating to ecological factors affecting hoverfly species at both larval and adult life-history stages, with a particular focus on factors relating to biodiversity change in the plant community. Hypotheses are based on both results from the preceding chapters and the scientific literature.

5. **How are the plant and insect communities of Studland likely to change in the coming decades under proposed management interventions?**

   Here I use Bayesian Belief Networks to synthesise the results from preceding chapters and information from the scientific literature in order to project future change under various management interventions.

6. **Thesis Discussion and Conclusions**

2. Improving estimates of environmental change using multilevel regression models of Ellenberg indicator values

2.1 Abstract

Ellenberg indicator values (EIVs) are a widely used metric in plant ecology comprising a semi-quantitative description of species‘ ecological requirements. Typically, point estimates of mean EIV scores are compared over space or time to infer differences in the environmental conditions structuring plant communities – particularly in resurvey studies where no historical environmental data are available. However, the use of point estimates as a basis for inference does not take into account variance among species EIVs within sampled plots, and gives equal weighting to means calculated from plots with differing numbers of species. Traditional methods are also vulnerable to inaccurate estimates where only incomplete species lists are available.

I present a set of multilevel (hierarchical) models – fitted with and without group-level predictors (for eg. habitat type) – to improve precision and accuracy of plot mean EIV scores, and to provide more reliable inference on changing environmental conditions over spatial and temporal gradients in resurvey studies. I compare multilevel model performance to GLMM’s fitted to point estimates of mean EIVs. I also test the reliability of this method to improve inferences with incomplete species lists in some or all sample plots.

Hierarchical modelling led to more accurate and precise estimates of plot-level differences in mean EIV scores between time-periods, particularly for datasets with incomplete records of species occurrence. Furthermore, hierarchical models revealed directional environmental change within ecological habitat types, which less precise estimates from GLMM’s of raw mean EIVs were inadequate to detect. The ability to compute separate residual variance and adjusted R^2 parameters for plot mean EIVs and temporal differences in plot mean EIVs in

multilevel models also allowed us to uncover a prominent role of hydrological differences as a driver of community compositional change in our case study, which traditional use of EIVs would fail to reveal.

Assessing environmental change underlying ecological communities is a vital issue in the face of accelerating anthropogenic change. I have demonstrated that multilevel modelling of EIVs allows for a nuanced estimation of such from plant assemblage data changes at local scales and beyond, leading to a better understanding of temporal dynamics of ecosystems. Further, the ability of these methods to perform well with missing data should increase the total set of historical data which can be used to this end.

2.2 Introduction

Resurvey studies, where communities are resampled after years or decades have elapsed, are becoming increasingly common in ecology due to interest in how ecosystems are responding to global environmental change (e.g. Diaz *et al.* 2013; Krause *et al.* 2015). However, contemporaneous environmental data alongside historical data on species records are often lacking, which can hamper attempts to identify drivers of community change. As one solution, Ellenberg Indicator Values (EIVs) are widely used to infer environmental change over time where no data are available for abiotic conditions (Prach 1993, McGovern et al. 2011, Newton et al. 2012, Wesche et al. 2012, Häring et al. 2014, Krause et al. 2015). EIVs score plant species on an ordinal scale based on estimated optimal environmental conditions for moisture, light, soil nutrient levels, reaction (pH) and salt tolerance (F, L, N, R and S respectively) (Ellenberg 1988; Hill et al. 2004). Typically, ecologists compare mean EIV scores of plants sampled from stands of vegetation to infer differences in abiotic conditions (Diekmann 2003). However, use of point-estimate plot mean EIVs fails to account for variation in EIV scores of plant species within sample plots, which I hypothesise could improve accuracy of inferences if included. Furthermore, incomplete species occurrence records for some or all plots may lead to inaccurate estimates of plot means and thus poor inference of environmental changes over time.

The population parameter one attempts to estimate when calculating a mean EIV score from plant occurrence records – for example describing soil reaction (EIV R) – is the mean EIV score for all plant species able to establish at this plot given the soil pH, all other things being equal (Ellenberg 1988, Dupré 2000). However, as well as environmental filtering for pH, a myriad of factors, including abiotic conditions and interactions with other species present in the community, will affect the probability of a particular species establishing a local population (Grime 1977, Keddy 1992, Vellend 2016). This complex filtering process leads to the diverse plant assemblages I see in nature, which in turn lead to variation in EIV scores of species within and between plots.

Environmental heterogeneity is an important factor in plant ecology studies generally (e.g. Maslov 1989), and by failing to account for different levels of variation within a system, traditional methods discard much information, which may result in over- or underestimation of the extent of change over time (Gelman and Hill 2006). *Figure 2.1* depicts three distinct levels of variation that can be identified within a typical ecological study estimating environmental change using EIVs: i) variation among EIV scores of species recorded within sampled plots ($\sigma_{species}$); ii) variation between plots in mean EIV scores (σ_{α}), and; iii) variation in between time-period differences in plot mean EIVs as environmental conditions change differentially across a landscape over time (σ_{β}). Traditional methods using point estimates of mean EIVs from sampled plots (the $\bar{x}$*'s* in *Figure 2.1*) to infer differences between groups of plots in space or time – either broken down by a grouping factor (eg. habitat type), or on average across all sample plots – fail to incorporate variation within plots in species EIV scores ($\sigma_{species}$).

The suitability of hierarchical modelling to account for structure and variability in ecological systems is well established (Royle and Dorazio 2008, Cressie et al. 2009, Kéry and Royle 2016), and this approach provides an ideal framework to account fully for the structure and variability identified in *figure 2.1*. Instead of using point estimates of mean EIVs, data enter the model as species-specific EIV scores, and inferred plot means – with all of their associated uncertainty – are estimated and used at a higher level within the model to infer differences between groups of plots in space and time (McElreath 2016a). In this way information is shared between plots, with mean EIV estimates augmented through partial pooling – that is, plot-level estimates being pulled towards the overall mean to an extent dependant on the number of species a mean estimate is composed of, and the variability of estimates between plots (Gelman and Hill 2006). More fully accounting for uncertainty in this way should lead to more reliable estimates of individual plot mean values, and of differences between groups of plots in space and time (Gelman and Hill 2006). Furthermore, because estimates are pooled according to shared information content, differences between any pair or combination of individual plots or habitats in the system can be inferred without having to contend with the issue of multiple comparisons, which should provide more power to detect change over time in conventional null hypothesis testing frameworks (Gelman et al. 2012).

A multilevel (hierarchical) modelling approach may also help to improve estimates of plot mean EIVs in instances where lists of recorded species are incomplete for some or all plots. Incomplete sampling is a common nuisance in ecological studies as some species are more difficult to detect than others, and ease of detection may vary depending on the time of year a particular plot is sampled, and among species (Kéry and Gregg 2003, Kéry 2004, Chen et al. 2013). This issue may be further compounded if recorders with differing botanical skills sample different plots, or in resurvey studies where it can be difficult to confirm the completeness of records, and where differing sampling methods may have been used. As long as data are not missing systematically across all plots, multilevel modelling should improve mean estimates for plots with missing data – and any inference based on these estimates – by pooling information across plots.

The aim of this paper is to demonstrate how hierarchical modelling can lead to higher discriminatory power than traditional methods when using EIVs to assess environmental changes underlying plant communities. This is achieved by accounting for uncertainty at all levels of the ecological system and by explicitly identifying and estimating components of temporal and spatial variation in plot mean EIVs.

I demonstrate the utility of this method in studies with both complete and incomplete plot records for species occurrence by fitting models to a real resurvey dataset. The models describe two scenarios: 1) A set of plots across a landscape, resampled in a second time-period, assumed to be replicates of a similar habitat type; and 2) A similar set of plots sampled in two time-periods, but in this case groups of plots differ by some grouping factor (eg. habitat type in our case study). I ask: 1) Do inferences on changes in environmental conditions in space and between time-periods differ between hierarchical models of EIVs with a full multilevel structure and models using point estimates of raw mean EIVs from sampled plots as data, to an extent that will effect conclusions about change in the system? 2) Do hierarchical models improve mean estimates – and consequently inferences on temporal differences based on these estimates – for datasets where the full cohort of species is not recorded in all sampled plots? I provide code in the Appendix 2 to fit the models in R and Jags.

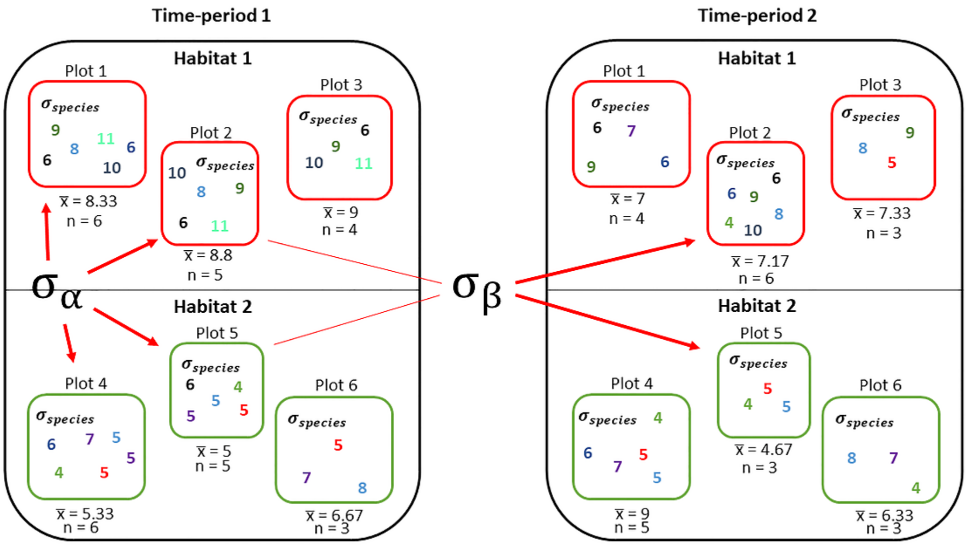

Figure 2.1 Typical spatiotemporal sampling structure of a resurvey study where Ellenberg Indicator Values (EIVs) are used to infer environmental differences underlying plant assemblages. Each colour/number combination represents the EIV score of a specific plant species. In this example plots are sampled within two separate ecological habitat types, and plant species occurrences are recorded for all plots in two separate time-periods. The σ values denote components of variation i) in EIVs among species within sampled plots (σ_{species}), ii) in mean EIVs between plots (σ_α), and iii) in differences in plot mean EIVs between time-periods (σ_β). Methods using pre-averaged mean values (x̄'s) as a starting point for inference fail to account for σ_{species}, and as a result can lead to less reliable plot mean estimates and inferences across the wider landscape and between time-periods

2.3 Methods

2.3.1 Data

All models were fitted to a real ecological dataset for EIVs describing moisture, light, soil nutrient levels, reaction (pH) and salt tolerance (F, L, N, R and S respectively) from the PLANTATT dataset which provides EIVs adjusted for use in the UK and Ireland (Hill et al. 2004). Historical data were collected by Cyril Diver and contemporaries in the 1930s from the Studland Peninsula, Dorset, UK (Lat: 50.66, Lon: -1.9) (Good 1935, Diver 1938). The

Peninsula consists of a habitat mosaic ($\sim 3km^2$) characterised as dune, dune heath, tertiary heath, woodland, harbour shore, marsh and edge aquatic plant assemblages. Diver and colleagues recorded lists of species occurrences in 74 sample plots ("compartments") which varied in size and shape (size in m^2: min = 899.98, max = 200764.4, mean = 44452.52), and were based on the topographical properties and local ecological characteristics of Studland (Diver 1938). The sampling compartments of Studland fall somewhere between Permanent and Quasi-permanent categories by the framework presented in Kapfer *et al.* 2017, as though they were relocated using various physical indicators and detailed ordinance survey maps, the precise boundaries between them may not always be in the exact same positions for historical and contemporary sampling. The National Trust resurveyed the area between 2013 and 2015 in a citizen science initiative coined "The Cyril Diver Project" following Divers' original sampling plots. (https://www.nationaltrust.org.uk/studland-beach/features/the-cyril-diver-project). Both sampling and resampling efforts aimed to record all species present in their respective time-periods by repeatedly visiting plots throughout the year and scouring them carefully in teams for the duration of respective study periods. The number of species in each sample in each plot time-period, area and coordinates of sample plots are detailed in Appendix 2.

2.3.2 Models

2.3.2.1 *Estimating environmental change over time in resurvey studies*

The first scenario I consider is one in which I estimate between time-period differences in mean EIVs for a resurvey study, where sample plots are considered replicates of similar, homogenous stands of vegetation in the same type of habitat. As such, model M2.1 below is equivalent to compiling a series of t-tests, one for each plot, to estimate differences in mean EIV scores at plot level – though to use it for statistical testing in this manner would require major corrections for multiple testing. I formulate this simple linear model to emphasise fully the progression from fixed effects models with no-pooling, to those with partial pooling under a multilevel structure – and to use as a baseline against which to compare plot mean estimates from hierarchical models. The appropriateness of using mean values of ordinal EIVs and means of ordinal values more generally has been widely discussed in the literature and is not the topic of this paper, however I agree that it has proven a useful method in applied plant ecology and should continue to be so (Diekmann 2003, Pasta 2009).

M2.1

$$y_i \sim N(\alpha_{j[i]} + \beta_{j[i]} x_i, \sigma_{species}), \text{ for } i = 1, \ldots., n$$

y_i is the EIV score for species *i* in plot j, and $\sigma_{species}$ is the estimated residual variance for EIV scores of *n* species within sampled plots. In this no-pooling model the α_j values are the plot means from time period 1, and each β_j parameter is an estimate of the difference in mean EIV in compartment j between time-periods 1 and 2. x_i is the binary (0,1) predictor for the time-period that species y_i was sampled in.

To move from “no-pooling” to hierarchical models I allow the $\alpha_j's$ and β_j’s from model M2.1 to share information through partial pooling, changing them from fixed to random effects. As such, model M2.2 below can be viewed as a type of mixed effects model which allows us to use more conservative estimates of plot-level between time-period differences (slopes) by sharing information content across plots, and thus arrive at a more accurate estimate of overall change.

M2.2

$$y_i \sim N(\alpha_{j[i]} + \beta_{j[i]} x_i, \sigma_{species}), \text{ for i} = 1, \ldots., \text{n}$$

$$(\alpha_j, \beta_j) \sim MVN\big((\mu_\alpha, \mu_\beta), (\sigma_\alpha, \sigma_\beta,\ \rho\sigma_\alpha^2\sigma_\beta^2)\big)\text{, for j = 1,…., j}$$

Slope and intercept parameters are constrained to come from bivariate normal distribution (MVN) with mean vector (μ_α, μ_β) to account for correlation between them (Gelman and Hill 2006). The covariance matrix is defined by the variance in plot intercepts (σ_α) and slopes(σ_β), and the covariance between the two sets of parameters $(\rho\sigma_\alpha^2\sigma_\beta^2)$, where ρ is the correlation coefficient. Allowing information on temporal differences across plots to be shared in this way makes sense particularly if the sampled plots come from a spatial area within which I expect abiotic drivers of change to be linked.

2.3.2.2 *Inferences between plots differing by a grouping factor*

Sampled plots may differ by some categorical factor (eg. Habitat type, grazing regime etc...). I can extend model M2.2 to include a group-level predictor within the sub-models of $\alpha_j{}'s$ and $\beta_j's$. Thus plot-level estimates in model M2.3 below are improved when groups of plot differ by habitat, as now the estimates are pooled towards the habitat-level mean value rather than the mean across all plots. M2.3 also allows us to estimate differences in mean changes at habitat level.

M2.3

$$y_i \sim N(\alpha_{j[i]} + \beta_{j[i]}x_i\ , \sigma_{species})\text{, for i = 1,…., n}$$

$$(\alpha_j, \beta_j) \sim MVN\big(\mu_{\alpha[k]}, \mu_{\beta[k]}\big), (\sigma_\alpha, \sigma_\beta,\ \rho\sigma_\alpha^2\sigma_\beta^2))\text{, for j = 1,…., j}$$

In hierarchical model M2.3 the data (y_i) still enter the model at the level of plant species within plots, and the plot intercepts and slopes are still constrained to come from a multivariate normal distribution. Here however, the means of this distribution $(\mu_{\alpha[k]}\ and\ \mu_{\beta[k]})$ take on a different value for each of *k* groups (habitat types in our case study). σ_α and σ_β now estimates variation in plot-level intercepts and slopes respectively, after taking habitat type into account.

Model M2.3 allows us to estimate differences between groups of plots by essentially nesting a two-way ANOVA within the model structure. To compare inferences on habitat level differences from the hierarchical model with those using point estimates of mean EIVs as data, I fitted Generalized Linear Mixed Models (GLMM's) with plot ID as a random effect nested in time-period to account for repeat sampling. While this technically is a hierarchical model, it does not incorporate the multilevel structure which is the focus of this paper. I compared these models to their hierarchical (multilevel) counterparts in terms of differences in magnitude, precision and sign of habitat level estimates, and whether differences in habitat-level EIVs between time-periods were significant at the standard α= 0.05 significance level. To perform these tests of significance, habitat-level differences in EIVs for each GLMM were corrected for multiple comparisons using the multcomp package in R (Hothorn et al. 2008). I also calculated Bayesian R^2 for each level within the hierarchical models (data level, varying intercepts and varying slopes) (Gelman and Pardoe 2006).

2.3.2.3 *Analyses with incomplete species records*

I refitted the models with incomplete sets of species artificially subsampled from a selection of plots to test model performances in predicting plot mean EIVs where not all species present in a plot are recorded. Since improving plot mean EIV estimates by pooling information across plots – and thus improving inferences based on these estimates – is the mechanism by which I suggest that multilevel modelling is an improvement on methods using point estimates of plot mean values as data, this missing species analysis also served as our most important validation procedure (following Lin *et al.* 1999). If these methods can accurately estimate plot mean values primarily from information shared across plots, with most of the species missing from the focal plot, then it is clear that the models use the pooled information in a valuable way.

Plots were chosen in a random stratified manner; one plot with >50 recorded species from each habitat type in each time-period (14 total). 90% of species in each of these 14 plots were selected at random and excluded from the dataset, representing severe undersampling. Models M2.1, M2.2 and M2.3 were refitted and model outputs compared to the raw mean values when all data were included, under the assumption that plots with >50 species provided an adequate estimate of the “true mean” value. This process was repeated iteratively 120 times with a different random 90% of species removed from each plot during each iteration. Model performances were compared graphically, and using calculated summary statistics to assess precision and accuracy of plot level estimates for plots with missing species. Precision was assessed as the mean width of 50% and 95% credible intervals of plot estimates, and as the inverse variance of plot mean estimates. Accuracy was assessed as the proportion of times the “true mean” value was within the 50% and 95% credible intervals, and as the mean distance of point mean estimates from the “true mean” value.

2.3.3 Software and validation

Models were fitted in JAGS and R version 3.3.1 using package runjags with minimally informative priors following Gelman & Hill 2006 (see Appendix 1 for a description of the models in the Jags language) (Denwood 2016, R Core Team 2017). Additional R packages were used for analyses of mcmc chains and graphics (Plummer et al. 2006, Wickham 2009). In addition to the validation discussed in section 3.2.3 I performed a range of posterior predictive checks and comparisons between simulated and real world datasets to assess model adequacy (following Gelman & Hill 2006; Kéry & Schaub 2012).

2.4 Results

2.4.1 Analyses with incomplete species records

Multilevel model estimates from both models M2.2 and M2.3 were consistent across separate runs of the simulation, regardless of which 10% species remained, with high levels of precision and accuracy (*Figure 2.2, Table 2.1*). Plot mean estimates with missing species were closer to the true means for hierarchical vs. non-hierarchical models for all four EIVs, often by more than a factor of two – averaging across replications and depleted plots (*Table 2.1*). The proportions of "hits" for 50% and 95% credible intervals about the mean estimates differed between models and EIVs, but underperformed for some hierarchical models due to consistent misses across replications for some individual sample plots (*Figure 2.2*). Models without group-level habitat predictors performed slightly better in this respect (Table 2.1).

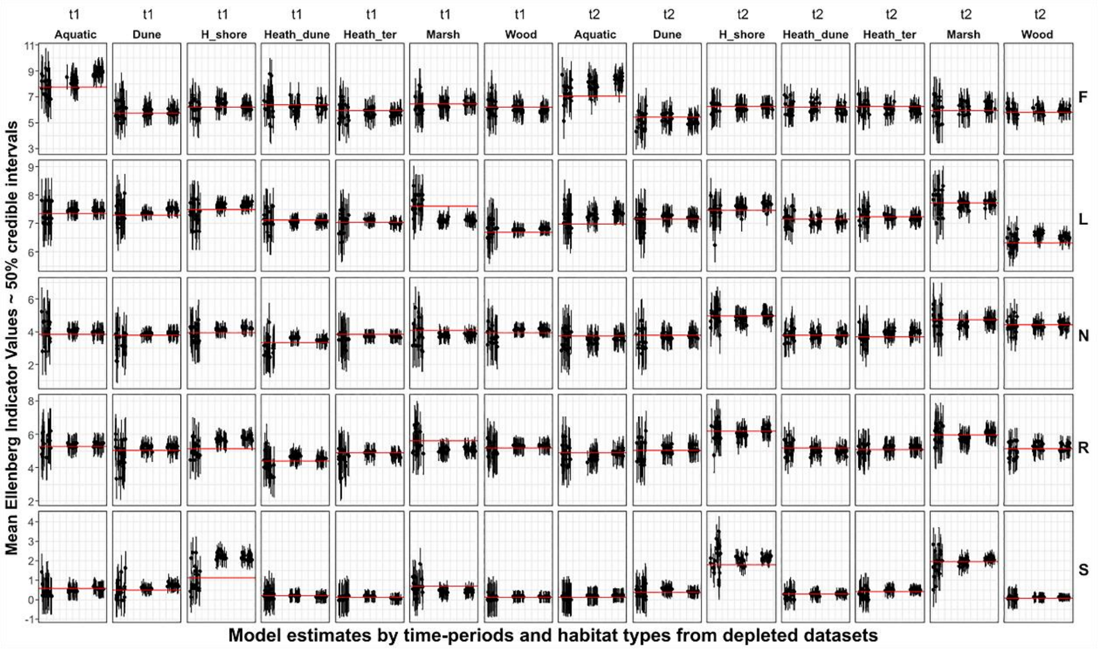

Figure 2.2 Mean estimates with 50% uncertainty intervals of plot-level Ellenberg Indicator Values (EIVs) F, L, N R and S from plots with a random 90% of species removed. One plot with 50 or more recorded species was randomly chosen from each habitat type in each of two sampling periods. Red lines are plot mean EIVs with full cohort of species remaining. The three clouds of points from left to right in each grid panel display uncertainty intervals from: 1) No-pooling models, representing raw mean estimates of 10% of species randomly remaining in each iteration; 2) Estimates from hierarchical models with partial pooling of plot intercept and slope parameters, and; 3) Estimates from hierarchical models with partial pooling including group level habitat predictors. Plot shows a subset of 20 out of 120 iterations run in total for clarity.

Table 2.1 Model performances from analyses of plots with a random 90% of species removed. All statistics were calculated for 14 depleted plots over 130 simulations of the validation analysis.

Model	Mean width 50% CI	Mean width 95% CI	Mean precision	Proportion of hits 50% CI	Proportion of hits 95% CI	Avg. dist. from true mean
EIV F						
RV M2.1	0.87	2.54	3.97	0.53	0.96	0.51
RV M2.2	0.61	1.77	14.58	0.58	0.96	0.32
RV M2.3	0.51	1.5	27.48	0.53	0.87	0.36
EIV L						
RV M2.1	0.46	1.33	11.52	0.52	0.96	0.25
RV M2.2	0.2	0.6	412.84	0.46	0.89	0.15
RV M2.3	0.19	0.57	429.94	0.39	0.82	0.17
EIV N						
RV M2.1	0.83	2.41	4.02	0.54	0.97	0.46
RV M2.2	0.36	1.07	193.62	0.45	0.99	0.2
RV M2.3	0.39	1.05	170.69	0.58	1	0.16
EIV R						
RV M2.1	0.78	2.25	4.45	0.5	0.97	0.44
RV M2.2	0.39	1.16	77.89	0.5	0.92	0.26
RV M2.3	0.37	1.09	96.02	0.55	0.9	0.21
EIV S						
RV M2.1	0.54	1.58	32.99	0.64	0.92	0.3
RV M2.2	0.24	0.72	671.08	0.66	0.89	0.18
RV M2.3	0.21	0.62	605.52	0.55	0.85	0.19

2.4.2 Plot-level inference

Out of sample predictive accuracy was markedly better in hierarchical vs. non-hierarchical models for all five EIVs as estimated by DIC (ΔDIC between 8.6 and 40), and models including group-level habitat predictors (M2.3) were invariably the best by this criteria (*Table 2.2*). Estimates of variance among species EIVs within sample plots ($\sigma_{species}$) from hierarchical models were much larger in all cases than between plot (σ_α) and between time-period (σ_β) variance estimates. The inclusion of ecological habitat type in the M2.3 models significantly reduced residual variance in plot-level intercepts and slopes ($\sigma_\alpha \; and \; \sigma_\beta$) for models of all EIVs. The extent to which intercepts and slopes were pooled (λ_α and λ_β) differed between models of the five EIVs, but was much higher for model M2.3 vs. M2.2 in all cases, which exemplifies how adding habitat type provided a better target for pooled estimates by reducing residual variance in plot-level parameter estimates (*Table 2.2*). The inclusion of ecological habitat type in the M2.3 models explained over 40% of variation in the pooled plot-level slope parameters for EIVs L, N, R and S, while it explained 33% for EIV F, which also had higher estimates of σ_β both before and after the inclusion of habitat than the other EIVs (*Figure 2.3*).

Table 2.2 Residual variance (σ), Bayesian R^2, mean pooling of estimates (λ), effective number of parameters (pD), and DIC values for models fit to Ellenberg Indicator Values F, L, N, R and S of plant species from a re-visitation study on the Studland peninsula between the 1930's and 2010's. NP are "no-pooling", H are "hierarchical", and HG are "Hierarchical with group-level predictor" models. Parameters with subscripts α and β were estimated at the level of varying intercepts and slopes respectively.

Model	σ_{plant}	σ_α	σ_β	R^2_{plant}	R^2_α	R^2_β	λ_α	λ_β	**pD**	**DIC**
EIV F										
M2.1(NP)	1.74	-	-	0.22	-	-	-	-	149.1	36391.8
M2.2(H)	1.74	1.09	0.62	0.22	0	0	0.05	0.25	127.5	36383.2
M2.3(HG)	1.74	0.47	0.53	0.22	0.83	0.33	0.3	0.38	117.8	36371.2
EIV L										
M2.1(NP)	0.91	-	-	0.12	-	-	-	-	148.9	24561.4
M2.2(H)	0.91	0.28	0.18	0.12	0	0	0.13	0.41	98.7	24526.8
M2.3(HG)	0.91	0.18	0.15	0.12	0.63	0.41	0.36	0.61	94.7	24521.9
EIV N										
M2.1(NP)	1.64	-	-	0.06	-	-	-	-	148.8	35330.1
M2.2(H)	1.64	0.33	0.3	0.06	0	0	0.24	0.42	90.4	35290.8
M2.3(HG)	1.64	0.25	0.24	0.06	0.42	0.44	0.43	0.62	87.1	35289.5
EIV R										
M2.1(NP)	1.56	-	-	0.08	-	-	-	-	148.9	34100.7
M2.2(H)	1.54	0.45	0.35	0.08	0	0	0.17	0.42	107.5	34071.4
M2.3(HG)	1.54	0.34	0.28	0.08	0.43	0.44	0.33	0.6	100.9	34068.6
EIV S										
M2.1(NP)	1.08	-	-	0.22	-	-	-	-	148.9	27596.9
M2.2(H)	1.08	0.56	0.21	0.22	0	0	0.06	0.52	108	27577

M2.3(HG)	1.08	0.27	0.18	0.19	0.76	0.43	0.29	0.62	95	27563.6

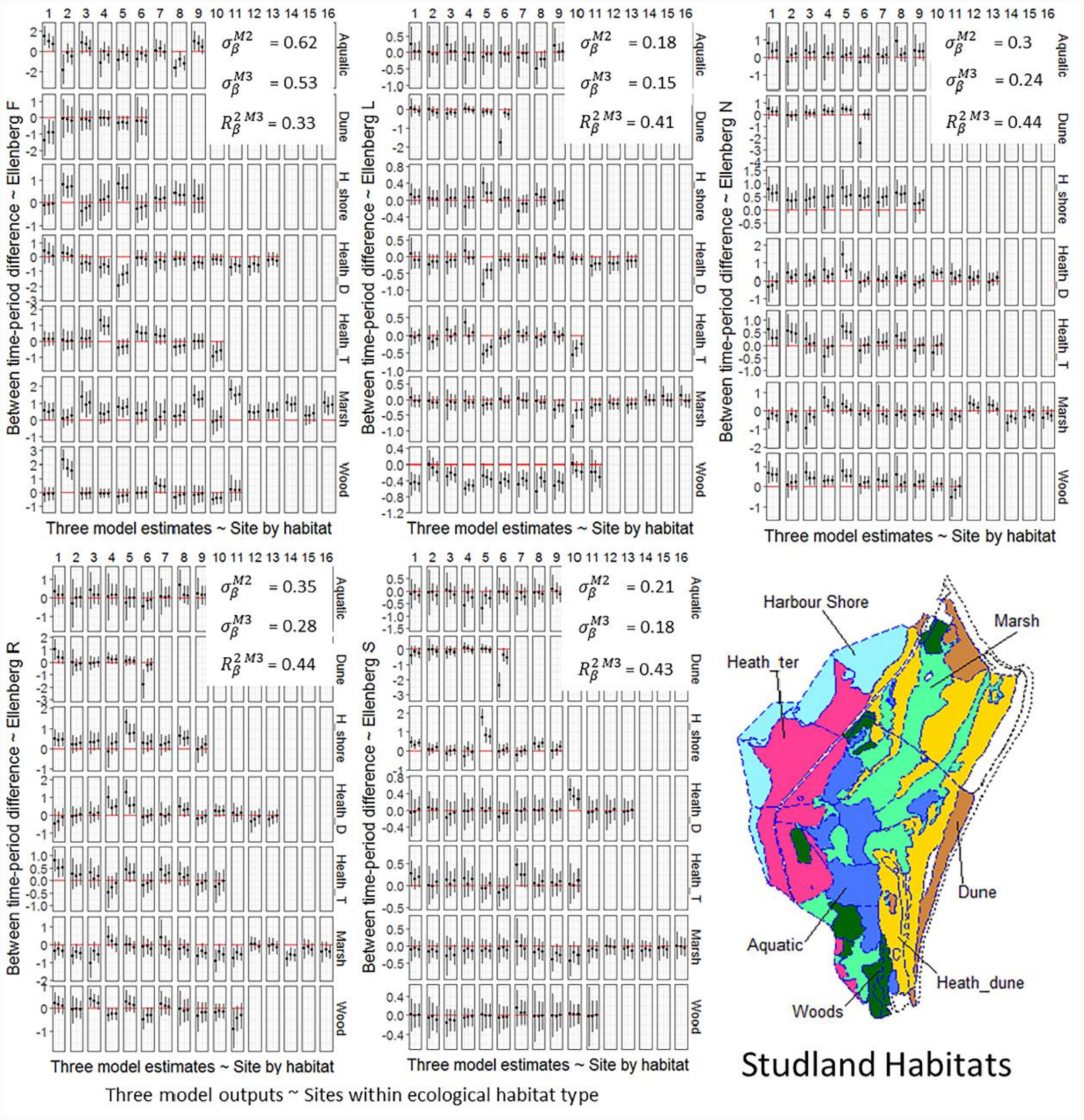

Figure 2.3 Changes in Ellenberg Indicator Values (EIVs) between sampling in the 1930s and resampling in 2010s. Plots show mean and 95% Bayesian credible intervals for estimates of plot-level changes between sampling-periods for each of seven habitats (Map inset). Each grid cell contains varying slope parameters (β's) from models M2.1 (no-pooling), M2.2 (hierarchical), and M2.3 (hierarchical) from left to right respectively. Horizontal red lines indicate zero change between sampling-periods. White textboxes show unexplained variance in slope parameters in hierarchical models with and without habitat as a predictor (σ_β^{M2} and σ_β^{M3} respectively) and the estimated proportion of variance explained by habitat as a group-level predictor for slope parameters (Bayesian R^2). Each column represents numbered plots within habitat types.

2.4.3 Habitat-level inference

Estimates of change in mean habitat-level EIVs between time-periods 1 and 2 differed to a large extent between full multilevel models (M2.3) and GLMM's using raw mean EIVs as data (*Figure 2.4*). While mean estimates of habitat level change were often similar between the two sets of models, hierarchical model estimates were more precise with narrower 95% Bayesian credible intervals than GLMM estimates. Furthermore, to infer differences at the standard α = 0.05 level as commonly practiced, GLMM confidence intervals need to be adjusted for multiple comparisons, whereas pooled estimates from hierarchical models do not (Gelman et al. 2012), which led to a rejection of a null hypothesis of no change in environmental conditions in six of 35 instances in this system using estimates from the full multilevel model where I would have to accept the null hypothesis of no change using the GLMM estimates (*Figure 2.4*). This may lead one to conclude that there has been no significant change in the harbour shore habitat from GLMM results for instance, whereas hierarchical model results show strong, precise directional change in soil nutrients (N), pH (R) and salinity (S) underlying these assemblages. Similarly, GLMM results would underestimate the extent of change in the marsh, woodland and dune heath habitats compared with the more precise hierarchical estimates. However, despite the adjusted confidence intervals in the GLMM's, pooling of estimates in the multilevel models led to more conservative estimates of change in the dune habitat, which would lead us to conclude minimal change over time (accept the null hypothesis of no change) for EIVs L and S, while I would conclude stronger negative change from GLMM estimates (reject the null hypothesis of no change).

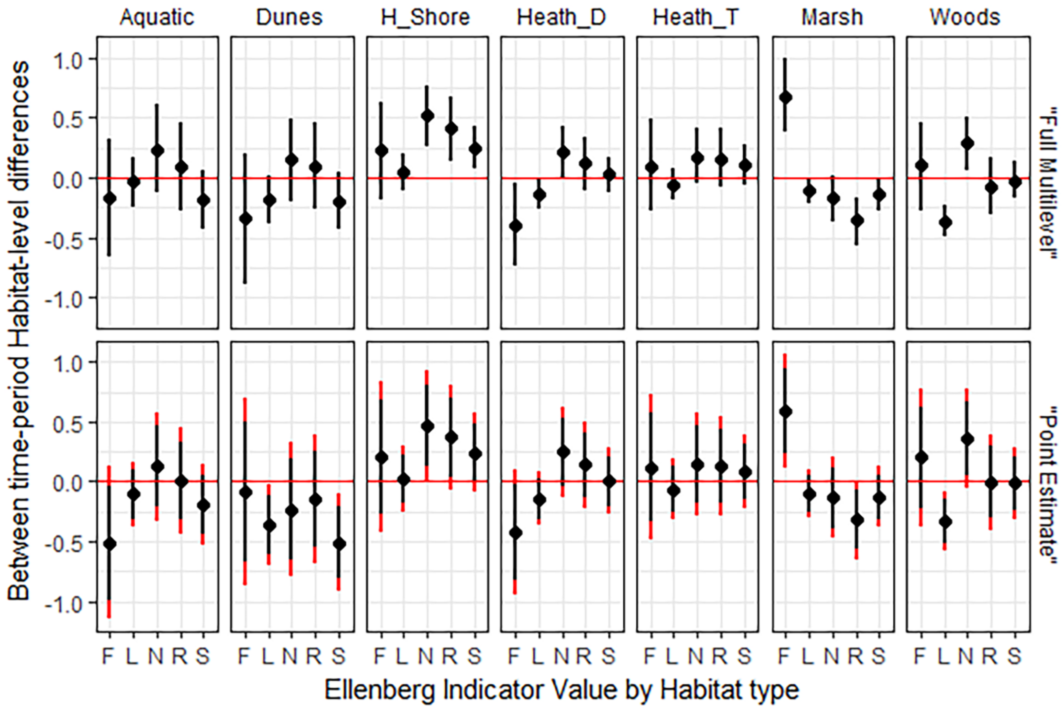

Figure 2.4 Mean and 95% Bayesian credible intervals (top) and confidence intervals (bottom) for habitat level differences in mean Ellenberg Indicator Values (EIVs) for Moisture (F), Light (L), Nutrients (N) Reaction (R) and Salinity (S) on the Studland peninsula between the 1930s and 2010s. Top row shows estimates from multilevel models with recorded species EIVs as data (model M2.3 from text), while the bottom row shows estimates from mixed effects models using raw means of plot EIVs as data. Red extensions to the GLMM confidence intervals represent corrections for multiple testing; hierarchical estimates do not need to be corrected due to pooling of estimates.

2.5 Discussion

I have shown that multilevel modelling provides improved discriminatory power when estimating differences in mean Ellenberg indicator values between historical and contemporary plant assemblages, both at the level of individual plots and across the wider community. Multilevel models suggested a prominent role of hydrological changes – alongside succession processes – in driving compositional change between sampling periods in our case study, the extent of which would not be revealed by inference using point estimates of plot mean EIVs as data. When I removed 90% of plant species from a selection of species rich plots, estimates of plot mean EIVs from hierarchical models were very close in the majority of cases to mean values with the full cohort of species remaining. This was in stark contrast to raw means for randomly remaining species, and it demonstrates the rich potential for improving estimation and inference by pooling information across plots in hierarchical models in instances of non-systematic missing data, which are common in ecological studies. Taken together these findings highlight the potential value of information discarded when point estimates of plot mean EIVs are used as the starting point for inference, and show how hierarchical modelling can increase the utility of EIVs in suggesting the nature of environmental factors likely underlying changes in plant community composition.

2.5.1 Model performance with missing data

The phenomenon of recorders overlooking species present when performing surveys is a consistent feature of ecological sampling and can lead to bias in estimates of many ecological rate and state variables (Kéry and Gregg 2003, Kéry 2004, Chen et al. 2013). While missing species may not be an issue when using weighted averages of EIVs (Ewald 2003), our analyses on artificially depleted plots for presence/absence data show the utility of hierarchical models to help alleviate inaccuracy in estimates due to imperfect sampling and non-systematic missing data. The ability of the multilevel models to estimate plot mean EIVs accurately when the majority of species are missing should also allay any apprehensions over using the ordinal EIVs fit to a Gaussian distribution at the data level of these models; improvement in plot mean values is the primary aim of this paper, and results from analyses on depleted datasets demonstrate that this has been achieved.

2.5.2 Habitat-level inference

Hierarchical model performances improved with habitat type as a group-level predictor by providing better targets for pooled estimates. Furthermore, the ability to infer change over time from resulting habitat estimates without correcting for multiple comparisons allows us to build a more nuanced and precise picture of environmental change over time. Effect sizes for changes in habitat level mean EIVs in the Studland case study were small (<1) in all cases, but as these specify average changes across entire habitats they still indicate meaningful directional changes in environmental conditions. With small effect sizes – as will usually be the case given the scale on which EIVs are quantified – the increased precision of estimates gained from hierarchical modelling is a major advantage in revealing the direction and magnitude of environmental change in a study system.

Broad increases in EIV N across the habitats of Studland are in-line with studies over a similar period both across the county of Dorset (Newton et al. 2012) and further afield (Bennie et al. 2006), possibly resulting from atmospheric nitrogen deposition. Other trends are likely more specific to Studland, including wetter conditions across the marsh habitat, and decreases in EIV L across the woodland and dune heath habitats probably indicating ecological succession. Such location specific changes in the environment could have important effects on co-occurring animal assemblages. For example, changes in precipitation levels can lead to shifts in vegetation structure and resulting changes in rodent community composition (Ernest et al. 2008). The wetter marshes of Studland may have similarly affected local invertebrate and mammal assemblages, and we have shown that hierarchical modelling is better suited to uncover such effects when using EIVs.

While pooled habitat level estimates from multilevel models suggested more widespread change across the Studland system than did estimates from the GLMM’s, they were also more conservative than the GLMM estimates in an important way, exemplified by the dune habitat.

Larger changes estimated from the GLMM's in dune plots result from a large influence of one plot (dune plot number 6, *Figure 2.3*), whereas in the multilevel models the influence of this plot was dampened by the pooling of this plot's slope (β) estimate. In time-period 1 this was a newly formed dune which only seven plant species had colonised. From typical dune succession I would expect this plot to become more shaded, more acidic and more nutrient rich over time (Jones et al. 2008). While the raw mean estimates do suggest that it has become more shaded and more acidic by time-period 2, they would also suggest that it has become less nutrient rich. It seems likely that the apparent decrease in soil nutrient levels in this plot is a confounded estimate driven by the strong correlation between EIV R and N (Diekmann 2003), at a plot where soil pH was probably a stronger driver of species recruitment in time-period 1 (Jones et al. 2008). I would suggest that without specific ecological knowledge of a plot, in general it is a worthwhile trade-off to underweight plot mean values as the multilevel models should do, rather than overweighting it as is probable using point estimates from plots with sparse data. This should reduce overconfidence in specific plot values, giving a more accurate estimate of change in this plot despite the few plant species present in the 1930s, while also reducing the effect of outliers on habitat level estimates of change (McElreath 2016a).

2.5.3 Plot-level inference

By using hierarchical models to account explicitly for different variance components in a study system, I can build a more in-depth picture of changes that have occurred. In the Studland case study, variance in EIV scores among plant species within sample plots ($\sigma_{species}$) was larger in all cases than variance between plots (σ_{α}) and variance in plot-level changes between time periods (σ_{β}) for all EIVs, which illustrates the value in pooling information between plots in this way to improve estimates of plot mean values. High variance estimates within plots reflect the fact that the environmental parameter an EIV represents tends to play just a small role in determining whether a plant species occurs in a given area, and that in any sample plot only a subset of species likely to occur despite environmental constraints will do so at a given time (Pärtel 2014). Species may be absent from plots they could potentially occupy for various stochastic and mechanistic reasons (Callaway and Walker 1997, Chave 2004, Leibold et al. 2004), or they may be missed by recorders in a given sampling instance as previously discussed (Kéry & Royle 2010). Computation of separate R^2 values for variance explained by habitat type for intercept and slope parameters is also highly valuable, as practitioners will often be interested only in the changes over time, and not the baseline differences between habitat types.

The ability to provide a plot specific picture of local change alongside estimates of average trends across the wider landscape should also prove valuable to those wishing to concentrate on finer details to aid management, or to use as indicators of dynamics affecting ecological communities contemporaneous with plant assemblages. For example, when I look at changes in plot mean EIVs over the 80 year period across the Studland Peninsula (β parameters), I see it was far more variable for EIV F (moisture) than for the other EIVs both before and after accounting for habitat type. While some changes in this system – such as levels of shade (EIV L) across the woodland plots – may have clear ecological explanations (e.g. succession) specific to habitat types, highly variable changes in plot mean EIV F estimates suggest that changes in the hydrological profile of the peninsula is an important abiotic driver of change in community composition across habitat boundaries. With hierarchical models, I can pinpoint outliers or plots within which change does not match plots in a similar habitat because pooling allows us to view each estimated plot mean in isolation with more confidence that it is a balanced estimate (Gelman et al. 2012). Inspection of these plot values could lead one to develop new hypotheses about drivers of change – for instance spatial proximity to a body of water, or height above sea level – which can be easily incorporated back into the model once data is compiled on them to assess their influence. In this way hierarchical models can be used in conjunction with knowledge of the details of a specific system to uncover drivers of change as part of an iterative scientific process.

2.5.4 Model extensions and flexibility

The multilevel models presented here, particularly fitted in a flexible Bayesian framework, can be extended or adapted to specific study systems in many useful ways. For instance, other grouping factors – in place of or in addition to habitat type – may be added to the sub-models for intercepts and/or slopes (e.g. natural vs. semi-natural, grazing regime, management practice). Similarly, continuous predictors could be added if they are of interest (e.g. plot elevation, plot area). One could also add predictors at the level of species within plots such as %cover or invasive vs. non-invasive species, depending on specific study aims. Informative or regularising priors may be used, which could be particularly useful in instances of small sample sizes in terms of numbers of plots or species richness within plots (McElreath 2016a). Finally, the method could be adapted for use on any quantitative trait values which are averaged across species, which may help address issues of robustness (Aiba et al. 2013).

2.5.5 Conclusions

The increasing prevalence of resurvey studies in plant ecology, coupled with the importance of understanding accelerating environmental change, has led to Ellenberg indicator values becoming an important tool in the ecologists' kit. I have demonstrated how multilevel modelling can provide a more powerful discriminatory framework when using EIVs to hypothesise the nature of environmental dynamics underlying compositional change in plant communities. These methods also perform very well in situations where some or all plots sampled do not have the full cohort of species recorded. Our contribution describes one more way hierarchical modelling, particularly applied in a flexible Bayesian framework, provides an ideal way to describe the multitude of hierarchical structures we see at all levels in biological systems, from cells to meta-communities. Furthermore, I contest that identifying and explicitly modelling components of variation within an ecological system in this way can lead to the development of further hypotheses about environmental drivers shaping plant community functional characteristics in a way that is difficult using traditional statistical techniques, as our case study demonstrates.

3. Congruent change over 80 years in plant and insect communities across a dynamic habitat mosaic

3.1 Abstract

Changes in the abiotic and biotic environment are important drivers of biodiversity change by causing species losses and gains. However, the extent to which distinct co-occurring taxa experience similar long-term patterns in species richness and compositional differences when exposed to environmental change is unclear, as historical data on co-occurring taxa are extremely rare.

Using the CDP data, I investigated whether local communities display cross-taxon congruence – correlated patterns of species richness and compositional change – across six co-occurring plant and insect taxa: vascular plants, non-vascular plants, grasshoppers and crickets (Orthoptera), ants (Hymenoptera: Formicinae), hoverflies (Diptera: Syrphidae), and dragonflies and damselflies (Odonata). Using hierarchical logistic regression (HLR) and multivariate statistical analyses, I also examined to what extent observed congruencies were explained by shared responses to abiotic environmental change vs other causal factors (e.g. biotic interactions).

All taxa displayed high levels of turnover across the *ca.* 80-year time period, though overall species richness did not change substantially. I found widespread evidence of cross-taxon congruence in species richness change across the study system, with HLR results suggesting a prominent role for shared responses to environmental change underlying many of these congruencies. HLR models also indicated stronger congruencies between vascular plant and their direct consumers, suggesting a role for biotic interactions between these groups.

In this chapter, I have provided a unique illustration of cross-taxon congruence in biodiversity change across an 80-year period, likely driven both by abiotic and biotic environmental change. Results highlight the potential for cascading community effects of environmental change on local plant and insect communities. Such effects need to be accounted for when planning biodiversity management in the face of projected anthropogenic disturbances.

3.2 Introduction

Species losses and gains are a widespread consequence of environmental change, with poorly understood repercussions for long-term biodiversity patterns and ecosystem functioning (Sax and Gaines 2003, Wardle et al. 2011). In local communities undisturbed by major human encroachment, long-term monitoring has indicated as much as 10% turnover in species composition per decade (Dornelas et al. 2014). Understanding connections between patterns of such changes across co-occurring taxa is vital in order to assess the probability of cascading effects of environmental change, as anthropogenic disturbances continue throughout the 21st century. However, a paucity of historical records has meant the majority of long-term biodiversity studies have focused on one or very few taxa (but see: Ernest et al. 2008, Özkan et al. 2014, Ewald et al. 2015), and as such, the prevalence and drivers of correlated biodiversity trends in locally co-occurring taxa are not well understood.

Ecological communities commonly display cross-taxon congruence (CTC) – correlated patterns in species richness or composition – over spatial extents (Westgate et al. 2014). However, the strength of such congruencies is variable and depends on the taxa involved and on the spatial scale of analysis (Pearson and Carroll 1999). When correlations are strong, cross-taxon congruence can be used as an ecological indicator, whereby easily surveyed taxa indicate approximate richness or composition in more cryptic taxa (Fattorini *et al.* 2012). It follows then, that correlated biodiversity trends across taxa could similarly be used for ecological indication of temporal biodiversity change.

Temporal CTC in species richness and compositional change could occur due to abiotic or biotic mechanisms, or to a combination of both. Temporally variable abiotic conditions play a dominant role underlying biodiversity change across a range of taxa and systems (Mutshinda et al. 2009), and therefore environmental change may be expected to drive congruent biodiversity trends in taxa which co-occur locally as they respond in tandem to a changing abiotic environment. Interactions between taxa – particularly those with strong trophic or mutualistic dependencies – also play a key role in determining species composition, with plant community richness and composition in particular often associated with biodiversity in higher taxa (e.g. Scherber *et al.* 2010). Thus biodiversity change in interacting taxa could drive negative or positive changes in the interaction partners depending on the nature of the interaction (Pace et al. 1999, Kiers et al. 2010).

To assess temporal CTC at relevant time-scales, resurvey or time-series data over long periods are needed, as many important drivers of environmental change act over decades (e.g. climate (Vázquez et al. 2017) and agriculture (Robinson and Sutherland 2002)). Plant and insect occurrence data from the Cyril Diver Project provide an ideal opportunity to do so. Using these data, I assessed the degree of temporal CTC across plant and insect taxa in the dynamic Studland system with *ca.* 80 years between sampling periods.

I aimed to investigate whether local plant and insect communities display cross-taxon congruence in species richness and compositional change over an approximately 80 year period, and to what extent revealed congruencies are driven by shared responses to abiotic environmental change (inferred from the plant community (Chapter 1; Carroll *et al.* 2018)). I assessed temporal CTC across six taxa which represent distinct evolutionary histories, ecological requirements, and trophic characteristics (*table 3.1.*), at three relevant local scales within the study system (*figure 3.1.*). I expected distinct responses to environmental change among these taxa at group level due to niche conservatism within clades (Wiens et al. 2010).

To quantify temporal CTC and its probable drivers, I asked: i) To what extent have species richness and composition in each taxon changed between sampling-periods, and how do changes compare across taxa?; ii) What environmental factors best predict species composition within each taxon during each sampling-period, and have composition/environment relationships changed between sampling-periods?; iii) Do plant and insect groups display temporal congruence in local species richness change among sampling compartments? (*figure 3.1.*); iv) To what extent is congruence between taxa in species richness change associated with shared responses to environmental change?

I hypothesised that changes in composition of herbivore communities would correlate more closely with changes in plant community composition with than would the changes in the omnivore and carnivore groups due to trophic dependencies. I further hypothesised that congruencies observed in pairwise comparisons among the other five taxa would be driven largely by shared responses to abiotic changes, as no strong trophic dependencies exist between these groups.

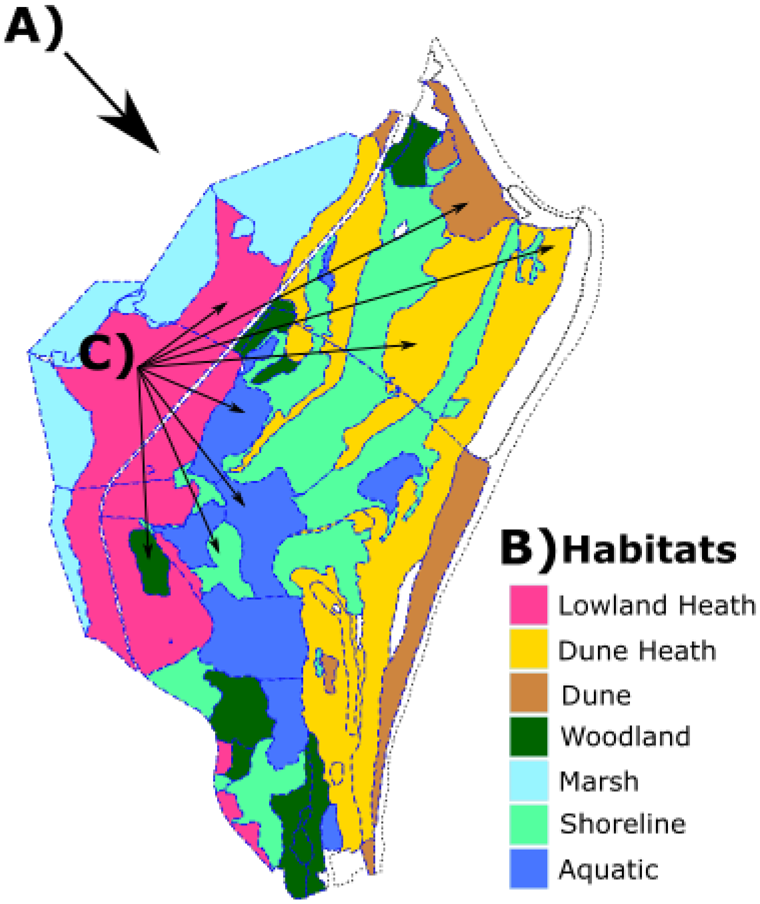

Figure 3.1 The Studland peninsula in Dorset consists of a mosaic of ecological habitats surveyed in the 1930s and 2010s. Dashed lines separate the sampling compartments of historical and contemporary surveys, and colours denote habitat types. Even within this small peninsula (~$3km^2$), biodiversity change in plant and insect communities can unfold in differing ways at distinct spatial scales: A) Changes at the level of the whole study system; B) Changes within the distinct ecological habitat types, and; C) Changes within and among the sampling compartments. Species richness and compositional changes may correlate across taxa (Cross-taxon congruence) at any or all scales due to shared responses to a changing environment or biotic interactions.

Table 3.1 Focal taxa and their trophic status.

Taxon	**Trophic status**
Vascular Plants	Primary producers
Non-Vascular plants	Primary producers
Orthoptera (Grasshoppers/Crickets)	Herbivores
Hymenoptera Formicidae (Ants)	Omnivores (herbivorous/carnivorous diet depends on species)
Diptera Syrphidae (Hoverflies)	**Larva:** Omnivores (diet varies by species) **Adult:** Herbivores (strong dependency on nectar/pollen)
Odonata (Dragonflies/Damselflies)	Carnivores

3.3 Methods

See chapter 1 for details on species occurrence data collection.

3.3.1 Environmental data

Between sampling periods in the 1930s and 2013-2015 the peninsula underwent considerable and heterogeneous change driven by hydrological differences, vegetative succession and nitrogen deposition (Carroll et al. 2018). Environmental data used in statistical analyses consisted of categorical variables describing the ecological habitat type (*figure 3.1.*), and compartment mean Ellenberg Indicator Values (EIVs) for moisture (F), Light (L), Soil Nutrients (N), pH (R) and Salinity (S) derived from hierarchical regression models with improved accuracy by pooling information across compartments in chapter 1. EIVs provide a species-specific score which grades plant species according to observed environmental associations, and site mean EIVs are widely used in re-visitation studies as proxies for alternative environmental drivers (e.g. Newton *et al.* 2012; Diaz *et al.* 2013) in the absence of directly measured environmental data.

3.3.2 Statistical analyses

To quantify temporal CTC and drivers thereof, I performed a set of analyses at three different scales: the whole study system, ecological habitat types, and local sampling compartments (*fig 1.*). I first quantified absolute biodiversity change (species losses and gains) within each taxon at study system and habitat levels to provide a context of the overall change to compare between taxa. I then assessed taxon-specific relationships between species composition and environmental conditions within each sampling-period at sampling compartment level to identify important environmental predictors which may have driven community change and underlie congruencies between taxa. I examined pairwise correlations in species richness differences between sampling-periods at sampling compartment level as a measure of temporal CTC. Finally, I re-estimated these correlations after accounting for species richness change associated with environmental change (EIVs & Habitat type) to assess the degree of congruence due to shared responses to the abiotic environment between each pair of taxa.

3.3.2.1 *Compositional change between time-periods (species losses and gains)*

To quantify changes in species richness and composition at the levels of study system and ecological habitat type between sampling-periods, I used the Temporal β-diversity Indices (TBI) of Legendre & Salvat (2015). TBI are a simple but intuitive and information rich method based on breaking down components of the classical dissimilarity indices used in community ecology, in this case the Jaccard similarity. For presence/absence data this amounts to simply counting the number of species losses and gains between two sampling periods in a sampling unit (whole peninsula, habitat), and calculating the sum of species gains plus losses as a proportion of the total number of species present in either or both time-periods (losses + gains + species found in both time-periods) to find the proportional change in species composition between sampling periods. I calculated TBI for each taxonomic group within each ecological habitat type, and for the peninsula as a whole, to compare proportional changes in community composition between sampling-periods across taxa. I also calculated species richness differences as the difference between the number of losses and gains for each sampling unit.

3.3.2.2 *Species composition in relation to the environment*

To identify environmental factors underlying compositional differences between the 1930s and 2010s, I assessed relationships between species composition and environmental conditions for each taxon within each sampling period and how these relationships changed between sampling periods. To quantify composition/environment relationships, I performed redundancy analyses (RDA) and variation partitioning on multivariate Hellinger transformed species-by-compartment occurrence matrices for each taxon within sampling periods 1 and 2 (Legendre and Gallagher 2001, Legendre and Legendre 2012). RDA is a form of constrained ordination analogous to multivariate regression, which allows the user to quantify proportions of explained variance in species composition (adjusted R^2) attributable to continuous or categorical predictor variables across a set of sampling units (Legendre & Legendre 2012).

I fitted RDAs for each of the six focal taxa using two sets of environmental explanatory variables across the sampling compartments: 1) broad ecological habitat types as categorical predictors, and 2) mean within sampling-period EIVs for moisture (F), Light (L), Soil Nutrients

(N), pH (R) and Salinity (S) (Carroll et al. 2018). EIVs for nutrients (N) and pH (R) were highly collinear across sampling compartments, so final models only included EIV R (not EIV N) as EIV R explained more variance (by adjusted R^2 criteria) in almost all cases. I selected statistically significant EIV predictors at the alpha = 0.05 level for each taxon using the forwardsel function from package VEGAN in R (Oksanen et al. 2013). Finally, I used multivariate variation partitioning with VEGAN's varpart function for each set of models to determine the shared and unique contributions to the explanation of variation in species composition attributable to Habitat type vs EIV explanatory variables.

3.3.2.3 *Cross-taxon congruence in pairwise comparisons of species richness change*

To quantify temporal CTC in species richness change between sampling compartments – that is, the magnitude of correlations in richness differences between pairs of taxa – I used a hierarchical logistic regression (HLR) based approach. I extracted just the species lost and gained between sampling periods for each compartment and coded them as 0 and 1 respectively. I fitted a HLR with intercepts varying by compartment for the vascular plant taxonomic group, and five separate sets of slope parameters, also varying by compartment, for each of the other five focal taxa (coded as dummy variables) (Model M2.1, Appendix 3). I included a random effect for species ID to ensure I estimated the average change of species within taxa for comparison. I reconstructed intercepts from the fitted model for each taxon on the inverse logit scale, corresponding to the proportion of species gained vs lost in each sampling compartment after controlling for species ID. This proportion provided me with a proxy for species richness change that I could compare across taxa: a proportion greater than 0.5 represents an increase in richness, while a proportion less than 0.5 represents a decrease. I then computed Pearson's correlations of the intercepts between each pair of taxa over the full posterior distribution of estimates from the models *across the subset of sample plots with records for both taxa within a pair*. This provided a measure of cross-taxon congruence for average richness change between taxa.

3.3.2.4 *Congruence due to shared responses to environmental change*

To assess whether correlations in species richness change between taxa were driven by shared responses to environmental change, I fitted a second HLR model (M2.2 Appendix 3), extending the variable intercept and slope parameters of M2.1 to include predictors for habitat type and for the change in mean EIVs between sampling periods. The inclusion of habitat type as a proxy for environmental change entails the assumption that environmental conditions in distinct habitat types changed in different ways to one another as indicated in chapter 1.

The additional predictor terms were included as varying offsets for habitat type with varying slopes for change in EIV scores and were fitted using a Multivariate Normal distribution with an associated variance/covariance matrix with a non-centred parameterization to aid model fit (McElreath 2016a, Stan Development Team 2018b). EIV predictors included in this model were those found to be significant predictors of community composition from RDA analyses in section 3.3.2.2 for each taxon (see *figure 3.3.*), so that we were only using environmental covariates found to have an association with assemblage composition for a specific taxon, and to help avoid overfitting. Pairwise correlations were then recomputed over the posterior distributions having controlled for these components of environmental change.

In order to test for potential sampling bias and bias introduced due to rare, cryptic or transient species, I refitted the hierarchical models from sections 3.3.2.3 and 3.3.2.4 including species loss/gains only for species present in 20% or more sampling compartments in the time-period in which a species was more widespread (taxon-specific). I then re-computed cross-taxon correlations to check if they differed substantially to correlations computed under the full dataset. This should serve to minimise effects of rare or "vagrant" species on cross-taxon correlations, and increase the likelihood that species recorded as lost or gained were legitimately present in one time-period and not the other under this analysis.

Hierarchical models were fitted with MCMC in Stan using the rethinking package in R version 3.5.0 with 4 parallel chains of 4000 iterations each (McElreath 2016b, R Core Team 2018, Stan Development Team 2018a). Details of fitted models and validation including posterior predictive checks can be found in Appendix 3**.**

3.4 Results

3.4.1 Compositional change between time-periods (species losses and gains)

All six taxa displayed large proportional differences in species composition between sampling periods, both across the peninsula as a whole, and within ecological habitat types (*figure 3.2.*). Peninsula-wide differences in species composition were of a similar order of magnitude across taxa (proportional difference in species composition ≈ 0.5) with the exception of Odonata (proportional difference = 0.24), but proportions of species losses vs gains which contributed to differences were less uniform across the groups. Orthoptera, ants and Odonata in particular showed larger species gains than losses, but these were from much smaller total species numbers than the other three groups (*figure 3.2.*). At the level of ecological habitat types, compositional differences were variable both within and between taxa, but the total differences tended to be larger than at the whole peninsula level.

Species richness marginally increased at the study system level for all taxa apart from hoverflies (net loss of 5 species), but net gains or losses in richness across the peninsula as a whole were composed of gains in some ecological habitat types and losses in others for five of the six taxa (excluding Orthoptera which experienced no net losses) (*figure 3.2.*). In general, gains dominated in the heath, dune heath, harbour shore and aquatic habitats, while losses tended to be more prominent in the wood and marsh habitats.

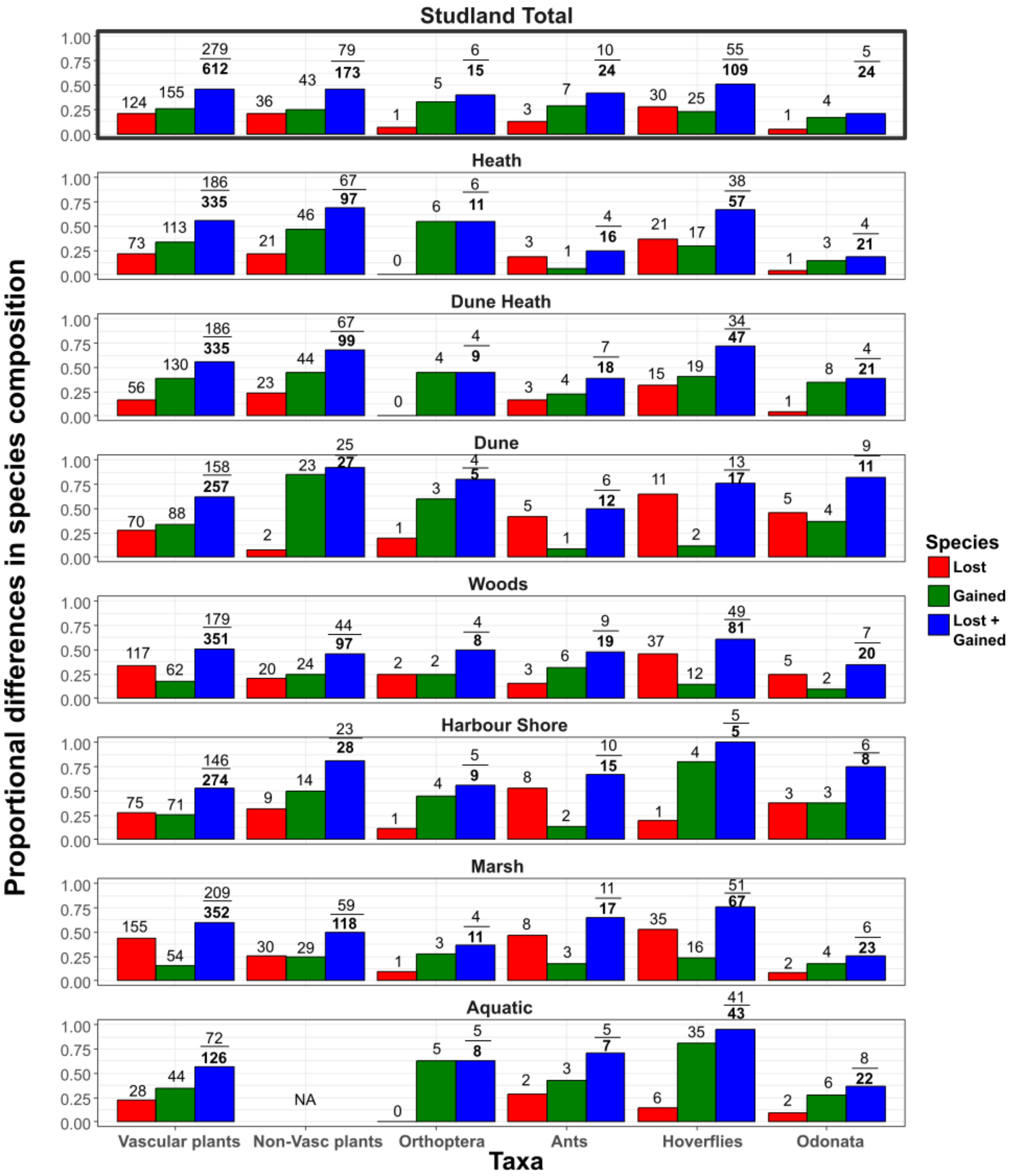

Figure 3.2 Between time-period compositional change for six plant and insect taxa within ecological habitat types and for the whole Studland peninsula for sampling-periods in the 1930s and 2010s. Proportional differences (y-axes) in species composition (blue) are computed as the number of species losses (red) + gains (green) as a proportion of the total number of species present in either or both time-periods combined, and are identical to the Jaccard dissimilarity index computed between two time-periods. A value of 1 on the y-axis for blue bars indicates that the identity of every species in the assemblage has changed between sampling-periods, while a value of 0 indicates the exactly the same species were present in each time-period. Numbers labelling the bars are the raw species counts for each sampling unit from which the proportions were derived. Change in species richness can be calculated as gains minus losses in each instance.

3.4.2 Species composition in relation to the environment

The most influential factors in predicting species composition across taxa at compartment level within each sampling-period were wetness and light availability (EIVs F and L), along with ecological habitat type, though composition/environment relationships showed widespread changes for all six taxa between sampling-periods (*figure 3.3.*). Variation partitioning revealed that habitat type and EIVs shared a large amount of explained variation for models of all taxa in time-period 1, and for five of the six taxa in time-period 2 (excluding Odonata). Explained variance (adjusted R^2) increased in the 2010s vs the 1930s for vascular plants, non-vascular plants and Orthoptera (by 0.07, 0.07 and 0.04 respectively) – mostly explained jointly by habitat type and EIVs, rather than being exclusively explained by either set of predictors. This indicates that species composition differed more among habitats in the 2010s for these groups, possibly due to a greater contrast in environmental conditions compared with the 1930s. Adjusted R^2 for ant and hoverfly groups showed decreases between sampling-periods in the 2010s vs the 1930s (by 0.08 and 0.04 respectively), and both groups exhibited a shift towards variance explained jointly by habitat and EIVs in the latter time-period.

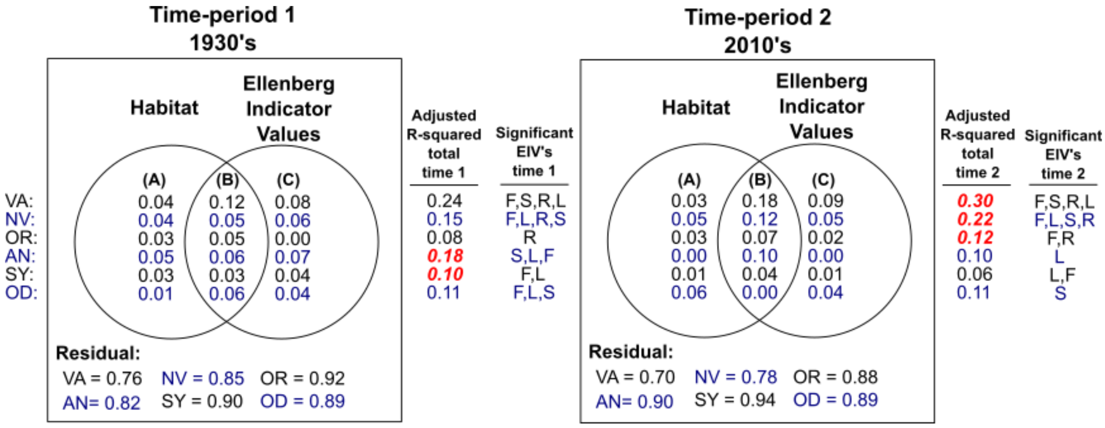

Figure 3.3 Relationships between species composition and the environment across the Studland peninsula derived from Canonical Redundancy analyses (RDA) and multivariate variation partitioning performed separately on Vascular plants (VA), Non-vascular plant (NV), Orthoptera (OR), Ant (AN), Hoverfly (SY) and Odonata (OD) assemblages for sampling periods in the 1930s and 2010s. Venn diagrams display proportions of variation explained (adjusted R^2) by A) ecological habitat type alone, B) jointly by habitat type and site mean Ellenberg indicator values (EIVs), and C) EIVs alone. EIVs F, L, R and S represent soil moisture, light availability, pH and salinity respectively. Only significant EIVs included in the final models were used for calculations of adjusted R^2. Red numbers indicate that more variation was explained by environmental predictors in that time period for a taxon.

3.4.3 Cross-taxon congruence in pairwise comparisons of species richness change

HLR models revealed strong evidence for cross-taxon congruence in temporal species richness change across the study area, illustrated by pairwise correlations between plant and insect taxa in *figure 3.4*. Mean pairwise correlations between taxa in species richness change were non-negative in all cases before accounting for environmental change, and the 95% credible intervals were fully positive (did not cross zero) in 7 of the 15 comparisons (analogous to frequentist statistically significant congruencies at the α = 0.05 level, black intervals *figure 3.4.*). Correlations between vascular plants and other taxa (excluding ants) were strong and positive, and correlations between vascular plants and the two herbivorous groups (hoverflies and Orthoptera) were stronger than those with non-herbivores. Non-vascular plants displayed the weakest correlations with other taxa, with the only notable correlations between them and vascular plants, and a weaker (mean ≈ 0.25) correlation with Odonata. Pairwise correlations between insect groups were broadly positive, with 3 out of 6 of the distributions "statistically significant" before accounting for environmental change.

3.4.4 Congruence due to shared responses to environmental change

When environmental covariates were controlled for, 8 of the 15 pairwise correlation distributions shifted in a negative direction, including all 6 insect-insect group comparisons (*figure 3.4.*, blue intervals). Correlations between vascular plants and herbivores stayed strong and positive, but the correlation between vascular plants and Odonata shifted to centre at approximately zero. Correlations between non-vascular plants and all other groups shifted in a positive direction, but remained weak in all comparisons apart from correlations with vascular plants and with Odonata.

Both models fitted for the partial dataset with species present in 20% or more compartments produced cross-taxon correlations that were strikingly similar to those under the full dataset (Appendix 3). This is almost certainly due to the species level random effect, which means that correlations were computed for an average species within a taxonomic group, and therefore rare and transient species will not have made large contributions.

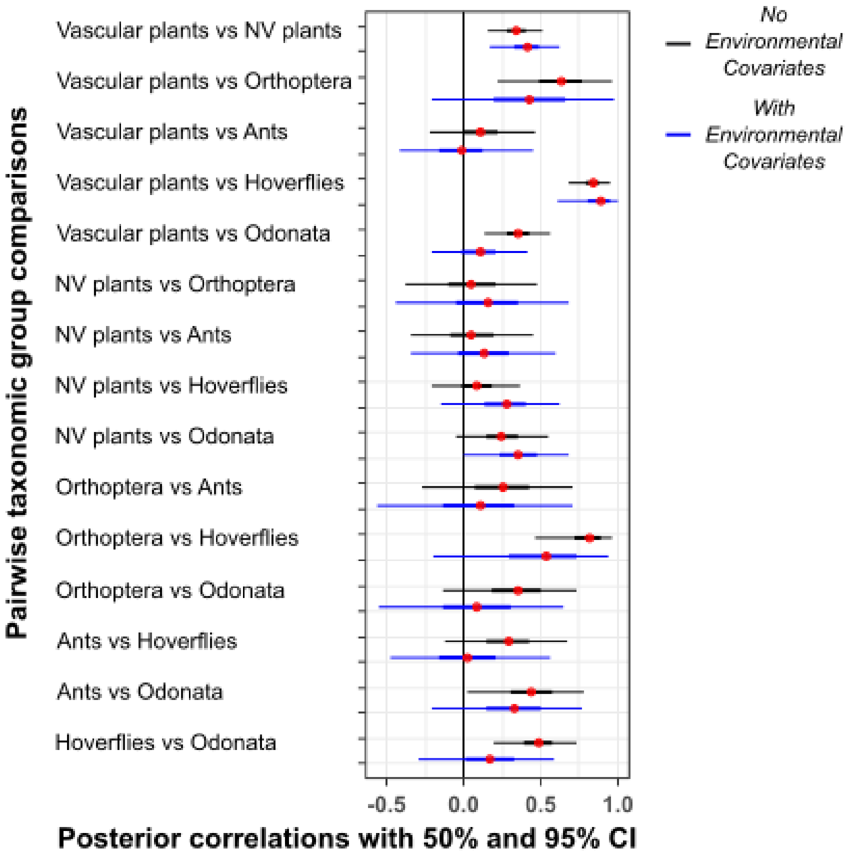

Figure 3.4 Pearson correlations between pairs of taxa in average proportions of species gained vs lost across the sampling compartments of the Studland peninsula between the 1930s and 2010s. Black credible intervals are pairwise correlations derived from a hierarchical logistic regression model including a varying compartment level intercept for vascular plants, varying slopes for the other five taxa, and a random offset for species ID. Blue credible intervals are pairwise correlations from the same model extended to include habitat and environmental change covariates and hence give residual correlations after controlling to some extent for shared responses to environmental changes between time-periods. Correlations were computed over the full posterior distribution of Bayesian models with plot showing medians (red dots), 50% credible intervals, and 95% credible intervals (thick lines and thin lines respectively).

3.5 Discussion

In this chapter, I have shown strong evidence of cross-taxon congruence in species richness and compositional changes in plant and insect communities over a period of *ca.* 80 years. The study system experienced high levels of turnover for all taxa, both within habitat types and across the system as a whole. However, overall species richness did not change substantially for any group at the study system level. Hierarchical model estimates suggest a prominent role for shared responses to environmental change underlying observed congruencies in richness differences at the sampling compartment level. Furthermore, biotic interactions between plants and herbivores were also likely drivers of biodiversity change, as these correlations were stronger than were correlations between plants and non-consumer groups. They were the only correlations to remain positive after accounting for environmental change.

High levels of compositional change are in line with findings from meta-analyses of biodiversity trends over this time period across a wide range of taxa (Vellend et al. 2013, Dornelas et al. 2014, McGill et al. 2015). Proportional changes were remarkably similar for five of the six taxa at the study system level (excluding Odonata), suggesting cross-taxon congruence in compositional change. This result reflects findings of CTC in species composition across spatial extents in contemporary communities (Westgate *et al.* 2014). However care must be taken when comparing raw proportions, as total numbers of species in each group differed. Compositional differences were much more variable within and between taxa within ecological habitat types than at the study system level, which also highlights the importance of scale and habitat classification in studies of cross-taxon congruence (Westgate et al. 2014, Schuldt et al. 2015).

Cross-taxon congruence in sampling compartment level species richness differences was widely prevalent in pairwise comparisons between taxa, adding to the few studies which have documented temporal CTC in biodiversity change. Ewald et al. (2015) found that extreme weather events had interannual effects on abundances in 11 out of 26 insect taxa in a 42 year time-series of insects recorded at genus, family and class level in cereal fields. They also found correlations in temporal abundance trends with temperature and precipitation, and detrimental effects of pesticide use across taxa, which could be interpreted as temporal CTC driven by shared responses to abiotic change. Özkan *et al.* (2014) also reported temporal CTC in phytoplankton and zooplankton, apparently driven by environmental factors and trophic interactions.

HLR models revealed strong congruencies between vascular plants and all other groups except for ants, and pairwise congruencies were stronger between vascular plants and herbivores (hoverflies and Orthoptera) than with other insect groups. Although causation cannot be determined from these results, the fact that this hypothesis was borne out suggests a role for bottom up effects of the plant community on composition of at least these herbivore groups – a finding in-line with previous experimental and observational results (Schaffers *et al.* 2008; Scherber *et al.* 2010; Rzanny *et al*. 2013). This is because I have already shown in chapter 1 that changes in the abiotic environment likely had large effects on plant community composition. However, I can not rule out the possibility of bottom-up causation, or a combination of top-down and bottom-up.

The relationship between vascular plants and hoverfly richness differences was particularly strong, and echoes the national trend over this time-period (Biesmeijer et al. 2006). Adult Hoverflies feed exclusively on nectar and pollen from flowering plants and some species have associations with specific vegetation types while attempting to attract mates (Gilbert and Rotheray 2011). Larva of many species also have trophic associations with particular plant species, either feeding on them directly or searching for invertebrate prey which feed upon them (Almohamad *et al.* 2009), Some plant species may also rely on hoverflies as pollinators

(Rader et al. 2016). Due to the number of potential pathways underlying this correlation more work is needed to determine the nature of underlying mechanisms, which may comprise a combination of the above.

Changes in the abiotic environment likely played a key role underlying observed compositional changes, as soil moisture (EIV F) and light availability (EIV L) were important predictors of species composition across taxa (RDA results). Abiotic environmental forcing is often an important driver of biodiversity change in dynamic environments (Mutshinda *et al.* 2009; Vellend 2016), and hydrology and vegetation structure are both important determinants of plant and invertebrate community composition (De Szalay & Resh 2000; Silvertown *et al.* 2015). As the study system has undergone widespread hydrological change and varying degrees of vegetative succession between the sampling-periods (Carroll et al. 2018), changes in these factors have likely affected which species occupy the study system.

Effects of environmental forcing were further underlined by congruent species richness differences at the sampling compartment level. Controlling for environmental factors broadly reduced model estimates of temporal CTC in species richness differences, suggesting a prominent role for shared responses to environmental change underlying observed congruencies. Abiotic factors drive CTC across contemporary plant and insect communities (Duan et al. 2016), and it is therefore not surprising that environmental changes would have similar effects on temporal richness differences across insect groups.

Non-vascular plants and ants were outliers to some extent in analyses of biodiversity change. Accounting for environmental factors increased congruence estimates between non-vascular plants and all other groups, which may suggest an opposing response to environmental changes when compared with the other taxa, masking temporal CTC in the original correlations (McElreath 2016a). Many non-vascular plant species thrive in wetter conditions (Silvertown *et* *al.* 2015), and increases in soil moisture at Studland (Carroll et al. 2018) may have increased species richness in this group while causing reductions in species richness across other taxa. Meanwhile RDA models described far more variance in ant community composition in the 1930s than in the 2010s (0.18 and 0.1 respectively), and they were also the only group not to display any congruence with vascular plant changes. Widespread gains across the study area made by the now dominant ant species *Formica rufa* may go some way to explain the idiosyncratic trend in this group, as competitive and predatory effects of this species may have had overwhelming effects on ant community structure through dominance hierarchy effects (Halaj and Wise 2001).

When comparing data collected under non-identical sampling regimes biased estimates of ecological phenomena are an inherent danger. This can be due, for example, to differences in sampling effort causing rare or cryptic species to be differentially represented (Chen et al. 2013), or spatiotemporal variance in sampling effort throughout the study area (e.g. (Fithian et al. 2015). By refitting hierarchical models for only species present in 20% or more sampling compartments I have at least partially mitigated such concerns, as cross-taxon correlations computed from these models were very similar to models under the full dataset (see **Appendix 3.**). This convergence of models under full and depleted datasets is likely due to the species level random effect giving less weight to rare and transient species, and estimating correlations between the "average" species within taxa. However, if sampling effort differed among sampling compartments in a consistent manner across taxa, spurious cross-taxon correlations in species loss/gain patterns remain a possibility I cannot rule out.

Assessing the relative contributions of different drivers of biodiversity changes can be difficult, even with good estimates of environmental change at hand, as positively or negatively correlated responses can mask the true nature of relationships (Ranta et al. 2008b). The hierarchical modelling framework used here circumvents this issue by modelling separate intercept and slope parameters for each taxon with associated predictors of taxon-specific effects of environmental change. However, it cannot account for possible effects of missing predictors, and neither can it account for the fact that estimates of environmental change were derived from the plant community. Consistent sampling bias across taxa could also have the potential to produce spurious shared responses to environmental change.

In conclusion, I have shown that congruent biodiversity change occurs across diverse plant and insect taxa, and is likely driven by changes in both abiotic and biotic environmental factors. These drivers do not act independently from one another, as demonstrated by apparent effects of biotic interactions between the plant community and herbivores, which were also responding to abiotic changes. These results therefore strongly point towards the existence of interacting effects of abiotic and biotic drivers on richness and compositional changes across co-occurring taxa. Further, as communities of disparate taxa respond in tandem to environmental change, these results suggest that the wide ranging anthropogenic environmental changes projected to continue throughout the 21st century are likely to have cascading effects on species richness and composition across local communities.

4. Abiotic and Biotic drivers of biodiversity change in a local hoverfly community over an 80-year period

4.1 Abstract

As insect communities adapt to continuing environmental change, component species face distinct ecological challenges as larval and adult individuals. However, a lack of long-term data documenting biodiversity change has meant that studies of community level effects of long-term environmental change are rare. In addition, the consequences of distinct ecological pressures acting on different life-history stages have remained largely unstudied in local insect communities. These species provide vital ecosystem services including pollination, biocontrol and decomposition, and as such, it is important to establish how long-term environmental changes affect temporal biodiversity patterns.

I investigated abiotic and biotic drivers of species richness and species compositional change in a local hoverfly community using the CDP data. I used a hierarchical logistic regression approach at local and wider landscape scales, combined with species level trait data, to examine effects of: *i)* hydrological change; *ii)* biodiversity change in the vascular plant community, and *iii)* ecological habitat type on species losses and gains. A particular emphasis was placed on distinct ecological pressures exerted at larval and adult life-history stages.

I found strong evidence for an effect of hydrological change on hoverfly composition at the peninsula level. Species whose larvae overwinter on or under the ground surface, and are also intolerant to flooding, have largely declined or been excluded from the community. However, more localised changes in soil moisture, indirectly estimated from the plant community (chapter 1), did not predict hoverfly species richness differences in observed adult flies between time-periods. Species richness differences at this localised scale were strongly associated with changes in vascular plant species richness. This effect was likely to have been driven via trophic

interactions between adult flies and the plant community, as there was no clear pattern in species loss/gains in larval feeding guilds. Species richness change in observed adult flies also varied by ecological habitat type, with higher richness in the 2010s in aquatic edge habitat types, and lower richness in marsh habitats. There was a small negative effect of habitat specialisation on hoverfly composition.

Together, these results suggest that species richness in hoverfly assemblages is limited by adult resource availability at highly localised scales, while compositional change is strongly affected by the availability of suitable larval microhabitat at the wider scale of a few kilometres. This work provides a unique empirical example of long-term community change which supports findings in contemporary systems highlighting the need to cater for idiosyncratic needs across the life-cycles of holometabolous insect species at relevant spatial scales under environmental change.

4.2 Introduction

Species richness and composition are undergoing substantial change in modern ecological communities, as human induced pressures cause widespread disturbances across a range of scales and taxa (Thomas et al. 2004, Potts et al. 2010, Barnosky et al. 2011). Mechanisms underlying such biodiversity change within communities can become particularly complex when species have contrasting ecological requirements at different life-history stages (Chesson 2000). Holometabolous insects – with egg, larval, pupal and adult forms – experience specific ecological pressures at each life-history stage, any or all of which can affect long-term abundance of individual species, leading to changes in species richness and composition. These species provide vital ecosystem services including pollination, biocontrol and decomposition, and as such, it is important to establish how long-term environmental changes affect temporal biodiversity patterns (Oliver et al. 2015). However, few studies have examined the effect of long-term change in the abiotic and biotic environment on different life-history stages, and how these impact on local species richness and composition.

There is an argument to suggest that an overemphasis has been placed on changes in species richness within the ecological literature, with too little concern for compositional change (McGill et al. 2015). Both richness and compositional changes can have important implications for ecosystem functioning (Oliver et al. 2015). Thus, as climate and land use changes proceed to alter the environment throughout the 21st century (Foley et al. 2005, Watts et al. 2015), it is important to understand factors affecting which species are recruited and excluded from communities, as well as monitoring the total numbers of species present.

Though there is evidence that declines in species richness have slowed across some holometabolous insect taxa in recent decades across Western Europe (Carvalheiro et al. 2013b), declines persist in many populations (eg. Hallmann *et al.* 2017). Compositional change also prevails in many such communities (e.g. Aguirre-Gutiérrez *et al.* 2016), including evidence for taxonomic homogenisation in some taxa and regions (Eskildsen et al. 2015). However, the full consequences of such change for community structure and functioning are as yet unclear. Establishing the drivers of change across spatial scales, taxa, and life-history stages are important goals to help mitigate effects of impending environmental change.

A multitude of biotic and abiotic drivers can underpin richness and compositional change in holometabolous insect communities. The availability of flowering plants as nectar and pollen food resources is vital for adult individuals of many species (Carvell et al. 2006). Larval individuals may also display strong dependencies on the plant community through direct or indirect trophic interactions; feeding either directly on plants (Gilbert and Rotheray 2011), or on herbivorous insects or microorganisms inhabiting them (Honěk 1983; Almohamad *et al.* 2009).

Habitat specific environmental change can play an important role in determining biodiversity patterns, as species display varying degrees of habitat specialisation (Casey et al. 2015). More resilient habitats with higher complexity may be less susceptible to species losses (Tscharntke et al. 2012). Differing micro- and macro-habitat requirements for adult and larval individuals must also be considered, as changes in either can affect biodiversity trends in differing ways (Moquet et al. 2018).

Another important factor in terrestrial ecological communities is how ecosystems differ along hydrological gradients, as component species will be morphologically adapted to suit specifically wet or dry conditions (Silvertown *et al.* 2015). Thus hydrological change can be an important driver of biodiversity change, to the extent that composition of plant and invertebrate communities is commonly used as an ecological indicator of environmental conditions at a specific location and time (eg. De Szalay & Resh 2000).

Finally, the scale of analysis is a vital factor to be taken into account when inspecting drivers of biodiversity change, as governing processes will act at differing scales (Keil et al. 2011, 2012, Chave 2013). This may be especially true in communities where species display large differences in dispersal abilities at different points in their life-cycle.

Hoverflies (Diptera, Syrphidae) represent an ideal taxon within which to study biodiversity change in holometabolous insect communities, as they comprise a group of species sensitive to all of the prevalent drivers of biodiversity change outlined above, as well as being particularly amenable to analysis with respect to such drivers. This is due to a combination of diverse ecological requirements and relative ease of monitoring within this group (Gilbert and Rotheray 2011), which make hoverflies useful ecological indicators (Sommaggio 1999, Dziock

2006, Burgio and Sommaggio 2007). Further, the diverse ecological requirements of hoverflies resulting from species specific traits and preferences have been particularly well documented, due to a combination of wide ranging academic research and fervent amateur interest in studying and recording (Speight and Sarthou 2014).

Dispersal abilities vary greatly among hoverflies, from highly localised to migratory species, but availability of suitable larval microhabitat and adult resources within 2 to 5 km in the landscape context can have large effects on hoverfly biodiversity (Gatter and Schmid 1990, Schönrogge et al. 2006, Jauker et al. 2009, Rotheray et al. 2014). Adult dispersal abilities are exponentially greater than that of larvae, and as such, larval microhabitat availability across the wider landscape can be an important predicter of hoverfly biodiversity, while adult resources may be more important in the immediate local vicinity, as adult flies can more freely disperse to meet their needs (Moquet et al. 2018). It thus seems clear that a variety of long-term changes across an ecosystem could have wildly differing effects on the biodiversity of subgroups of hoverfly species depending of their larval and adult needs.

The aim of this study was to determine which factors influenced long-term (*ca.* 80 years) species richness and compositional change in local hoverfly communities, particularly in relation to larval and adult ecological requirements. Using CPD species occurrence data, I identified three types of biotic and abiotic environmental drivers likely to affect hoverfly diversity across life-history stages, and asked the following questions to determine their importance:

1) How does hydrological change drive biodiversity change in the hoverfly community? *In chapter 1, I showed that Studland has become wetter across much of its area in the 2010s vs the 1930s. I hypothesised that i) Areas which have increased in wetness would display lower hoverfly species richness in the 2010s than the 1930s via exclusion of*

species susceptible to disturbance by flooding at this scale, and ii) Changes in seasonal hydrology would predict compositional change in hoverflies through exclusion of species susceptible to disturbance by flooding at the larval stage across the wider peninsula.

2) How are long-term changes in hoverfly richness and composition affected by biodiversity change in the local plant community?

   I hypothesised that iii) Reductions in species richness in the hoverfly community would be associated with reductions in vascular plant species richness via trophic interactions between adult hoverflies and their food plants, and iv) Changes in the plant community would affect hoverfly species composition by favouring some larval feeding guilds. Larval feeding guilds are here defined in terms of how larvae directly or indirectly interact (or not) with the plant community. Further, these two components of plant community driven biodiversity change may interact, with species richness in differing larval feeding guilds displaying distinct associations with changes in vascular plant species richness. This interaction is explored as hypothesis v).

3) Do richness and compositional changes in hoverflies differ by ecological habitat type, and by the degree to which hoverfly species specialise on specific habitats?

   I hypothesised that vi) Species richness changes in hoverflies would differ between habitat types, and vii) Habitat generalists would fare better than habitat specialists (compositional change), as their populations would be more robust to habitat specific drivers within the study area.

4.3 Methods

4.3.1 Study Area

The peninsula has undergone considerable and heterogeneous change between sampling-periods driven by hydrological change, vegetative succession and nitrogen deposition, as shown by analysis of differences in mean Ellenberg Indicator Values (EIVs) (Chapter 1). Most notably for the present study, the indicator values for soil moisture (EIV F) have displayed increases across many sampling compartments, particularly in the marsh habitat type, indicating generally wetter conditions in the 2010s compared with the 1930s. I used these EIV F change estimates to test *hypothesis i).*

4.3.2 Data

4.3.3 Hoverfly and plant surveys

Both historical and contemporary surveys aimed to sample and record the full cohort of hoverfly and plant species present in each compartment across the peninsula. This chapter, only sampling compartments for which full species lists for both hoverflies and vascular plants are available in both time-periods were used (Appendix 1).

4.3.4 Hoverfly trait data

To test hypotheses concerning factors driving change in species composition (*Hypotheses ii, iv, and vii*), I compiled hoverfly trait data from the "Syrph the Net" (StN) database (Speight and Sarthou 2014), and "Britain's Hoverflies" (Ball and Morris 2015). Compiled traits describe how individual hoverfly species interact with the biotic and abiotic environment, and aggregate changes in the nature of such traits between time-periods can reveal environmental factors underlying changes in species composition.

To test *Hypothesis ii)* on the effects of hydrological change on larval hoverflies, I classified species as 1) susceptible to, and 2) tolerant of disturbance by flooding. For susceptibility to flooding, I identified species whose larvae are classified as being active on or under ground-surface debris (GS), species whose larvae are active in the root zone of herb layer plants (RZ), and species whose hibernation/overwintering zone is under or in terrestrial ground surface microhabitats (WGS) (Speight and Sarthou 2014). Of these only WGS was a useful predictor in preliminary modelling, so RZ and GS were dropped from the final set of models presented in the results. For tolerance to flooding we used the Inundation tolerance variable (Inun) from the StN database.

To test whether the plant community affected hoverfly composition through larval feeding associations (*Hypotheses iv & v)*), I categorised the hoverfly species present during either or both sampling-periods into six separate larval feeding guilds based on how larvae interact directly or indirectly (or do not interact) with the plant community as follows: 1) Larvae which feed in decaying materials. These are primarily wet adapted and will generally feed around plants at the water's edge; 2) Larvae with direct or indirect trophic interactions with trees. These include species whose larvae feed in sap runs, on tree aphids, or in decaying timber; 3) Larvae which feed on a wide variety of aphids, and therefore are dependent on a wide variety of aphid host plants; 4) Larvae which are generalist ground layer and leaf litter predators, including root aphids; 5) Larvae which are brood parasites of various Hymenoptera 6) Larvae with species-specific associations with plants on which they feed directly. I used both StN and "Britain's Hoverflies" to derive these associations.

I used the total number of broad habitat types hoverfly species were associated with (Speight and Sarthou 2014) (StN database) as a measure of habitat specialisation to test *Hypothesis vii)*. Habitat specialisation may be due to associations between hoverfly species and specific habitats at larval or adult stages of development, or both. This numeric variable was standardised for use as a predictor in models described below.

4.3.5 Statistical methods

4.3.5.1 *Hierarchical logistic regression*

To assess the influence of factors on changes in species richness and composition across the hoverfly community of Studland, I used Bayesian hierarchical logistic regression (HLR) models. I subset the cohort of species from each sampling compartment representing biodiversity change by extracting just species lost or gained between sampling-periods, and coding them as 0's and 1's respectively to use as a response variable. This allowed me to use grouping factors of sample compartment and species ID as random offsets in HLR models to quantify the probability that a species was gained rather than lost on average in a given compartment, or that a given species was gained rather than lost on average across the study area respectively.

Compartment-level gain/loss probabilities are directly proportional to changes in species richness at this scale, and thus factors affecting these probabilities will be associated with hoverfly richness change within sampling compartments across the study area (*figure 2.1*). Similarly, factors affecting species-level gain/loss probabilities are those contributing directly to compositional change, as species losses and gains directly change composition in the hoverfly community. Compositional changes linked with species specific traits in these models concern the wider scale of the whole peninsula, as they relate the proportion of sampling compartments across the peninsula in which a species was lost or gained to trait values across species (*figure 2.1*).

I specified a baseline model with the species gain/loss response variable, and varying offsets for sample plot and species ID as follows:

Eqn 1

$$Gain\backslash Loss_i \sim Bernoulli(p_i)$$

$$logit(p_i) = \alpha^0 + \alpha_{j\,[i]}^{Plot} + \alpha_{k\,[i]}^{Species}$$

$$\alpha_j^{Plot} \sim Normal(0, \sigma_{Plot})$$

$$\alpha_k^{Species} \sim Normal(0, \sigma_{Species})$$

α^0 here is a global intercept, with α_j^{Plot}a varying offset for sampling compartments, and $\alpha_k^{Species}$ a varying offset for species. σ_{Plot} and $\sigma_{Species}$ are residual variance parameters for plot and species intercepts respectively.

To test hypotheses relating to factors driving species richness and compositional changes in the hoverfly community I extended the compartment-level and species-level submodels respectively to include the relevant predictors. The compartment-level submodel was extended as

Eqn 2

$$\alpha_j^{Plot} \sim Normal(\mu_j^{\alpha^{Plot}}, \sigma_{Plot})$$

$$\mu_j^{\alpha^{Plot}} = X * Beta\_plot$$

Where $\mu_j^{\alpha^{Plot}}$ replaces 0 as the mean value of the compartment offset, and is a product of the predictor for compartment j (X) and the estimated predictor coefficients ($Beta\_plot$).

The species-level submodel was extended as

Eqn 3

$$\alpha_k^{Species} \sim Normal(\mu_k^{\alpha^{Species}}, \sigma_{Species})$$

$$\mu_k^{\alpha^{Species}} = X * Beta\_species$$

Where $\mu_k^{\alpha^{Species}}$ replaces 0 as the mean value of the species offset, and is a product of the predictor for species k (X) and the estimated predictor coefficients ($Beta\_species$).

Q1. Effects of hydrological change on hoverfly diversity

To test *Hypothesis i)*, that compartment level hoverfly species richness was affected by changes in soil moisture at that scale, I included a standardised predictor for compartment level EIV F estimates derived from chapter 1 to the compartment-level submodel (M4.1). To test *Hypothesis ii)*, that changes in seasonal hydrology would predict hoverfly compositional change I included binary categorical predictors to the species-level submodel (Eqn 3) for species whose larvae overwinter at ground surface level (WGS), and for larval inundation tolerance, as well as an interaction term between these two variables (M4.2).

Q2. Effects of the plant community on hoverfly diversity

To test *Hypothesis iii)*, I expanded the compartment-level submodel (Eqn 2) to include the standardised difference in plot-level plant species richness, derived from the "Cyril Diver Project" data, as a continuous predictor variable (M4.3).

In Chapter 2 I found a strong correlation between species richness change in the hoverfly and plant communities of Studland, which suggested the possibility of a direct biotic interaction between these taxa. There may be a number of drivers behind this correlation, including trophic dependencies of adult hoverflies feeding on nectar and pollen, other species-specific hoverfly/plant associations like use as larval feeding sites, or unquantified shared responses to environmental change. To assess whether the trophic association of adult hoverflies was the dominant factor, I fitted the model described in *Eqn 2* using two separate plant species richness predictor variables; one with all plant species included ($PlantSP\_richDiff\ (A)$), and another with only plant species suitable for use as adult hoverfly food sources ($PlantSP\_richDiff\ (B)$). I postulate that if the relationship were primarily due to the adult hoverfly trophic dependencies $PlantSP\_richDiff\ (B)$ would explain a higher proportion of variation given that a significant relationship is found. However, this was not the case, as R^2 values for plot level submodels were higher in every instance for models including $PlantSP_{richDiff}(A)$ rather than $PlantSP\_richDiff\ (B)$. In the remainder of the manuscript I present results for models including $PlantSP\_richDiff\ (A)$.

To test *Hypothesis iv)* I included plant related larval feeding guild as a categorical predictor to estimate a varying intercept for this factor (M4.4). To test *Hypothesis v)* I extended this varying intercept model to also include a slope parameter which also varied by plant related larval feeding guild, in which the correlation was also modelled between the varying intercept and slope parameters (M4.7). This model was fitted using a non-centred parameterisation with the rethinking package in R, following McElreath (2016).

Q.3 Effects of Ecological Habitats on hoverfly diversity

To test *Hypothesis vi),* assessing the effects of the habitat type a compartment occupied on changes in hoverfly species richness, I included a variable offset for habitat type as a categorical predictor in the compartment-level submodel (Eqn 2, M4.8). To test *Hypothesis vii)* that habitat generalists would do better than habitat specialists I extended the species-level submodel *(Eqn 3,* M4.9*)* to include the predictor for standardised number of broad habitats a species is associated with.

Models with overlap between questions

As well as the models described in preceding subsections alluding to our specific questions, I present three models with parameters including overlap between questions, in order to assess potential confounding effects of predictors on one another. These were i) a model including the standardised difference in plot-level plant species richness and an offset for habitat type; ii) a model including the standardised difference in plot-level plant species richness and the soil moisture proxy (EIV F), and iii) a model including the plant related feeding guild offset and the predictors for *Hypothesis ii)* on the effects of seasonal hydrology (M4.11, M4.12 and M4.13). Finally, I fitted a “full” model including all predictors except the soil moisture proxy (EIV F), as this was not a useful predictor in any model fitted (M14).

4.3.6 Software and model evaluation, comparison and validation

Hierarchical logistic regression models were fitted using the probabilistic programming language stan with package RStan in R version 3.5.0 (R Core Team 2018, Stan Development Team 2018a). Models were evaluated using a combination of loo information criteria and inspection of parameter values. Loo is a form of information criteria based on leave one out cross validation, which can be used in a similar manner to the classic AIC whereby a smaller loo value indicates a better fitting model (Vehtari *et al.* 2017). All model comparisons were contrasted with the baseline model in ***Eqn 1***, as any simpler model without plot and species level offsets would have suffered from pseudoreplication. Parameters were evaluated by conducting a Bayesian analogue to significance testing using means and central 95% percentiles of the posterior parameter samples as Bayesian credible intervals (CRI) (Chen et al. 2013). I assessed the utility of group level parameters by computing explained variance for plot and species level submodels ($R^2_{richness}$ and $R^2_{composition}$ respectively) (Gelman and Pardoe 2006). Model validation was performed using posterior predictive checks and examination of mean residuals.

4.4 Results

4.4.1 Results overview and model comparisons

Hoverfly species richness largely decreased across the study area, with more species losses than gains recorded in in 23 of the 34 sampling compartments. Compositional change was high within every sampling compartment, with a minimum proportional change in species composition of 0.64, and 13 out of 34 compartments where the identity of every species recorded differed between the two time-periods. All these compartment-level losses and gains culminated in 30 species being lost and 25 gained across the whole study system out of 109 total species found in both time-periods combined (as was reported in chapter 3). These 109 species represent a substantial proportion of the roughly 270 hoverfly species found in the UK.

Changes in the plant community, hydrology and ecological habitats of Studland all contributed to change in the hoverfly community; as assessed via loo information criteria, Bayesian R^2 values and inspection of model parameters (*table 4.1*). Effects of changes in the plant community on local hoverfly richness (*Hypothesis iii), M4.4 table 4.1*) had the greatest predictive utility from a model concerning a single hypothesis, with a Δloo of 3.8 and a $R^2_{richness}$ value of 0.44. This was closely followed by the effects of hydrological change on hoverfly composition across the wider peninsula (*Hypothesis ii*, *M4.2 table 4.1*; Δloo of 3.4 and $R^2_{composition}$ of 0.11).

In general, effects of changes in the plant community and hydrological change were more useful predictors of hoverfly richness and compositional change than ecological habitat type, though habitat level effects were also apparent (*table 4.1*). The full model including all predicters (except EIV F) was by far the best model for out of sample predictive performance and explained variance (R^2), with a Δloo of 10.2 (M4.14 *table 4.1*). However, it should be noted that while parameter estimates obtained from the full model were generally similar to those of simpler models, the estimate of the global intercept was highly uncertain due to collinearity with mean parameters for habitat and feeding guild offsets. This resulted in wide uncertainty intervals from the full model when uncertainty in the intercept was included.

Table 4.1 Summary of fitted hierarchical logistic regression models with plot-level submodels describing changes in species richness and species-level submodels describing changes in species composition between sampling-periods in the 1903s and 2010s. Whether changes are driven by ecological pressures at larval or adult stages is shown where possible.

Model	Predictors	Adult / Larva	Richness / Composition	$R^2_{richness}$	$R^2_{composition}$	looic	Δloo
Baseline model							
M0	*NA*	**A + L**	**NA**	**-**	**-**	**452.4**	**-**
***Q1.** Hydrological change effects models*							
M4.1	*EIV F*	A + L	Rich	0.05	-	452.7	0.3
M4.2	*Hydro*	L	Comp	-	0.11	449	-3.4
M4.3	*EIV F, Hydro*	A + L	Rich + Comp	0.05	0.11	449.8	-2.6
***Q2.** Plant community effects models*							
M4.4	*PLNT.A*	A	Rich	0.44	-	448.6	-3.8
M4.5	*F.guild*	L	Comp	-	0.06	450.6	-1.8
M4.6	*F.guild + PLNT.A*	A + L	Rich + Comp	0.44	0.06	447.4	-5
M4.7	*F.guild X PLNT.A*	A + L	Rich + Comp	NA	NA	447.1	-5.3
***Q3.** Habitat effects models*							
M4.8	*HAB*	A + L	Rich	0.4	-	450.5	-1.9
M4.9	*Hab.gen*	A + L	Comp	-	0.03	449.8	-2.6
M4.10	*HAB, Hab.gen*	A + L	Rich + Comp	0.4	0.03	448.4	-4
***MISC.** Models with overlap between questions*							
M4.11	*PLNT.A, HAB*	A + L	Rich	0.7	-	446.4	-6
M4.12	*EIV F, PLNT.A*	A + L	Rich	0.42	-	450.1	-2.3
M4.13	*F.guild, Hydro*	A + L	Comp	-	0.16	449.2	-3.2
Full model							
M4.14	*NA*	**A + L**	**Rich + Comp**	**0.69**	**0.16**	**442.2**	**-10.2**

4.4.2 *Q1)* Effects of hydrological change on hoverfly richness and composition

4.4.2.1 *Hypothesis i) Effects of local soil moisture changes on hoverfly species richness*

Changes in soil moisture as measured by the Ellenburg Indicator Value proxy (EIV F) had no effect on hoverfly species richness differences at the level of sampling compartment (Mean parameter estimate = -0.96, 95% Bayesian CRI = -2.45 to 0.52). This null effect was further highlighted when the EIV F predictor was included in a model which also included the plant species richness difference predictor (M4.12, Mean parameter estimate = -0.15, 95% Bayesian CRI = -1.43 to 1.16), as the parameter centred even more closely on a value of zero. This suggests that any apparent effect of soil moisture was probably due to confounding effects of losses of plant species.

4.4.2.2 *Hypothesis ii) Effects of hydrology on hoverfly composition via larval exclusion*

Changes in hydrology across the study area showed a clear influence on changes in hoverfly species composition between the two time-periods (*figure 4.1*). Species which are active on the ground surface during winter, and are also inundation intolerant, displayed clear proportional declines between time-periods, while species in the other three flood susceptibility/tolerance categories showed no distinct trends ($R^2_{composition}$ = 0.11, *figure 4.1,* Blue shaded uncertainty intervals). This effect was maintained in model M4.13 including offsets for plant related larval feeding guilds (*figure 4.1,* Grey shaded uncertainty intervals), and in the full model M4.14. While R^2 value for the hydrological hypothesis is smaller than for plant effects, it is explaining a smaller proportion of a larger variability in species level effects vs compartment level effects.

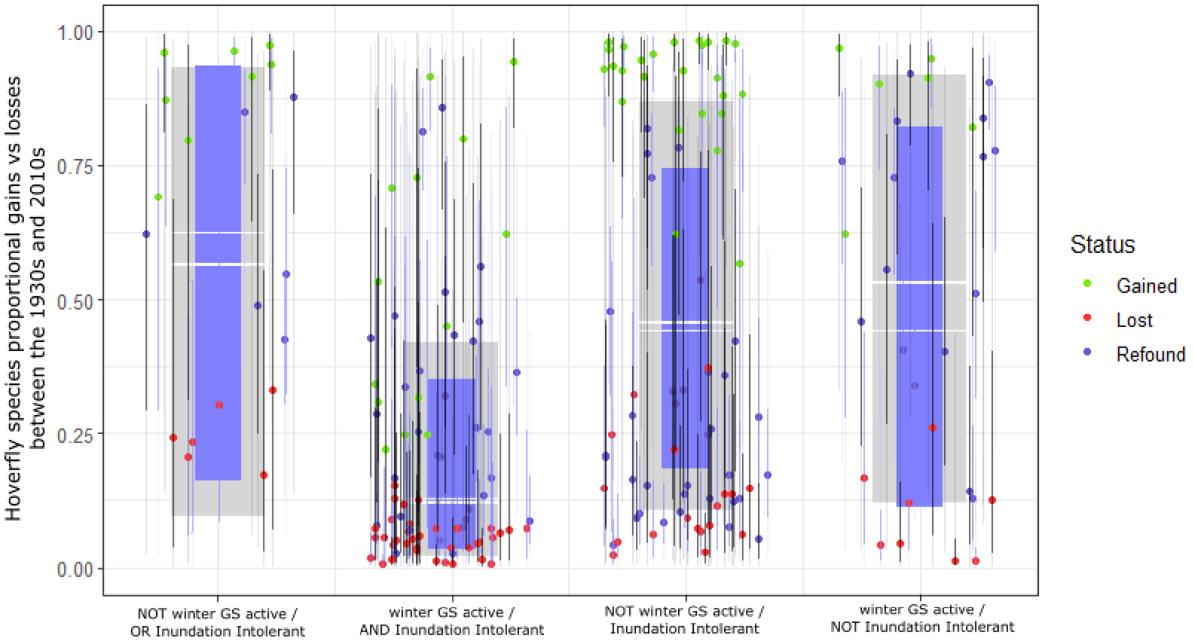

Figure 4.1 Effects of hydrological change on hoverfly species composition across the Studland peninsula between sampling-periods in the 1930s and the 2010s. Species are divided into four categories depending on whether they overwinter on/under the ground surface and whether they tolerant of flooding (inundation) or not. Posterior distributions are displayed for Bayesian hierarchical logistic regression models with i) just hydrological hypothesis predictors (95% uncertainty interval as blue shaded region and thin white line as median estimate), and ii) hydrological hypothesis predictors and an offset for species' plant related larval feeding guilds (95% uncertainty interval as grey shaded region and thick white line as median estimate). Species intercepts (with 50% (unshaded) and 95% (shaded) uncertainty intervals) show the probability a species was lost or gained across the study area for species which were gained (green), lost (red), or found in both time-periods (blue) within the peninsula between time-periods. Species which overwinter on or under the ground surface, but which are not inundation tolerant were largely excluded by the 2010s

4.4.3 *Q2)* Plant community effects on hoverfly richness and composition

4.4.3.1 *Hypothesis iii) Effects of plant species richness difference on hoverfly richness*

Species richness differences in hoverflies had a strong association with richness differences in vascular plants using both $R^2_{richness}$ and Δloo criteria, bearing out our *Hypothesis iii)* (M4.4, *table 4.1*). This relationship remained strong and positive when estimated from models M1 with only the plant species richness difference predictor (*figure 4.2*, blue shaded region, Mean slope parameter = 1.29, 95% Bayesian CRI = 0.68 to 1.93), and the full model M4.14 (*figure 4.1*, grey shaded region, Mean slope parameter = 1.34, 95% Bayesian CRI = 0.71 to 2.01).

A compartment level increase of 1 standard deviation of plant richness differences across compartments (41 plant species) equated to an increase in the proportion of hoverfly species gained, rather than lost, of approximately 0.3 around the midrange. Though the slope estimate remained approximately the same under models M4.4 and M14, compartment level proportional gain estimates were invariably higher from M14 (faded blue intervals, *figure 4.2*) compared with M4.4 (black intervals, *figure 4.2*). This is because estimates displayed from M4.14 are counterfactual estimates after accounting for detrimental effects of hydrological change (see section 4.5.2.2 above). The wide uncertainty interval around the regression line of M4.14 in *figure 4.2* is an artefact of uncertainty in the global intercept of this model rather than the slope parameter.

Figure 4.2 Association between hoverfly species richness differences and vascular plant species richness differences in sampling compartments between sampling-periods in the 1930s and 2010s. Regression lines (with 95% uncertainty intervals) show relationship between the standardised difference in plant species richness and the proportion of hoverfly species gained vs lost from a given compartment (logistic scale) from hierarchical logistic regression models with i) just plant richness difference predicter (Thick line, Blue shade, M4.4), and ii) all predictors (Thin line, Grey shade, M14). Compartment-level intercepts from models M4.4 (black intervals) and M4.14 (shaded intervals) are also shown on the logistic scale (with 50% uncertainty intervals), and the associated proportional gain vs losses are shown on the right axis. Intercepts above proportion of 0.5 on right axis represent compartments which have gained more species than they've lost. Absolute values for plant species richness differences are shown on the top axis for clarity. Compartment intercepts are coloured by ecological habitat type.

4.4.3.2 *Hypothesis iv) Larval related plant community effects on hoverfly composition*

Of the six plant related larval feeding guilds of hoverfly species, three saw notable overall proportional declines across the study area between sampling periods; generalist ground predators, Hymenoptera nest parasites and herbivores of specific plant species (*figure 4.3* A, M4.5). Of these three groups, generalist ground predators showed the strongest evidence for declines, with the full 95% CI lying below 0.5 proportional gains, while the 95% CI's of the other two crossed 0.5, indicating small probabilities of proportional gains (*figure 4.3.* A, M4.5). However, once species level predictors for the hydrological effects of ground surface winter activity and inundation tolerance were added (*Hypothesis ii)*), model estimates of proportional losses in generalist ground predators and herbivores of specific plant species were negated (*figure 4.3* A, M4.13), suggesting that these effects were confounded and actually due to flooding of these species' larval habitat. This was also true, though to a slightly lesser extent, for Hymenoptera nest parasites. Wet adapted species and those with larvae associated with trees showed the least evidence of declines (*figure 4.3* A).

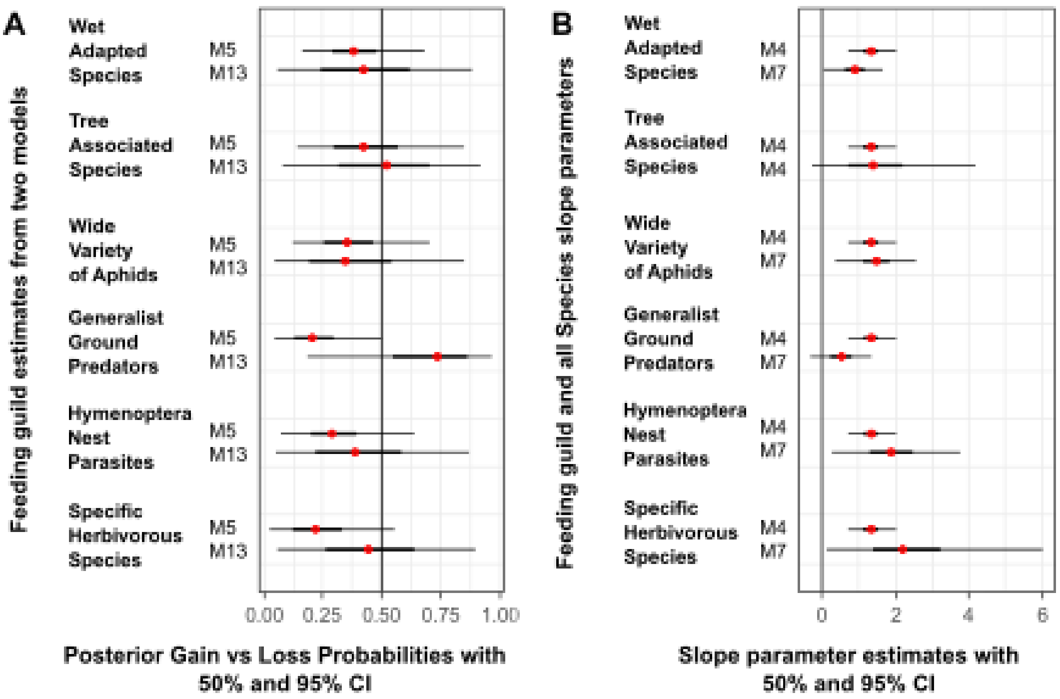

Figure 4.3 Effects of plant related larval feeding guilds on proportions of hoverfly species gains vs losses on the Studland peninsula between the 1930s and 2010s. A) Proportions of species gained vs lost in sampling compartments at the peninsula level in hierarchical logistic regression models including just the feeding guild offset (M5), and species level predictors for inundation tolerance and susceptibility (M13). B) Association between hoverfly species richness differences and vascular plant species richness differences in sampling compartments between sampling-periods on average across feeding guilds (M4, constant), and broken down as slope parameter varying by plant related larval feeding guilds (M7).

4.4.3.3 *Hypothesis v) Interacting effects of plant community change*

When broken down by plant related larval feeding guilds, all groups retained positive median associations with species richness differences in the vascular plant community at the sampling compartment level (*figure 4.3* B). However, the posterior slope estimated for the relationship with plant richness differences displayed some negative probability for the generalist ground predator guild (Mean estimate = 1.34, 95% Bayesian CRI = 0.71 to 2.01), which suggests that wider species losses in this group driven by hydrological change (section 4.5.2.2 above) may have overridden effects of plant diversity. Interestingly, the other guild to show a slightly more negative relationship with plant richness differences than the average (*figure 4.3* B, M4.14) across guilds were wet adapted species, while uncertainty ballooned in estimates for tree associated species and herbivores of specific plant species.

4.4.4 Q3) Effects of habitat type on hoverfly richness and composition

4.4.4.1 *Hypothesis vi) Effects of ecological habitat type on hoverfly richness*

Ecological habitat type was a strong predictor of compartment-level hoverfly species richness change both before and after including the effects of plant species richness differences (*table 4.1, M4.8 before plant richness difference, M4.11 after plant richness difference)*. The most notable habitat differences were a strong positive richness increases in aquatic edge habitat type, and a strong negative offset in the marsh habitat type, where all 11 compartments saw reductions in species richness (*figure 4.4*). While the woodland compartments also saw reductions in hoverfly richness in every sample plot, the mean offset for this habitat type shifted towards zero when plant richness differences and habitat type were included in the same model, suggesting that species richness loss may be largely due to reduced flower availability in this habitat type. The reverse was true in Dune heath, and to a lesser extent in the Heath habitats, where the effect of plant species richness differences may have masked a decline in hoverfly richness (McElreath 2016a).

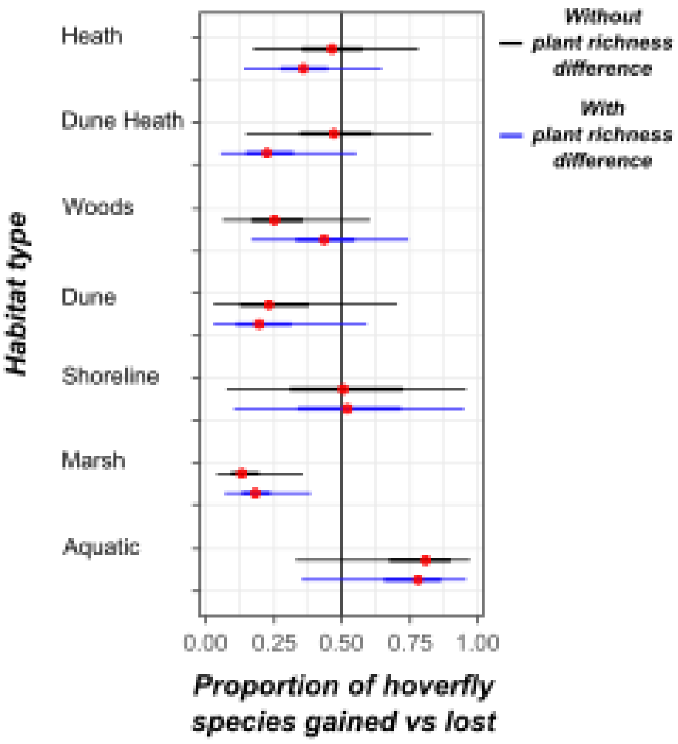

Figure 4.4 Proportion of hoverfly species gained vs lost in sample plots in different ecological habitat types between sampling-periods in the 1930s and 2010s from hierarchical logistic regression models including (blue) and not including (black) predictors for change in vascular plant species richness. Thick lines represent 50% Bayesian uncertainty intervals, thin lines represent 95% uncertainty intervals, and red dots the medians of posterior distributions of effects.

4.4.4.2 *Hypothesis vii) Effects of habitat specialisation on hoverfly composition*

We found no support for *Hypothesis vii)* that habitat generalists would fare better than habitat specialists, in fact the relationship went in the opposite direction, though it was not significant at the 95% level (mean parameter estimate -0.5, 95% CRI = -1.18 to 0.14). However, a *Δloo* of -2.6 compared with the baseline model suggests that there may be some predictive power in this relationship (*table 4.1.*). Its possible that wetter conditions favoured species which specialise in fewer wetter habitats over more generalist species, as this effect centred further towards zero in the full model (M14 Appendix 4.1 *fig Hab Gen/Spe*)).

4.5 Discussion

Long-term changes in hoverfly species richness were strongly associated with changes in species richness in the vascular plant community across the sampling compartments of Studland. However, when species were categorised into plant related larval feeding guilds there was limited evidence of differing associations with plant species richness between guilds. This suggests that the association between plant and hoverfly richness differences is largely due to forces acting on adult flies. At the larval level, it appears that annual winter flooding by the 2010s – compared with the 1930s – has been a strong driver of compositional change across the wider peninsula. However, effects of hydrological change were not observed in more localised assemblages of observed adult flies in sampling compartments, with no association between adult hoverfly richness differences and approximated changes in soil moisture (via *EIV F*) at this scale. Together, these findings suggest that species richness in adult hoverfly assemblages is limited by adult resource availability at highly localised scales, while compositional change is strongly affected by the availability of suitable larval microhabitat at the wider scale of a few kilometres.

Wetter winter conditions in 2010s vs 1930s appear to have strongly driven compositional change at the peninsula level via the exclusion of maladapted larval flies (*Hypothesis ii)*), though increases in soil moisture levels had no apparent effect on observed adult species richness at the more localised scale of sampling compartments (negating *Hypothesis i)*). However, this assertion is derived only from the differential success of species with suitable traits and behaviours to exploit such conditions, and not from direct data on changes in hydrological conditions. In the Studland study system, species which are both susceptible to, and intolerant of, flooding have largely declined, suggesting wetter ground-surface conditions during winter months in the 2010s compared with 1930s. Species composition in invertebrate communities – particularly hoverflies – has been widely used as an ecological indicator

(Sommaggio 1999, Burgio and Sommaggio 2007), and here I have provided another method to do so in areas which have experienced hydrological change by combining species occurrence and trait data.

This indirect indication of wetter conditions in the 2010s vs the 1930s is in agreement with inferences based on the plant community across large swathes of the peninsula over the same period, particularly in the marsh habitat (Chapter 1; Carroll *et al.* 2018). However, the non-association between local hoverfly richness and changes in soil moisture at the more localised scale of sampling compartments seemingly points toward differing scales at which hydrological processes underlying biodiversity change have acted on larval and adult flies. Further, though much of the peninsula has gotten wetter in the intervening period, large sections have also retained similar levels of wetness, and some have even become drier (REF: Carroll et al. 2018). The present result would therefore suggest that many species lost had larvae reliant on the now wetter marsh habitats, otherwise the result would be called into question. Unfortunately species were not sampled at the larval stage in either time-period to verify or disconfirm this.

Strong associations between changes in hoverfly species richness and local richness differences in the vascular plant community is consistent with *Hypothesis iii*) which posited a trophic association with the plant community driving long-term changes in hoverfly species richness. However, while the trophic link may have contributed to hoverfly richness differences, the fact that richness differences with models including all plant species produced higher explained variance that models with hoverfly pollinated species suggests that it is not the sole underlying driver. Model estimates of proportional changes in both vascular plant and hoverfly species richness both displayed temporal autocorrelation and this may have contributed to the vascular plant richness effect (see Appendix 5.). It is also possible that sampling issues could have played a role. For instance, if both hoverflies and vascular plant sampling efforts were spatially biases in a similar way, this could manifest as an association in model estimates. However, it seems unlikely that this would be solely responsible for such a strong and consistent effect.

The association between hoverfly and plant species richness change mirrors national trends in the UK and Netherlands over the same period, where hoverflies and out-crossing plant species relying on insect pollination have declined in parallel (Biesmeijer et al. 2006). Further, I found only limited evidence of differences in local richness – or wider compositional changes – among plant related larval feeding guilds (*Hypotheses iv) & v)*), particularly once the above-mentioned effects of winter flooding had been accounted for. This result adds credence to the likelihood that the association with plant richness differences was driven by processes acting on adult rather than larval flies.

Species richness in contemporary hoverfly communities is also positively associated with floral resource diversity (Meyer *et al.* 2009), but there may be a number of mechanistic causes underlying trophic links between adult flies and the plant community. Morphological differences in feeding apparatus can lead pollinating species to specialise on differing groups of plant species, and thus increases in floral diversity may increase the probability that more hoverfly species' preferred food plants are present (Branquart and Hemptinne 2000). Temporal niche complementarity can also be an important factor, whereby the flight periods of different species are staggered throughout the year, overlapping flowering periods of differing plant species (Martínez-Falcón *et al.* 2011). Such temporal niche complementarity in floral exploitation is also common in other holometabolous insect groups including bees (Dante *et al.* 2013; Scriven *et al.* 2016), and may be a vulnerability under future climate change if the phenology of insect species and their host food plants diverge (Watt and McFarlane 2002, Thuiller et al. 2008, Wolkovich et al. 2012). It is also possible that local hoverfly richness in our study system was limited by more direct interspecific competition for fewer floral resources, though this was unmeasured here.

The dichotomy of scale suggested between adult food resources limiting highly localised species richness differences and changes in larval microhabitat availability due to flooding altering species composition at wider spatial scales closely mirrors contemporary findings on hoverfly biodiversity in Belgian heathlands (Moquet *et al.* 2018). There, species richness decreased with distance to larval habitat and increased with floral density, but distance to larval habitat was relevant at the landscape scale, while floral density was relevant at the scale of sample plots. Not only did analyses reveal the potential for differing effects of scale between adult floral resource limitation and hydrology related larval conditions, but within the hydrological analyses local richness in observed adult flies was not at all influenced by adjacent wetter conditions, even though the amalgamation of such local wetter conditions clearly influenced composition across the wider community. Biodiversity change in Dutch and UK hoverfly communities more generally over the time-scale of this study was scale dependent, local environmental changes thought to be important for hoverfly diversity dynamics (Keil et al. 2011). This chapter sheds further light on such dynamics, and highlights the way in which dispersal abilities at differing life-history stages contribute to biodiversity patterns across a landscape.

It is also possible that differences between habitat types in hoverfly species richness change at Studland (*Hypothesis v)*) were due to changes in availability of larval microhabitats among habitats (e.g. fallen trees (Rotheray et al. 2014), hymenopteran nests), which operate at a scale intermediate between sampling compartments and the whole peninsula in this study system. Aquatic habitat compartments were less saline in the 2010s vs the 1930s (Chapter 1), and also saw large gains in hoverfly species richness, which may be partly due to less saline conditions being more suitable for aquatic larvae. Further, it is possible that processes linking plant related larval feeding guilds to hoverfly biodiversity change operate at this intermediate scale between sampling compartments and the whole peninsula level, though this is speculative without further investigation.

In conclusion, long-term changes in hoverfly species richness were strongly associated with changes in species richness of the vascular plant community, likely due to a trophic link with adult flies; while composition was influenced by changes in seasonal hydrology excluding species with larval individuals exposed to, and unsuited for, wetter conditions. This chapter provides evidence for two mechanisms for how resource limitation and environmental change act at contrasting life-history stages to determine overall diversity in hoverfly communities: 1) a strong influence of adult resource limitation on species richness at highly localised scales; 2) marked effects of larval microhabitat availability on community composition at a broader scale of a few kilometres. As a charismatic and popular species group with well understood microhabitat requirements and relative ease of monitoring, hoverflies should increasingly be used as ecological indicators in the face of future environmental change, and I have highlighted another method by which to do so. This work provides a unique empirical example from long-term community change which supports findings in contemporary systems highlighting the need to cater for species idiosyncratic needs across the life-cycle at relevant spatial scales.

5. Projecting effects of local management interventions under three regional metacommunity scenarios using a Bayesian Belief Network

5.1 Abstract

In order to restore and conserve ecological networks, practitioners need both to provide strong management and maintenance of ecosystems at local scales and maintain connectedness between ecological communities. However, conservation managers can often find themselves in the position of making decisions with limited empirical data to inform quantitative models on processes affecting populations and communities. As a result, semi-quantitative techniques for producing predictive models to inform management decisions, integrating whatever data are available, can be important tools.

Here, I use a recent adaptation of classical Bayesian Belief Networks (BBNs), synthesising results from previous data chapters and information from peer-reviewed literature to project probable outcomes of management on future biodiversity trends at Studland under three regional metacommunity scenarios. I investigate potential effects of management on species richness of plants and insects in functional groups and broad ecological habitats. I examine three broad categories of management intervention: 1) Increased drainage to influence hydrology; 2) Management of sika deer and cattle grazing, and; 3) Artificial disturbances induced to slow down ecological succession. I project the effects of these local management interventions under three regional scenarios in which metacommunity richness and connectivity are assumed to be stable, in decline or increasing respectively.

Under the assumption of a stable metacommunity, BBN models projected modest probabilities of increasing species richness in functional groups and ecological habitats for all three management intervention strategies. The only exceptions were projected reductions in richness of wetland species in scenarios increasing drainage to reduce flooding, and reductions in

richness in woodland habitats in scenarios in which ecological succession was curtailed. However, projections of positive probabilities of increasing species richness under local management were small in comparison to effect of regional metacommunity. Scenarios in which the regional metacommunity was assumed to be deteriorating or increasing in connectivity and richness, predicted widespread declines and increases in biodiversity respectively no matter what local management was included.

These results suggest that the range of local management strategies explored here can provide useful contributions to biodiversity conservation and management at Studland. Increased drainage is predicted to increase species richness across the plants and insects of Studland if past trends are reversible. However, such increases would come at the expense of wetland species, and the potential of losses of priority species should be weighed up before implementing this management practice. Management to control grazing and succession could also have beneficial effects, but without any specific losses foreseen. However, BBN projections also highlight the crucial importance of maintaining the health of the regional metacommunity in order to maintain a healthy local system, as local practices were negligible in comparison with metacommunity effects. Therefore it seems that effective conservation on Studland can only be achieved in conjunction with responsible regional practices.

5.2 Introduction

Although the international community has begun taking steps to assuage human induced biodiversity declines, collectively we are falling short of stated targets both within nations and internationally (Tittensor et al. 2014). Downward trends are pervasive across taxa and regions (Chamberlain *et al.* 2000; Dunn *et al.* 2009; Barnosky *et al.* 2011; Ceballos *et al.* 2017), but there is mounting evidence to suggest that insects are facing even more serious declines than vertebrates and plants (Thomas et al. 2004, Dirzo et al. 2014, Sánchez-Bayo and Wyckhuys 2019). Insect declines have the potential to cause cascading effects across ecosystems via collapses of trophic and mutualistic interaction networks (Kiers et al. 2010, Sánchez-Bayo and Wyckhuys 2019), and may also interrupt vital ecosystem services including decomposition and pollination (Oliver et al. 2015). System specific projections of biodiversity trends in insects are therefore urgently needed to inform local management for conservation, as are projections for the plants upon which they depend. In preceding chapters I used compositional change in plant and insect communities to infer how abiotic and biotic changes have driven biodiversity change across the Studland peninsula (chapter's 2-4). Here, I synthesise these results, in combination with information from peer-reviewed literature, to project possible outcomes of management strategies on the future health of plant and insect biodiversity across Studland.

Effective management for conservation is difficult to implement, and although management strategies informed by data intensive studies are highly desirable (e.g. Gormley *et al.* 2012), high quality, systematically collected data are not always available to inform quantitative models. As a result, techniques to produce predictive models integrating whatever eclectic data are available to inform management decisions are potentially very useful. A recent adaptation of classical Bayesian Belief Networks (BBNs) for ecological systems is one such method (Stafford et al. 2015). This approach allows for the combined use of data – sparse or otherwise – along with expert opinion and results derived from the scientific literature, to project scenarios with which to inform management for conservation (Spiers et al. 2016, Stafford et al. 2016).

A review of the state of England's wildlife sites reported in 2010 made clear the need to both provide strong management and maintenance of ecosystems at local scales, and to maintain connectedness between ecological communities, in order to restore and conserve ecological networks in the UK (Lawton et al. 2010). Results from preceding chapters have identified a number of local abiotic and biotic drivers of biodiversity change in the plant and insect communities of Studland between the 1930s and the present day (Ref: Ch's 1-3). These provide a strong foundation upon which to parameterise BBN models to project future trends in species richness across the taxa and habitats of Studland under proposed management interventions. High rates of observed turnover across taxa recorded by the Cyril Diver Project also highlighted the relevance of dispersal from the surrounding metacommunity for species to exploit ecological opportunities presented in the face of local environmental change over this time-scale. Given that habitat fragmentation across landscapes is a serious and pervasive driver of biodiversity declines in plant and insect taxa (Thies *et al.* 2008; Potts *et al.* 2010), BBN projections should also take potential trajectories of the surrounding metacommunity into account.

The aim of this chapter is to project possible biodiversity outcomes for Studland under proposed local management implementations, under scenarios where the regional metacommunity is assumed to be in differing states. Biodiversity outcomes are quantified as directional changes in species richness for key species groups and habitat types. The broad management strategies I will project are those already under consideration – and in some instances under implementation – by the National Trust to aid in conservation and maintenance of biodiversity at Studland. These are grouped into three broad categories of management practice: 1) Increased drainage to influence hydrology; 2) Management of sika deer and cattle grazing, and; 3) Artificial disturbances induced to slow down ecological succession. As the effectiveness of management interventions applied locally will also depend on regional processes, I project the effects of local management under three regional scenarios; firstly, a scenario in which richness and connectivity in the metacommunity is assumed stable; secondly where it is assumed that the metacommunity is in decline and colonisation of species is more problematic, and finally where it is assumed the metacommunity is increasing in richness and connectivity.

5.3 Methods

5.3.1 Conceptual models of the study system

To begin constructing a BBN to project probable outcomes of biodiversity trends under management interventions, I first broke down the Studland study system into a conceptual model with five broad levels (*figure 5.1*). These levels are: 1) Specific management interventions (subdivided from the three broad management categories above); 2) Direct effects of management interventions on processes driving ecological change; 3) Key species groups which should be affected by these processes; 4) The habitats of Studland composed of the key species groups, and 5) The metacommunity context within which the local ecosystem of Studland is embedded. The aim of the BBN introduced below is to project probable outcomes of species richness trends for Studland, quantified as directional changes in species richness for the key species groups and habitats specified in levels 3 and 4 of the conceptual model. A more detailed description of the components of each group is given in *table 5.1*. Each row in the table describes a node in the BBN.

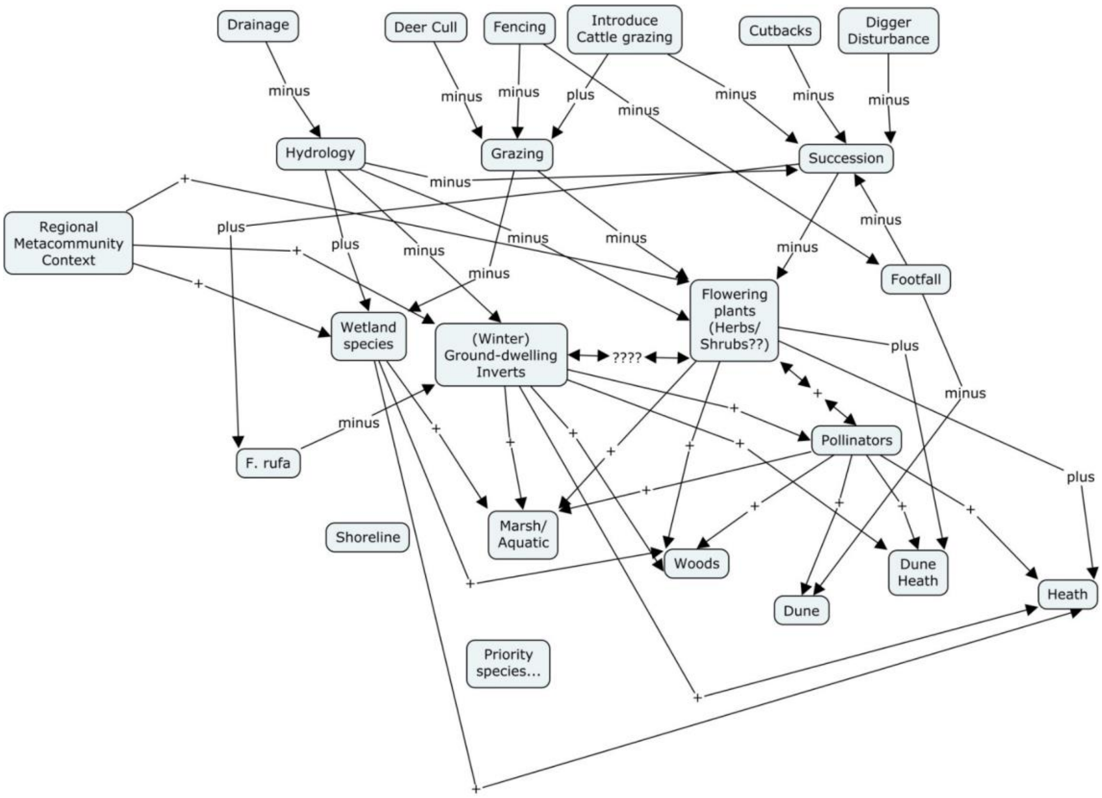

Figure 5.1 Conceptual model of the study system. Nodes are represented by text in boxes, while edges are arrows between nodes.

Table 5.1 Description of each node in the Studland conceptual model / Bayesian Belief Network.

Node	Definition
Marsh/Aquatic	Overall species richness of marsh and aquatic edge habitats
Woods	Overall species richness of woodland habitats
Heath	Overall species richness of heathland habitats
Dune Heath	Overall species richness of dune heath habitats
Dune	Overall species richness of dune habitats
Wetland species	Plant and invertebrate species specialising in wet conditions
Ground Inverts	Invertebrate species which spend some or all of their life cycle at ground level
Herbs/Shrubs	Herbaceous plants and shrubs
Pollinators	Invertebrate species which actively pollinate plants
Formica rufa	Abundance and spread of the red wood ant Formica rufa across the peninsula
Hydrology	The overall wetness of conditions across the peninsula
Grazing	Overall levels of sika deer and cattle grazing
Succession	Ecological succession, particularly with heath succumbing to woodlands
Footfall	Disturbance by footfall of humans and cattle
Drainage	Dig out old drainage ditches to reduce levels of flooding, particularly in winter
Deer cull	Culling to reduce deer populations
Fencing	Erection of fencing to exclude deer and/or people
Cattle grazing	Introduction of cattle grazing in selected areas across the heaths
Disturbance	Disturbance of thick heather or bryophyte mats (Digger, cutbacks etc.) to encourage pioneer species
Metacommunity	Connectivity richness and abundance within regional metacommunity

5.3.2 Bayesian Belief Network of the study system

To project the effects of management on plant and insect richness at Studland I translated the conceptual model of Studland from *figure 5.1* into a modified Bayesian Belief Network following Stafford *et al.* (2015). Traditional BBNs consist of a collection of *nodes* (e.g. representing a management intervention or species richness of a functional group in the Studland system), each of which can have a prior probability of increasing or decreasing. Nodes are connected to each other in the network via connectors called *edges*, each of which specifies the probability of a directional effect of one *node* on another. For example, in the case of a Studland BBN derived from *figure 5.1*, it could be specified that if drainage (*node*) was definitely increasing (probability of 1), then there is a 0.8 probability of hydrology (*node*) decreasing, representing drier conditions on the peninsula. This probabilistic directional effect of drainage on hydrology is specified by the *edge* between these two *nodes*.

The modified BBN of Stafford *et al.* (2015) introduces a number of features useful to ecological studies, including the ability to include two-way reciprocal interactions, and individual computation of interactions rather than the need to compute combined effects. Further, under this BBN implementation, priors need only be specified for targeted nodes for which we wish to specifically examine the effects of change (e.g. management interventions, metacommunity state), whereas all other nodes are set to have an equal prior probability of increasing or decreasing before effects of change in targeted parameters occurs (prior of 0.5). These models can be fitted in an easy to use Microsoft Excel interface which requires minimal training to parameterise (Stafford and Williams 2014). *Table 5.2.* presents the structure and probabilistic relationships between nodes of the Studland BBN used in this chapter.

5.3.3 Determining parameters for the Bayesian Belief Network

BBNs utilise the concept of probability as a subjective degree of belief (De Finetti et al. 2017), using Bayes theorem to update prior probabilities given defined relationships among nodes within the network. However, such subjective probabilities can (and should) be informed by available data and results of scientific studies where possible. Parameter values for the Studland BBN were chosen using information from a combination of previous chapters of this thesis and published peer reviewed literature (Appendix 5, table 1), and are displayed in *table 5.2.* Parameters for which table 1 in Appendix 5 provides no evidence from either this thesis or the literature are assumed to be self-evident (e.g. the reduction in grazing with the addition of fencing, as deer cannot physically access an area in which to graze). In the remainder of this section I give an overview of results from chapter’s 2 to 4, outlining how they have logically informed BBN parameterisation in relation to the three management intervention strategies outlined above.

Chapter’s 2 and 4 (on plants and hoverflies respectively) both highlighted the impact of hydrological change on biodiversity trends on Studland over the 80-year time span. It is likely that a cessation of the maintenance of drainage tracts running along the peninsula between sampling-periods has contributed to wetter conditions (David Brown, Personal comms), although the effects of underground hydrological processes and runoff from the mainland are as yet unclear and may also be important. Wetter conditions have likely led to reductions in species richness in wetter areas of the peninsula, evidenced in chapter’s 3 and 4, but also allowed for colonisation of wet adapted species. Given these results, it seems likely that the reintroduction of drainage tracts is a management intervention which could have major effects on Studland’s biodiversity – probably increasing local richness at the expense of wet adapted species.

The development of plant assemblages which are better suited to conditions of reduced light availability in the 2010s vs the 1930s, as inferred from EIV analysis in chapter 2, suggests that ecological succession has played an important role in biodiversity change at Studland in the interim period. Further, in chapter 3 I found that the EIV for light was the second most important EIV predictor of species composition across taxa within each time-period (after soil moisture), suggesting that changing vegetation structure due to succession may have played an important role in changing composition in plants and insects over time.

Studland’s Heath and Woodland habitats have undergone the highest levels of ecological succession between the 1930s and 2010s according to inferences from chapter 2. Heathlands are a plagioclimax successional stage – with woodlands and forests as the climax community

(Gimingham 1994, Bokdam and Gleichman 2000) – but they are highly valued for both ecological (e.g. conservation of heath adapted species) and cultural reasons (Gimingham 1994). The termination of historical land use practices has seen the widespread loss of heathlands across Europe in the 20th and 21st centuries (Loidi et al. 2010), and thus slowing or halting succession in heathlands is a common aim of conservationists and a stated conservation priority for the National Trust at Studland. Management interventions which could slow the progression of ecological succession include cutting vegetation, artificial physical disturbances (e.g. via diggers), and conservation grazing.

As well as influencing succession, a change in the grazing regime between the 1930s and 2010s may have limited the availability of adult food resources for hoverflies and other pollinators. Cattle grazing on the heathlands was widespread in the 1930s, but no longer occurs, while sika deer are now pervasive since their introduction in the 1940s (*David Brown personal comms*). The grazing behaviour of these two species are very different, and it seems likely that the loss of cattle grazing and trampling across the heathlands has encouraged succession, while deer grazing was likely a major component of the reduction of understory plant species across the woodlands. The loss of such understory plant species has had detrimental effects on the hoverfly community as seen in chapter 4, which suggests the potential for similar implications for other species of pollinators also relying on nectar and pollen food sources. Management interventions to offset these differing effects of grazing include fencing and deer culls to control for the effects of deer on herbaceous plants, and the re-introduction of cattle across the heathlands.

Finally, the metacommunity effect on wetland and ground invertebrates assumed under the models are greater than on herbs/shrubs and pollinators as the latter have generally higher dispersal abilities, and thus could likely colonise from further and/or sparser patches.

Table 5.2 Interactions in the Bayesian Belief Network. For each cell, the number is the probability of increase in the column variable, given that the corresponding row variable is increasing.

Values above 0.5 mean that there is a positive probability of increase, while values below 0.5 mean that a decrease is more probable.

Prob of column increasing give	**Marsh/Ac**	**Woods**	**Heath**	**Dune hea**	**Dune**	**Wetland**	**Ground I**	**Herb/Shr**	**Pollinato**	**Formica r**	**Hydrolog**	**Grazing**	**Successio**	**Footfall**
Marsh/Aquatic														
Woods														
Heath														
Dune heath														
Dune														
Wetland species	0.9	0.65	0.8											
Ground Inverts	0.65	0.85	0.85	0.85					0.85	0.75				
Herb/Shrubs	0.75	0.9	0.9	0.8	0.6		0.7		0.9					
Pollinators	0.75	0.9	0.9	0.9	0.7			0.75						
Formica rufa							0.15							
Hydrology						0.9	0.1	0.2					0.35	
Grazing						0.4		0.1						
Succession		0.6	0.4	0.4	0.4			0.2		0.8				
Footfall					0.2								0.4	
Drainage											0.25			
Deer cull												0.15	0.65	
Fencing												0.1	0.6	0.2
Cattle grazing												0.7	0.2	
Disturbance													0.1	
Mettacommunity						0.7	0.7	0.65	0.65					

5.4 Results

All of the results I present below are for probabilities of nodes in the Bayesian Belief Network increasing. Probabilities > 0.5 indicate that increases are more likely than not that, while probabilities < 0.5 indicate the opposite. Increasingly higher and lower probability values relative to 0.5 indicate an increasingly positive and negative chance respectively of nodes increasing following management scenarios under the model.

5.4.1 Management under a stable metacommunity

All probabilities in this subsection are given from model runs with the prior probability of the health of the regional metacommunity increasing set to 0.5 (increase or decrease equally likely) (*table 5.3 A*). In general, model predictions in the face of a stable metacommunity led to mostly modest negative and positive probabilities of increases of the key ecological outcome – species functional groups and overall richness of habitats – in the range of 0.33 to 0.63.

Increasing drainage to reduce flooding (by altering the prior for drainage to 0.8) resulted in increased probabilities of species richness gains for the functional species groups of ground invertebrates, herbs and shrubs, and pollinators (all posterior $p \geq 0.6$), and smaller but notable increases in the probabilities of increasing succession and abundance/distribution of *Formica rufa* (both $p = 0.57$ *table 5.3 A*). There was also an unsurprising reduction in the probability of wetland specialist species increasing due to drier conditions ($p = 0.35$). There were no reductions in richness in any of the broad habitat types under this management scenario, though a probability of increase of 0.55 was the highest probable outcome.

Management to reduce the effects of deer grazing by introducing widespread deer culls and fencing (alter prior of $p_{increase}$ to 0.9 for both parameters) resulted in similar probabilities of increases to the previous scenario in nodes for herbs and shrubs, pollinators and *F. rufa*, but no probable increase in richness of ground invertebrates ($p_{increase}$ = 0.5) (*table 5.3 A*). Similar outcomes are projected across the broad habitats as in the drainage scenario, except that the dune habitat is predicted do marginally better than dune heath. Perhaps the biggest difference between this management scenario and increasing drainage is a projected probable increase in richness in wetland species of 0.58.

In a management scenario designed to halt the progress of ecological succession (alter prior of $p_{increase}$ for introduction of cattle grazing and increased disturbance and cutbacks to 0.8 and 0.9 respectively) the most notable outcomes are increased probabilities for heath, dune heath and dune habitats increasing in richness ($p_{increase}$ = 0.56 for all three). However, we also see a slight probability of decrease in richness in the woodland habitats (0.45), and a more likely decrease in *F. rufa* abundance/distribution (0.33), both likely due to direct effects of succession on these nodes (*table 5.3 A*). The cattle have a direct positive effect on grazing (0.68).

I also projected the three management scenarios using pairwise combinations of two from the drainage, deer control and succession control management strategies reported in the preceding paragraphs with the same alterations to prior probabilities of increases to each management practice as before (*table 5.3 A*). Pairwise combinations of the introduction of drainage along with the other two management practices had the most wide-ranging positive effects of the three implemented strategy pairs, though the combination of drainage and disturbance saw decreases in probabilities for woodland richness, wetland species and *F. rufa* of 0.45, 0.41 and 0.44 respectively. The combination of deer and succession control management strategies predicted perhaps the most stable outcome of the three, with only *F. rufa* marginally predicted to decrease by the Bayesian Belief Network (0.45 *table 5.3 A*).

Finally, I ran a scenario implementing all three management strategies together. All functional species groups were predicted to increase with posterior probability values ≥ 0.6, apart from wetland species ($p_{increase}$ = 0.44). Dune and dune heath habitats were predicted to increase in this scenario, while the other habitats should remain stable (*table 5.3 A*).

5.4.2 Management under deteriorating/improving metacommunity

Deteriorating or improving metacommunity connectivity and richness completely outweighed the effects of local management interventions in BBN projections (*table 5.3 B & C*). In the face of a deteriorating metacommunity (prior of $p_{increase}$ for metacommunity node of 0.2), the probability of an increase in richness in all species functional groups and habitats was ≤ 0.45 under all local management combinations explored (*table 5.3 B*). The only exceptions were richness in the dune habitat for which the inland metacommunity was not deemed to be important source of species dispersal, and stable abundance/distributions of *F. rufa* in 2 of the 7 local management combinations ($p_{increase}$ = 0.5), where induced succession control presumably kept them stable.

When metacommunity connectivity and richness were assumed to be improving (prior of $p_{increase}$ for metacommunity node of 0.8) the converse was true, with the probability of an increase in richness in most functional groups and habitats ≥ 0.55 under all local management combinations (*table 5.3 C*). Again, the notable exceptions here were *F. rufa* and the dune habitats, although the dune habitat was projected to increase in 4 out of 7 local management scenarios, while the probability of increase/decrease of was more variable depending on the specific combination of local management interventions.

Table 5.3 Results of different management scenarios from the Bayesian Belief Network. Bold values represent probabilities of nodes increasing ≥ 0.55, light grey values in italics represent probabilities of nodes increasing ≤ 0.45 (or of nodes decreasing ≥ 0.55). All values in section A have prior probability of connectivity and richness in the metacommunity increasing of 0.5. All values in section B have prior probability metacommunity increase of 0.2 (probability decreasing = 0.8). All values in section C have prior probability of connectivity and richness in the metacommunity increasing of 0.8.

	Increase drainage ($P_{increase}$ = 0.8)	Increase Deer cull & Fencing ($P_{increase}$ = 0.9, 0.9)	Increase Cattle & Disturb ($P_{increase}$ = 0.8 & 0.9)	Increase Drainage, Deer cull & Fencing ($P_{increase}$ = 0.8, 0.9, 0.9)	Increase Drainage, Cattle & Disturb ($P_{increase}$ = 0.8, 0.8, 0.9)	Increase Deer cull, Fencing , Cattle, & Disturb ($P_{increase}$ = 0.9, 0.9, 0.8, 0.9)	All prev column combo
	A. $P_{increase}$Metacommunity = 0.5						
Marsh/Aquatic	0.51	0.54	0.5	0.52	0.51	0.53	0.52
Woods	0.54	0.54	*0.45*	**0.55**	*0.45*	0.49	0.49
Heath	0.53	0.49	**0.56**	0.49	**0.56**	0.54	0.54
Dune heath	**0.55**	0.49	**0.56**	0.49	**0.56**	0.54	**0.55**
Dune	0.51	**0.57**	**0.56**	**0.57**	**0.56**	**0.59**	**0.59**
Wetland species	*0.35*	**0.58**	0.47	0.46	*0.41*	0.54	*0.44*
Ground Inverts	**0.63**	0.5	**0.56**	**0.63**	**0.64**	0.53	**0.63**
Herb/Shrubs	**0.6**	**0.61**	0.53	**0.61**	**0.56**	**0.61**	**0.61**
Pollinators	**0.6**	**0.58**	0.53	**0.6**	**0.58**	**0.58**	**0.6**
Formica rufa	**0.57**	**0.57**	*0.33*	**0.58**	*0.44*	*0.45*	0.51
Hydrology	*0.28*	0.5	0.5	*0.28*	*0.28*	0.5	*0.28*
Grazing	0.5	*0.11*	**0.68**	*0.11*	**0.68**	*0.27*	*0.27*
Succession	**0.57**	**0.64**	*0.16*	**0.6**	*0.2*	*0.4*	*0.41*
Footfall	0.5	*0.17*	0.5	*0.17*	0.5	*0.17*	*0.17*
	B. $P_{increase}$Metacommunity = 0.2						
Marsh/Aquatic	*0.43*	*0.43*	*0.43*	*0.43*	*0.43*	*0.43*	*0.43*
Woods	*0.42*	*0.44*	*0.42*	*0.44*	*0.42*	*0.43*	*0.43*
Heath	*0.41*	*0.42*	*0.44*	*0.42*	*0.44*	*0.43*	*0.43*
Dune heath	*0.42*	*0.43*	*0.45*	*0.43*	*0.45*	*0.44*	*0.44*
Dune	0.47	0.52	0.5	0.52	0.5	0.53	0.53
Wetland species	*0.32*	*0.37*	*0.35*	*0.35*	*0.34*	*0.36*	*0.35*
Ground Inverts	*0.38*	*0.35*	*0.36*	*0.38*	*0.38*	*0.35*	*0.38*
Herb/Shrubs	*0.4*	*0.42*	*0.4*	*0.42*	*0.42*	*0.42*	*0.42*
Pollinators	*0.37*	*0.37*	*0.37*	*0.37*	*0.37*	*0.37*	*0.37*
Formica rufa	*0.44*	0.5	*0.36*	0.5	*0.37*	*0.43*	*0.43*
Hydrology	*0.28*	0.5	0.5	*0.28*	*0.28*	0.5	*0.28*
Grazing	0.5	*0.11*	**0.68**	*0.11*	**0.68**	*0.27*	*0.27*
Succession	**0.57**	**0.64**	0.16	**0.64**	*0.2*	*0.4*	*0.41*
Footfall	0.5	*0.17*	0.5	*0.17*	0.5	*0.17*	*0.17*
	C. $P_{increase}$Metacommunity = 0.8						
Marsh/Aquatic	**0.57**	**0.57**	**0.57**	**0.57**	***0.57***	**0.57**	**0.57**
Woods	**0.58**	**0.57**	**0.56**	**0.57**	***0.56***	**0.56**	**0.56**
Heath	**0.59**	**0.57**	**0.59**	**0.57**	***0.59***	**0.58**	**0.58**
Dune heath	**0.58**	**0.56**	**0.58**	**0.56**	***0.58***	**0.57**	**0.57**
Dune	0.53	**0.56**	0.54	**0.56**	0.54	**0.57**	**0.57**
Wetland species	**0.62**	**0.66**	**0.64**	**0.63**	***0.61***	**0.66**	**0.62**
Ground Inverts	**0.66**	**0.65**	**0.65**	**0.66**	***0.66***	**0.65**	**0.66**
Herb/Shrubs	**0.62**	**0.63**	**0.61**	**0.63**	***0.62***	**0.63**	**0.63**
Pollinators	**0.64**	**0.64**	**0.63**	**0.64**	***0.64***	**0.64**	**0.64**
Formica rufa	**0.58**	**0.58**	*0.45*	**0.58**	*0.45*	0.51	0.52
Hydrology	*0.28*	0.5	0.5	*0.28*	*0.28*	0.5	*0.28*
Grazing	0.5	*0.11*	**0.68**	*0.11*	***0.68***	*0.27*	*0.27*
Succession	**0.57**	**0.64**	*0.16*	**0.64**	*0.2*	*0.4*	*0.41*
Footfall	0.5	*0.17*	0.5	*0.17*	0.5	*0.17*	*0.17*

5.5 Discussion

Under the scenario of a stable metacommunity, all three management strategies predicted modest probabilities of increasing species richness in the key functional species groups and across the ecological habitats of Studland more broadly. The only exceptions to this general pattern were projected reductions in richness of wetland species in scenarios increasing drainage to reduce flooding, and reductions in richness in the woodland habitats in scenarios in which ecological succession was curtailed. However, these projections of modest effects of local management were completely swamped in scenarios in which the regional metacommunity was assumed to be deteriorating or increasing in connectivity and richness, where projections of widespread declines and increases in biodiversity respectively prevailed.

Results from the Bayesian Belief Network predicted that the potential management implementations under consideration are likely to accrue some benefits to the biodiversity of Studland such as increased species richness in understory vegetation and resulting increases in pollinator species richness. However, there is a high degree of uncertainty inherent in the various outcomes. While it would be desirable to have a higher degree of certainty, ecological systems are notoriously complex and in some cases even display chaotic dynamics (Hastings et al. 1993), and thus the uncertainty of BBN predictions may be apt. Stochastic environmental events, such as the predicted increasing frequency of flooding and freezing weather conditions under climate change (Watts et al. 2015, Blöschl et al. 2017), could perturb the desired outcomes of management, as could unexpected disturbances such as outbreaks of disease in plant or invertebrate populations (e.g. (Strauss *et al.* 2012)). Predictions from the Studland BBN are based primarily on results from preceding chapters of this thesis, with the implicit assumption that biodiversity change that has occurred in the last 80 years is somewhat reversible if appropriate management conditions are put in place. Such assumptions are bold in ecological systems, given that they often exhibit regime shifts (Hastings and Wysham 2010), and alternative stable states (Suding *et al.* 2004), whereby upon reaching a certain level of change a system may reach a tipping point beyond which it is difficult to return to conditions of old (Reyer et al. 2015).

The BBN models do, however, provide us with a useful quantification of the conceptual model of the study system and how its components are linked together, given what we have learned throughout this thesis. The models suggest that any or all of the proposed management strategies should benefit the biodiversity of Studland. Despite resulting projections being directional rather than estimates of effect sizes of proposed management strategies, these models can encourage practitioners to think probabilistically and in terms of second order (knock-on) effects of interventions. I would suggest that this conceptual model combined with BBN projections should be of greater value in the hands of in-house ecologists and rangers of the National Trust who have a better applied knowledge of the system, and of the implementation and outputs of management practices to date.

The key predictions of interest from the Studland BBN are concerned with broad species richness trends across key functional groups of species and ecological habitat types, but in reality management concerns may be more focused on individual species or species groups. There is a general desire to conserve species which are particularly at risk, or which are nationally rare, and it is possible that management which protects many species may damage some specific populations in need of protection – for example rare wetland species under the drainage management strategy. Some species are also objectively more important than others in the context of a healthy ecosystem; keystone species (Mills and Doak 1993) and ecosystem engineers (Jones *et al.* 1994) can have disproportionate effects compared to others. It is thus important to take such factors into consideration when introducing disruptive management strategies.

The most striking finding to emerge from the BBN projections were the overwhelming effect of the surrounding metacommunity. The fact that the metacommunity node was directly fed into the key functional species groups explains this effect, but I would argue that it is a very reasonable model assumption given the high rates of species turnover at the peninsula level over the past 80 years documented in chapter 2 of this thesis. Though it is unclear how much degradation or rejuvenation the metacommunity would have to undergo to see the projected effects of the BBN realised, its importance is well established both generally (Leibold and Chase 2018), and specifically in the context of Dorset county (Keith et al. 2011, Diaz et al. 2013a). Further, the importance of metacommunity dynamics in maintaining local biodiversity has also been widely documented in the recent decades (Harrison 1999, Fukami 2015), and the Cyril Diver Project data provide another striking example. However, the large number of species gained at Studland between the 1930s and 2010s may suggest that a stable metacommunity existed during this time in the vicinity of Studland from which species arrived. Thus high projected probabilities of increasing richness at Studland under increases in metacommunity richness and connectivity may be a less realistic scenario than the adverse effects in the case of reduced metacommunity richness and connectivity in future years.

To conclude, BBN models predict that each or any of the proposed management implementations would likely benefit the biodiversity of Studland via the metric of species richness, though the benefits of any management strategy for any given functional species group or habitat are highly uncertain. Crucially, it is likely that the health of the regional metacommunity is of the utmost importance in maintaining a healthy local system. I would thus suggest that local management strategies should be implemented using the conceptual model of the Studland system and BBN predictions to aid decisions, in conjunction with dedicated conservation efforts at the landscape scale.

6. Discussion and Conclusions

6.1 Introduction and Thesis Overview

Historical and contemporary occurrence data from the Cyril Diver Project revealed major differences in the composition of plant and insect species present on Studland between the 1930s and 2010s. Changes in aggregated traits of species indicated widespread change in the abiotic environment as an underlying driver of species compositional change. The most prominent abiotic driver was the transition to wetter conditions across the peninsula in the 2010s compared with the 1930s, which were independently inferred from plant and hoverfly traits. Within time-period analyses and correlated species loss/gains across taxa provided further indirect evidence to suggest that changes in the abiotic environment also contributed to biodiversity change in non-vascular plants, orthoptera, ants and odonata. Biotic interactions were also an important factor underlying biodiversity change, exemplified by a strong association between species richness differences in vascular plants and hoverflies. Taken together, these results show how effects of long-term abiotic and biotic changes can propagate through local plant and insect communities driving changes in species richness and composition. In conjunction with BBN projections, they underline the importance of conservation efforts focused on both local communities and surrounding landscapes, and highlight the need to improve understanding of interactions and feedbacks between local and regional communities.

6.2 Discussion: Main body

Results of analyses presented throughout chapters 2, 3 and 4 revealed that widespread species losses and gains across the study area resulted, at least in part, due to a suite of abiotic and biotic drivers acting locally at Studland. Although this finding is perhaps intuitive and unsurprising, long-term empirical examples of factors affecting biodiversity change are surprisingly rare (Magurran and Dornelas 2010, Leibold and Chase 2018). Where long-term studies of factors underlying biodiversity change have been undertaken, variability in abiotic conditions have been a dominant underlying driver (Mutshinda *et al.* 2009), and results herein seem to confirm their importance within local plant and insect communities. EIV analyses of chapter 2 indicated clear changes in plant community composition across the peninsula with respect to abiotic environmental change (Carroll et al. 2018). Differing composition/environment relationships between time-periods revealed through RDA analyses of chapter 3 also suggest that the other focal taxa investigated have experienced similar environmental pressures. Results from chapter 4 confirmed the existence of such abiotic and biotic drivers of change in Studland's hoverfly communities; a group of species for which factors underlying biodiversity change at wider spatial scales over this time-period have previously been demonstrated (Biesmeijer 2006, Keil et al. 2011).

Cross-taxon congruencies (CTC) in species richness differences (chapter 3) further implied a set of mechanistic factors underlying species losses and gains, as opposed compositional changes due purely to random drift, as there would be no reason to expect correlated changes across taxa if they occurred randomly with respect to abiotic and biotic environmental conditions (Vellend et al. 2014). Indeed, diminished correlations in species richness change across taxa in analysis including environmental and habitat predictors suggest a key role for shared responses to abiotic environmental change underlying congruencies.

Studies of long-term biodiversity change including multiple co-occurring taxa are very rare, but findings of existing research are not unsimilar to my results. Ewald et al. (2015) found correlations between abundance trends of multiple co-occurring invertebrate taxa and temperature, precipitation and pesticide use over a 42 year period. This result may point towards a shared responses to abiotic environmental changes driving cross-taxon congruence in biodiversity trends, similar to congruencies uncovered in chapter 2 of this thesis. Ernest et al. (2008) documented cascading effects of changing precipitation levels in desert ecosystems on occurrences of grass species, which in turn had knock-on effects on the rodent community mediated through trophic interactions. My results show that biotic interactions between plants and hoverflies may have been driven by hydrological changes in a similar fashion (discussed further below). While cascading effects on the vertebrate populations of Studland are unknown, risks of insect losses to insectivore populations are well documented (Brickle et al. 2000, Chamberlain et al. 2000, Hart et al. 2006, English et al. 2017).

Notwithstanding findings of mechanistic drivers, a large proportion of variation in species richness and compositional change was left unexplained in all analyses across chapters 2, 3 and 4. As such, effects of neutral processes cannot be ruled out as an important component underlying observed biodiversity change, though unmeasured abiotic and biotic factors may also have played a key role. For instance, it seems likely that changes in dominance hierarchies within the ant community altered by the spread of the dominant competitor *Formica rufa* have effected species richness and composition among ants and other ground-dwelling invertebrates (Halaj & Wise 2001; Hawes *et al.* 2002; Hawes *et al.* 2013). Similarly, the spread of the invasive moss *Campylopus introflexus* across Studland since the 1930s may also have affected plants and invertebrates (Ketner-Oostra & Sýkora 2004; Schirmel *et al.* 2011). Coastal erosion and trampling due to increased numbers of visitors using paths are examples of further abiotic and anthropogenic forces that may have affected the dune and shoreline communities of Studland (Ciccarelli 2014).

Hydrological change across the peninsula represents the most convincing finding of an abiotic factor affecting the plants and insects of Studland, as it was implied independently through trait based analyses of both vascular plants and hoverflies. As well as being the most robust finding of an abiotic driver of biodiversity change, changes in soil moisture (EIV F) was also found to drive compositional change in vascular plant communities in a manner independent of ecological habitat type (Carroll et al. 2018), and was a consistently important predictor of within time-period species composition across taxa (RDA analyses chapter 3). It is not surprising that such hydrological changes as have occurred on Studland have had wide ranging effects on the plant and insect communities present, as species composition of both groups are known to display distinct adaptations to wetter or drier conditions (Silvertown et al. 2015a, Turić et al. 2015). The exclusion of hoverfly species which were both susceptible to, and intolerant of, ground surface flooding in winter months provides a clear demonstration of a mechanism by which such a compositional change has occurred.

Biodiversity change across plant and hoverfly communities resulting from increased winter flooding underlines the complexity with which abiotic and biotic factors can combine to drive changes in species richness and composition. It is possible that wetter conditions in the 2010s have detrimentally affected Studland's hoverflies in two distinct ways; firstly, as previously discussed, via the direct exclusion of unsuited larval individuals, and secondly, indirectly via species richness limitation mediated through the loss of plant species. In chapter 4 I already discussed a range of mechanisms by which the loss of plant species could lead to an accompanying loss of hoverfly species. I will further outline here why I am inclined to think that this was the direction of causality underlying the hoverfly/plant richness association. Sampling compartments in the marsh habitat type lost 101 plant species between time-periods (*figure 3.2*), and EIV analysis in chapter 2 strongly suggests that this loss of species was driven largely by increases in soil moisture (*figure 2.4*). Though overall hoverfly species richness on Studland decreased by only five species, sampling compartments in the marsh habitat saw major proportional declines in richness. Model estimates of these proportional species richness declines remained consistently negative across all marsh compartments for hoverflies even after having accounted for the effects of flooding on susceptible hoverfly larvae (*figure 4.4*). Had plant species been present in the marsh habitat, it seems likely that the mobile hoverfly adults would have found their way from others parts of the peninsula to exploit them as food resources, and therefore that the loss of plant species limited the number of hoverfly species present. The fact that there was no general decline in the occurrence of wet adapted hoverfly species further bolsters the likelihood of this hypothesis.

The effects of wetter winter conditions on biodiversity change in co-occurring plant and insect taxa may prove to be a particularly pertinent case study in the face of climate change in coming decades. Increasing frequency of flooding and droughts are a major element of climate change projections (Trenberth 2011; Trenberth *et al.* 2015; Arnell & Gosling 2016; Winsemius *et al.* 2016), in regions including Europe and the UK (Watts et al. 2015, Blöschl et al. 2017). Such hydrological change is likely to have widespread effects on ecological communities (Medlock & Vaux 2015; Moor *et al.*

2015; Mainwaring *et al.* 2017), and as such, this threat demands a diverse array of research approaches to help mitigate negative ecological consequences (Leigh et al. 2015). I have shown that hydrological change can indeed cause major shifts in species composition in local communities, and that these effects may cascade through co-occurring taxa in unexpected ways. It seems that the plant and insect communities of Studland have had time to change in response to a changing hydrological context, as many suitably adapted species have colonised the peninsula between time-periods. However, rates of hydrological change may increase more rapidly in many areas in coming decades (Vitousek et al. 2017), and it is not clear that communities will have time to respond via compositional change, particularly if hydrological disturbances occur simultaneously over large spatial extents.

Bayesian Belief Network projections of chapter 5 further illustrate how rapid changes in local abiotic environments could interact with processes occurring at wider scales to the detriment of biodiversity in local communities. BBN projections suggest that a species rich meta-community is needed in order to provide a reservoir of suitably adapted species within dispersal range to exploit new conditions. However, widespread habitat fragmentation due primarily to agricultural intensification, both in Dorset (Hooftman and Bullock 2012, Jiang et al. 2013) and more broadly (Cordingley et al. 2015), limits the ability of species to disperse among local communities (Henle *et al.* 2004; Thompson *et al.* 2017). Such dispersal limitation, in conjunction with cascading effects of changing abiotic conditions on local biodiversity (chapter's 2, 3 & 4), may deprive local communities of necessary colonisers to compensate for species losses. It seems that this risk would be amplified if the direction of abiotic changes were variable throughout a landscape, with some ecosystems drying up while others became wetter, as this would lead to local losses of species adapted to both wet and dry conditions simultaneously. I would therefore suggest that research is needed into specific interactions between landscape fragmentation and dispersal limitation under changes in local abiotic conditions to investigate precisely how such local and regional dynamics interact.

Of course the research I have presented here suffers from a number of limitations as one would expect. Ideally research on factors affecting temporal biodiversity trends would consist of more than two time points. A lot may have happened in the 80 years between sampling, and it is even possible that trends observed here have played out multiple times. For instance, the peninsula may have gotten wetter, and drier, and wetter again. The snapshots of Studland in the 1930s have told us a lot about how plant and insect communities, but we still don’t know how long it took these processes to play out. Differing sampling methodologies in each time-periods are also less than ideal, and may have obscured certain signals from the analyses I conducted. However, I believe the plants and insects of the Studland have shed a lot of light on the processes affecting long-term changes in species richness and composition despite these limitations.

6.3 Final Conclusions

Throughout this body of work I have provided a rare empirical example of long-term environmental change propagating through co-occurring taxa in local communities, ultimately driving changes in species richness and composition. Richness and compositional change resulted both from direct effects of abiotic drivers – most notably due to wetter conditions – and from effects of interactions between co-occurring taxa, exemplified by the association between species richness differences in vascular plants and hoverflies. I also presented congruent trends in species richness change between diverse plant and insect taxa, which seem to have been driven at least partially by shared responses abiotic environmental change, and thus highlight the value of a whole system approach to management for conservation.

High observed turnover across the plant and insect taxa of the dynamic Studland environment – strongly influenced by underlying abiotic and biotic factors – may have troubling implications for ecological communities in coming decades. If, as climatologists predict, drought and flood conditions become increasingly frequent, the composition of species in local communities should adapt to track abiotic environmental change, as species colonise areas or become locally extinct depending on the possession of suitable traits to survive under new conditions. The CDP data shows that Studland's communities of plants and insects have had both time within which to adapt to a changing environment, and a reservoir of colonising species on hand within a distance over which they were able to disperse. However, we do not know how long it this took to unfold, only that it happened between the 1930s and 2010s in a biodiverse region of Dorset. More rapidly changing environments, particularly in fragmented landscapes which limit species dispersal, have the potential to allow local extinctions to overtake colonisations leading to ecological communities impoverished of species.

Therefore the take home message of this thesis must be to encourage an approach to conservation which maximises connectivity between local, species rich systems, which represent diverse ranges of abiotic conditions, as this may help insure communities against rapid changes in local abiotic environments.

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8. Appendices

Appendix 1.

Table A1.1 Compartment level data for six taxa. "c.n" is taxa specific compartment list.

Compartment	c.n_VA	c.n_NV	c.n_OR	c.n_AN	c.n_SY	c.n_OD	Eco.habitat	cmpt.area_m^2	x_coord_BNG	y_coord_BNG
Brands heath	1	1	1	1	1	1	Heath_T	72367.88	402378.5	84712.94
Curlew cottages	2	2	NA	NA	NA	2	Heath_T	899.5889	402577.2	85086.06
Curlew heath	3	3	3	3	3	3	Heath_T	74255.92	402704.5	85241.86
Little sea enclosure	4	4	NA	NA	4	4	Heath_T	10853.81	402690	84739.12
Pipley heath	5	5	NA	NA	5	NA	Heath_T	15024.35	402919.5	83773.62
Plateau heath north	6	6	6	6	6	6	Heath_T	97817.7	402884.5	85772.53
Plateau heath south	7	7	7	7	7	7	Heath_T	200764.4	402518.2	85397.56
Spur heath	8	8	8	8	NA	8	Heath_T	114452.2	402594.9	84582.95
Western Arm Heath	9	9	9	9	9	9	Heath_T	46662.21	402587.6	84965.55
Wood Heath	10	10	NA	10	NA	NA	Heath_T	6391.836	402853.3	84017.74
East heath pines	11	NA	NA	NA	NA	11	Heath_D	7744.334	403315.3	84887.3
First ridge north	12	12	12	12	NA	12	Heath_D	129864.2	403911.5	85617.07
First ridge south	13	13	13	13	13	13	Heath_D	172979.8	403478	84606.38
Inner Ridge	14	14	NA	14	NA	14	Heath_D	24413.98	403295.2	84417.08
Pipley hollow	15	15	15	15	15	NA	Heath_D	3204.267	403272.5	83961.11
Second ridge N	16	16	16	16	16	16	Heath_D	144635.4	403657.7	85675
Second ridge S	17	17	17	17	NA	17	Heath_D	29201.24	403411.7	85252.74
Southern heath	18	18	18	18	18	18	Heath_D	127788.7	403250.3	84240.32
Third ridge central	19	19	19	19	NA	19	Heath_D	67848.99	403334.6	85863.15

Third ridge north	20	20	20	20	NA	20	Heath_D	38697.82	403272.4	86066.33
Third ridge south	21	NA	21	21	NA	21	Heath_D	26285.42	403137.3	85339.74
Third ridge west	22	22	22	22	NA	NA	Heath_D	11127.94	403128.5	85555.2
Third ridge west heath	23	23	NA	NA	NA	NA	Heath_D	12711.96	403131.4	85727.11
Aspen wood	24	24	NA	24	24	NA	Wood	9446.228	403146.1	83713.37
Northern enclosure	25	NA	NA	NA	NA	25	Wood	24884.99	403561.7	86244.78
Northern Enclosure Extension	26	26	NA	26	NA	26	Wood	7066.84	403501	86283.17
Pipley enclosure	27	27	27	27	27	27	Wood	34921.55	403111.6	83743.02
Pipley wood	28	28	28	28	NA	28	Wood	30188.62	403194.8	83795.34
Plateau enclosure	29	29	NA	29	29	29	Wood	13318.97	403021.2	85607.95
Plateau enclosure extension	30	30	30	30	NA	30	Wood	7791.239	403001	85636.02
Third ridge pines	31	31	NA	31	31	31	Wood	7865.834	403044.4	85455.08
Three acre wood	32	32	NA	32	NA	NA	Wood	9910.083	402911.9	84003.27
Twelve acre wood	33	33	NA	33	33	33	Wood	50491.84	402914.2	84195.13
Western Arm Pines	34	NA	NA	34	NA	34	Wood	24283.05	402583	84743.82
Knoll Dunes	35	NA	NA	NA	NA	NA	Dune	4541.302	403391.7	83654.48
Lone dune	36	NA	NA	36	NA	36	Dune	5878.515	403243.5	84335.71
Northern dunes	37	NA	37	NA	NA	37	Dune	10973.43	403666.3	86262.08
Shell bay dunes	38	38	38	38	38	38	Dune	78455.08	403754.6	86154.26
South haven flats	39	NA	NA	NA	39	NA	Dune	6286.17	403451.5	86346.55
Zero ridge south	40	NA	NA	NA	NA	NA	Dune	104029.1	403608.7	84623.99
Bramble bush bay	41	NA	41	41	NA	41	H_shore	131970.6	403101.9	86109.75
Brands creek	42	42	42	42	NA	42	H_shore	26117.14	402276.8	84788.05
Dyke bay	43	43	43	NA	NA	NA	H_shore	76795.11	402703.1	85840.35
Dyke bay saltmarsh	44	NA	NA	NA	NA	NA	H_shore	6624.107	402531.3	85683.51
Gravel Spit	45	NA	45	45	NA	NA	H_shore	4574.459	402924.7	85982.3

Plateau bay	46	NA	NA	NA	NA	NA	H_shore	49603.62	402335.1	85642.19
Redhorn bay ex ciffs	47	NA	47	47	NA	NA	H_shore	65331.81	402255.8	85251.07
Redhorn quay ex shore	48	48	NA	48	NA	NA	H_shore	5514.588	402283.1	85493.83
Sandy point	49	NA	NA	NA	49	NA	H_shore	1170.44	402481	85708.04
Central marsh north	50	50	50	50	50	50	Marsh	131093.8	403488.1	85829.4
Central marsh south	51	51	51	51	51	51	Marsh	114065.2	403203.5	85228.98
Central tongue	52	52	NA	52	NA	52	Marsh	4295.939	403708.3	85316.46
East marsh	53	53	53	53	53	53	Marsh	64881.64	403228.7	84752.52
Eastern lake marsh	54	54	54	54	54	54	Marsh	89181.82	403394.1	85071.19
Little sea swamp	55	NA	55	NA	NA	55	Marsh	35265.17	402857	84740.26
Lone dunes marsh	56	NA	NA	NA	NA	NA	Marsh	1919.025	403203.6	84368.73
New pool marsh	57	57	57	NA	57	57	Marsh	49369.14	403076	85404.74
Northern dunes marsh	58	NA	58	58	NA	NA	Marsh	5918.71	403644.8	86198.01
Northern tongues	59	NA	59	59	NA	NA	Marsh	7408.769	403991.6	85868.52
One Acre Pool Marsh	60	NA	60	60	60	60	Marsh	22383.47	403204.4	85735.34
Pipley swamp	61	61	61	61	61	61	Marsh	57982.68	403011.1	83871.71
Saltings strip	62	62	62	62	62	62	Marsh	49044.66	403766.1	85581.13
Spur bog	63	63	63	63	63	63	Marsh	33773.25	402725.1	84294.74
Western Arm Marsh	64	64	NA	NA	64	64	Marsh	15544.56	402739.7	84998.22
Wood Marsh	65	65	NA	NA	65	NA	Marsh	3016.789	402843.8	83925.32
Eastern lake	66	NA	NA	NA	NA	66	Aquatic	25373.45	403469.7	85047.66
Little sea central	67	NA	NA	NA	NA	67	Aquatic	86303.72	402994.9	84876.4
LS Northern one	68	NA	NA	NA	68	68	Aquatic	6590.469	402984.4	85512.43
LS Northern two	69	NA	NA	NA	69	69	Aquatic	58613.8	402879.7	85235.29
LS Southern one	70	NA	NA	NA	NA	70	Aquatic	108148.2	402969	84469
LS Southern two	71	NA	NA	72	NA	71	Aquatic	41159.31	403082	84155.51
One acre pool main pool	72	NA	NA	NA	NA	72	Aquatic	4465.494	403237.4	85831.78
Pipley pools	73	NA	73	73	73	73	Aquatic	9825.182	403250	83748.87

Western Arm	74	NA	NA	NA	74	74	Aquatic	29835.04	402748.4	84844.74

Code to fit models in R and Jags

```
##================## Model 1 ~ No pooling

M1 <- "model{


 for(i in 1:n){

   y[i] ~ dnorm(yN.hat[i], tau)

   y.hat[i] <- alpha[Cmpt[i]]  + beta[Cmpt[i]]*Time[i]    # Cmpt and Time are sampling-compartment and sampling-period variables


     # Assess model fit using a sums-of-squares-type discrepancy

     resid[i] <- y[i] - y.hat[i]                    # residuals for observed data

     predicted[i] <- y.hat[i]                        # Predicted values

     sq[i] <- pow(resid[i], 2)                        # Squared residuals for observed data


     # Generate replicate data and compute fit stats for them

     y.new[i] ~ dnorm(y.hat[i], tau)                      # One new data set at each MCMC iteration

     sq.new[i] <- pow(y.new[i] - predicted[i], 2)          # Squared residuals for new data

 }


 ## Priors

 for (j in 1:max(Cmpt)){

   alpha[j] ~ dnorm(0,0.001)

   beta[j] ~ dnorm(0,0.001)
```

```
    alpha.t2[j] <- alpha[j] + beta[j]          ## Compute means for time-period two as derived variables.

  }


tau <- 1/(sigma * sigma)

sigma ~ dunif(0, 100)


s.y <- sd(resid[])        ## Data level finite-population standard deviation

  fit <- sum(sq[])                    # Sum of squared residuals for actual data set

  f.sim <- sum(sq.new[])             # Sum of squared residuals for new data set


#data# n, y, Cmpt, Time

#Inits# sigma

#monitor# alpha, alpha.t2, beta, sigma, s.y, fit, f.sim, resid, dic


}"


## Initial values

sigma <- list(rlnorm(1), rlnorm(1))


## Fit model using the "run.jags" function in R package runjags

results.M1 <- run.jags(M1, n.chains=3, sample = 10000)


## Calculate the Bayesian R^2 adjusted:

M1.resid <- as.mcmc(results.M1, vars="resid")

rsquared.yN <- 1 - mean(apply(M1.resid, 1, var))/var(y)


## Calculate summary of pooling factor
```

```
M1_y.lambda <- 1 - var(apply(M1.resid, 2, mean)) / mean(apply(M1.resid, 1, var))

##================## Model 2 ~ Partial pooling for group-level slopes and intercepts


M2 <- "model{


 for(i in 1:n){

  y[i] ~ dnorm(y.hat[i], tau)

  y.hat[i] <- alpha[Cmpt[i]]  + beta[Cmpt[i]]*Time[i]  # Cmpt and Time are sampling-compartment and sampling-period variables


    # Assess model fit using a sums-of-squares-type discrepancy

    resid[i] <- y[i] - y.hat[i]                    # Residuals for observed data

    predicted[i] <- y.hat[i]                       # Predicted values

    sq[i] <- pow(resid[i], 2)                      # Squared residuals for observed data


    # Generate replicate data and compute fit stats for them

    y.new[i] ~ dnorm(y.hat[i], tau)                # One new data set at each MCMC iteration

    sq.new[i] <- pow(y.new[i] - predicted[i], 2)          # Squared residuals for new data

 }


 ## Group-level model

 for (j in 1:max(Cmpt)){

  alpha[j] <- B[j,1]

  beta[j] <- B[j,2]


  B[j,1:2] ~ dmnorm(B.hat[j,], Tau.B[,])    ## Constrain the varying intercepts and slopes to come from a
```

```
                              # bivariate normal distribution to covariance between parameters.


   B.hat[j,1] <- mu.a             ## Mean EIV across all sampling-compartments for time-period 1

   B.hat[j,2] <- mu.b                  ## Estimated mean difference across all sampling-compartments between tp1 and tp2



    alpha.t2[j] <- alpha[j] + beta[j]        ## Mean for time-period two as a derived variable.


    for(k in 1:2){

      E.B[j,k] <- B[j,k] - B.hat[j,k]    ## Residuals from the group-level intercepts and slopes

    }

  }


## Priors

tau <- 1/(sigma*sigma)

sigma ~ dunif(0, 100)     ## Species-level residual variation


mu.a ~ dnorm(0,0.001)

mu.b ~ dnorm(0,0.001)


Tau.B[1:2, 1:2] <- inverse(Sigma.B[,])       ## Convert variance/covariance matrix to precision for jags.


Sigma.B[1,1] <- pow(sigma.a, 2)

sigma.a ~ dunif(0, 100)

Sigma.B[2,2] <- pow(sigma.b, 2)
```

```
sigma.b ~ dunif(0, 100)

Sigma.B[1,2] <- rho*sigma.a*sigma.b
Sigma.B[2,1] <- Sigma.B[1,2]
rho ~ dunif(-1,1)

s.y <- sd(resid[])        ## Data level finite-population standard deviation
s.a <- sd(E.B[,1])      ## Intercept level finite-population standard deviation
s.b <- sd(E.B[,2])      ## Slope level finite-population standard deviation      ## These are calculated as the residual standard deviation at each level of the model

  fit <- sum(sq[])                    # Sum of squared residuals for actual data set ## Plant level
  f.sim <- sum(sq.new[])              # Sum of squared residuals for new data set

#data# n, y, Cmpt, Time
#Inits# sigma, sigma.a, sigma.b
#monitor# mu.a, mu.b, B, Sigma.B, y.hat, B.hat, fit, f.sim, resid, E.B, dic

}"

## Initial values
sigma <- list(rlnorm(1), rlnorm(1))  ## Note rlnorm for positive variance component
sigma.a <- list(rlnorm(1), rlnorm(1))
sigma.b <- list(rlnorm(1), rlnorm(1))

## Run model
results.M2 <- run.jags(M2, n.chains=3, sample = 10000)
```

```
## Calculate the Bayesian R^2 adjusted:

# For the data level model
M2.resid <- as.mcmc(results.M2, vars="resid")
rsquared.y.M2 <- 1 - mean(apply(M2.resid, 1, var))/var(y.N)


## Calculate summary of pooling factors
# Data level model
M2_y.lambda <- 1 - var(apply(M2.resid, 2, mean)) / mean(apply(M2.resid, 1, var))

# Group level model
E.B <- as.matrix(as.mcmc(results.M2b_N_With_residuals, vars="E.B"))      ## Extract group level residuals
e.a_m2 <- E.B[,1:74]
e.b_m2 <- E.B[,75:148]

# Group level intercepts
M2_alpha.lambda <- 1 - var(apply(e.a_m2, 2, mean)) / mean(apply(e.a_m2, 1, var))
# Group level slopes
M2_betaN.lambda <- 1 - var(apply(e.b_m2b, 2, mean)) / mean(apply(e.b_m2b, 1, var))
```

```
##================## Model 3 ~ Partial pooling with group-level predictors for slopes and intercepts



M3 <- "model{


 for(i in 1:n){
   y[i] ~ dnorm(y.hat[i], tau)
   y.hat[i] <- alpha[Cmpt[i]]  + beta[Cmpt[i]]*Time[i]   # Cmpt and Time are sampling-compartment and sampling-period variables


     # Assess model fit using a sums-of-squares-type discrepancy
     resid[i] <- y[i] - y.hat[i]                      # Residuals for observed data
     predicted[i] <- y.hat[i]                          # Predicted values
     sq[i] <- pow(resid[i], 2)                          # Squared residuals for observed data

     # Generate replicate data and compute fit stats for them
     y.new[i] ~ dnorm(y.hat[i], tau)                      # One new data set at each MCMC iteration
     sq.new[i] <- pow(y.new[i] - predicted[i], 2)          # Squared residuals for new data
 }


 ## Group-level model
 for (j in 1:max(Cmpt)){
   alpha[j] <- B[j,1]
   beta[j] <- B[j,2]
```

```
   B[j,1:2] ~ dmnorm(B.hat[j,], Tau.B[,])    ## Constrain the varying intercepts and slopes to come from a
                                 # bivariate normal distribution to covariance between parameters.


   B.hat[j,1] <- gamma.a[Eco.hab[j]]             ## Habitat-level means for time-period 1
   B.hat[j,2] <- gamma.b[Eco.hab[j]]               ## Habitat-level differences between time-periods



     alpha.t2[j] <- alpha[j] + beta[j]         ## Means for time-period two as derived variables.


     for(k in 1:2){
       E.B[j,k] <- B[j,k] - B.hat[j,k]    ## Residuals from the group-level intercepts and slopes
     }
  }


## Priors
tau <- 1/(sigma*sigma)
sigma ~ dunif(0, 100)     ## Species-level residual variation


for(i in 1:7){
  gamma.a[i] ~ dnorm(0,0.001)       ## Ecological habitat-level Eberg means for time period one
  gamma.b[i] ~ dnorm(0,0.001)       ## Ecological habitat-level between time-period difference


   ## Derived means for habitat groups in time-period 2
```

```
   gamma.a.2[i] <- gamma.a[i] + gamma.b[i]     ## Habitat-level Eberg means for time period 2
}

Tau.B[1:2, 1:2] <- inverse(Sigma.B[,])       ## Convert variance/covariance matrix to precision for jags.

Sigma.B[1,1] <- pow(sigma.a, 2)
sigma.a ~ dunif(0, 100)
Sigma.B[2,2] <- pow(sigma.b, 2)
sigma.b ~ dunif(0, 100)

Sigma.B[1,2] <- rho*sigma.a*sigma.b
Sigma.B[2,1] <- Sigma.B[1,2]
rho ~ dunif(-1,1)

s.y <- sd(resid[])        ## Data level finite-population standard deviation
s.a <- sd(E.B[,1])      ## Intercept level finite-population standard deviation
s.b <- sd(E.B[,2])     ## Slope level finite-population standard deviation      # These are calculated ast the residual standard deviation at each level of the model

fit <- sum(sq[])                    # Sum of squared residuals for actual data set Species-level
f.sim <- sum(sq.new[])             # Sum of squared residuals for new data set

#data# n, y.N, Cmpt, Time, Eco.hab
#Inits# sigma, sigma.a, sigma.b
#monitor# alpha, alpha.t2, beta, sigma, sigma.a, sigma.b, s.y, s.a, s.b, gamma.a, gamma.b, rho, resid, E.B, dic
}"
```

```
## Initial values
sigma <- list(rlnorm(1), rlnorm(1))  ## Note rlnorm for positive variance component
sigma.a <- list(rlnorm(1), rlnorm(1))
sigma.b <- list(rlnorm(1), rlnorm(1))

## Fit the model
results.M3 <- run.jags(M3, n.chains=3, sample = 10000)



## Calculate the Bayesian R^2 adjusted:

# For the data level model
M3.resid <- as.mcmc(results.M3, vars="resid")
rsquared.y.M3 <- 1 - mean(apply(M3.resid, 1, var))/var(y.N)

# Group level model
E.B.M3 <- as.matrix(as.mcmc(results.M3, vars="E.B"))  ## Extract group-level residuals
e.a.M3 <- E.B.M3[,1:74]
e.b.M3 <- E.B.M3[,75:148]

# For the group-level intercepts
alpha.M3 <- as.mcmc(results.M3, vars="alpha")
rsquared.alpha.M3 <- 1 - mean(apply(e.a.M3, 1, var))/mean(apply(alpha.M3, 1, var))

# And the group-level slopes
```

```
beta.M3 <- as.mcmc(results.M3, vars="beta")

rsquared.beta.M3 <- 1 - mean(apply(e.b.M3, 1, var))/mean(apply(beta.M3, 1, var))



## Calculate summary of pooling factors:


# Data level model

M3.lambda <- 1 - var(apply(M3.resid, 2, mean)) / mean(apply(M3.resid, 1, var))


# Group level intercepts

M3_alpha.lambda <- 1 - var(apply(e.a.M3, 2, mean)) / mean(apply(e.a.M3, 1, var))


# Group level slopes

M3_beta.lambda <- 1 - var(apply(e.b.M3, 2, mean)) / mean(apply(e.b.M3, 1, var))
```

Supplementary materials submitted for publication of chapter 2.

Compartment	cmpt.num	cmpt.num_within.eco.hab.type	Eco.habitat	Eco.habitat.num	num.species	time.period	cmpt.area_m^2	x_coord_BNG	y_coord_BNG
Brands heath	1	1	Heath_T	1	73	0	72367.88	402378.5	84712.94
Curlew cottages	2	2	Heath_T	1	48	0	899.5889	402577.2	85086.06
Curlew heath	3	3	Heath_T	1	43	0	74255.92	402704.5	85241.86
Little sea enclosure	4	4	Heath_T	1	41	0	10853.81	402690	84739.12

Pipley heath	5	5	Heath_T	1	84	0	15024.35	402919.5	83773.62
Plateau heath north	6	6	Heath_T	1	69	0	97817.7	402884.5	85772.53
Plateau heath south	7	7	Heath_T	1	51	0	200764.4	402518.2	85397.56
Spur heath	8	8	Heath_T	1	64	0	114452.2	402594.9	84582.95
Western Arm Heath	9	9	Heath_T	1	99	0	46662.21	402587.6	84965.55
Wood Heath	10	10	Heath_T	1	81	0	6391.836	402853.3	84017.74

East heath pines	11	1	Heath_D	2	34	0	7744.334	403315.3	84887.3
First ridge north	12	2	Heath_D	2	80	0	129864.2	403911.5	85617.07
First ridge south	13	3	Heath_D	2	41	0	172979.8	403478	84606.38
Inner Ridge	14	4	Heath_D	2	32	0	24413.98	403295.2	84417.08
Pipley hollow	15	5	Heath_D	2	22	0	3204.267	403272.5	83961.11
Second ridge N	16	6	Heath_D	2	60	0	144635.4	403657.7	85675

Second ridge S	17	7	Heath_D	2	32	0	29201.24	403411.7	85252.74
Southern heath	18	8	Heath_D	2	44	0	127788.7	403250.3	84240.32
Third ridge central	19	9	Heath_D	2	111	0	67848.99	403334.6	85863.15
Third ridge north	20	10	Heath_D	2	116	0	38697.82	403272.4	86066.33
Third ridge south	21	11	Heath_D	2	74	0	26285.42	403137.3	85339.74
Third ridge west	22	12	Heath_D	2	63	0	11127.94	403128.5	85555.2

Third ridge west heath	23	13	Heath_D	2	33	0	12711.96	403131.4	85727.11
Aspen wood	24	1	Wood	3	73	0	9446.228	403146.1	83713.37
Northern enclosure	25	2	Wood	3	71	0	24884.99	403561.7	86244.78
Northern Enclosure Extension	26	3	Wood	3	93	0	7066.84	403501	86283.17
Pipley enclosure	27	4	Wood	3	268	0	34921.55	403111.6	83743.02
Pipley wood	28	5	Wood	3	56	0	30188.62	403194.8	83795.34
Plateau enclosure	29	6	Wood	3	124	0	13318.97	403021.2	85607.95
Plateau enclosure extension	30	7	Wood	3	55	0	7791.239	403001	85636.02

Third ridge pines	31	8	Wood	3	38	0	7865.834	403044.4	85455.08
Three acre wood	32	9	Wood	3	73	0	9910.083	402911.9	84003.27
Twelve acre wood	33	10	Wood	3	112	0	50491.84	402914.2	84195.13
Western Arm Pines	34	11	Wood	3	32	0	24283.05	402583	84743.82
Knoll Dunes	35	1	Dune	4	18	0	4541.302	403391.7	83654.48
Lone dune	36	2	Dune	4	12	0	5878.515	403243.5	84335.71
Northern dunes	37	3	Dune	4	45	0	10973.43	403666.3	86262.08
Shell bay dunes	38	4	Dune	4	62	0	78455.08	403754.6	86154.26
South haven flats	39	5	Dune	4	128	0	6286.17	403451.5	86346.55
Zero ridge south	40	6	Dune	4	7	0	104029.1	403608.7	84623.99
Bramble bush bay	41	1	H_shore	5	117	0	131970.6	403101.9	86109.75
Brands creek	42	2	H_shore	5	77	0	26117.14	402276.8	84788.05

Dyke bay	43	3	H_shore	5	46	0	76795.11	402703.1	85840.35
Dyke bay saltmarsh	44	4	H_shore	5	22	0	6624.107	402531.3	85683.51
Gravel Spit	45	5	H_shore	5	65	0	4574.459	402924.7	85982.3
Plateau bay	46	6	H_shore	5	57	0	49603.62	402335.1	85642.19
Redhorn bay ex ciffs	47	7	H_shore	5	54	0	65331.81	402255.8	85251.07
Redhorn quay ex shore	48	8	H_shore	5	86	0	5514.588	402283.1	85493.83
Sandy point	49	9	H_shore	5	42	0	1170.44	402481	85708.04
Central marsh north	50	1	Marsh	6	62	0	131093.8	403488.1	85829.4

Central marsh south	51	2	Marsh	6	70	0	114065.2	403203.5	85228.98
Central tongue	52	3	Marsh	6	44	0	4295.939	403708.3	85316.46
East marsh	53	4	Marsh	6	49	0	64881.64	403228.7	84752.52
Eastern lake marsh	54	5	Marsh	6	94	0	89181.82	403394.1	85071.19
Little sea swamp	55	6	Marsh	6	43	0	35265.17	402857	84740.26
Lone dunes marsh	56	7	Marsh	6	15	0	1919.025	403203.6	84368.73
New pool marsh	57	8	Marsh	6	38	0	49369.14	403076	85404.74
Northern dunes marsh	58	9	Marsh	6	67	0	5918.71	403644.8	86198.01
Northern tongues	59	10	Marsh	6	61	0	7408.769	403991.6	85868.52
One Acre Pool Marsh	60	11	Marsh	6	105	0	22383.47	403204.4	85735.34

Pipley swamp	61	12	Marsh	6	108	0	57982.68	403011.1	83871.71
Saltings strip	62	13	Marsh	6	99	0	49044.66	403766.1	85581.13
Spur bog	63	14	Marsh	6	112	0	33773.25	402725.1	84294.74
Western Arm Marsh	64	15	Marsh	6	68	0	15544.56	402739.7	84998.22
Wood Marsh	65	16	Marsh	6	63	0	3016.789	402843.8	83925.32
Eastern lake	66	1	Aquatic	7	50	0	25373.45	403469.7	85047.66
Little sea central	67	2	Aquatic	7	6	0	86303.72	402994.9	84876.4
LS Northern one	68	3	Aquatic	7	16	0	6590.469	402984.4	85512.43
LS Northern two	69	4	Aquatic	7	8	0	58613.8	402879.7	85235.29
LS Southern one	70	5	Aquatic	7	14	0	108148.2	402969	84469
LS Southern two	71	6	Aquatic	7	21	0	41159.31	403082	84155.51

One acre pool main pool	72	7	Aquatic	7	17	0	4465.494	403237.4	85831.78
Pipley pools	73	8	Aquatic	7	17	0	9825.182	403250	83748.87
Western Arm	74	9	Aquatic	7	35	0	29835.04	402748.4	84844.74
Brands heath	1	1	Heath_T	1	146	1	72367.88	402378.5	84712.94
Curlew cottages	2	2	Heath_T	1	49	1	899.5889	402577.2	85086.06
Curlew heath	3	3	Heath_T	1	59	1	74255.92	402704.5	85241.86
Little sea enclosure	4	4	Heath_T	1	49	1	10853.81	402690	84739.12

Pipley heath	5	5	Heath_T	1	72	1	15024.35	402919.5	83773.62
Plateau heath north	6	6	Heath_T	1	98	1	97817.7	402884.5	85772.53
Plateau heath south	7	7	Heath_T	1	98	1	200764.4	402518.2	85397.56
Spur heath	8	8	Heath_T	1	90	1	114452.2	402594.9	84582.95
Western Arm Heath	9	9	Heath_T	1	74	1	46662.21	402587.6	84965.55
Wood Heath	10	10	Heath_T	1	29	1	6391.836	402853.3	84017.74

East heath pines	11	1	Heath_ D	2	23	1	7744.334	403315.3	84887.3
First ridge north	12	2	Heath_ D	2	47	1	129864.2	403911.5	85617.07
First ridge south	13	3	Heath_ D	2	55	1	172979.8	403478	84606.38
Inner Ridge	14	4	Heath_ D	2	65	1	24413.98	403295.2	84417.08
Pipley hollow	15	5	Heath_ D	2	96	1	3204.267	403272.5	83961.11
Second ridge N	16	6	Heath_ D	2	67	1	144635.4	403657.7	85675

Second ridge S	17	7	Heath_D	2	47	1	29201.24	403411.7	85252.74
Southern heath	18	8	Heath_D	2	154	1	127788.7	403250.3	84240.32
Third ridge central	19	9	Heath_D	2	66	1	67848.99	403334.6	85863.15
Third ridge north	20	10	Heath_D	2	137	1	38697.82	403272.4	86066.33
Third ridge south	21	11	Heath_D	2	45	1	26285.42	403137.3	85339.74
Third ridge west	22	12	Heath_D	2	37	1	11127.94	403128.5	85555.2

Third ridge west heath	23	13	Heath_D	2	65	1	12711.96	403131.4	85727.11
Aspen wood	24	1	Wood	3	74	1	9446.228	403146.1	83713.37
Northern enclosure	25	2	Wood	3	34	1	24884.99	403561.7	86244.78
Northern Enclosure Extension	26	3	Wood	3	112	1	7066.84	403501	86283.17
Pipley enclosure	27	4	Wood	3	164	1	34921.55	403111.6	83743.02
Pipley wood	28	5	Wood	3	95	1	30188.62	403194.8	83795.34
Plateau enclosure	29	6	Wood	3	75	1	13318.97	403021.2	85607.95
Plateau enclosure extension	30	7	Wood	3	62	1	7791.239	403001	85636.02

Third ridge pines	31	8	Wood	3	24	1	7865.834	403044.4	85455.08
Three acre wood	32	9	Wood	3	29	1	9910.083	402911.9	84003.27
Twelve acre wood	33	10	Wood	3	105	1	50491.84	402914.2	84195.13
Western Arm Pines	34	11	Wood	3	17	1	24283.05	402583	84743.82
Knoll Dunes	35	1	Dune	4	44	1	4541.302	403391.7	83654.48
Lone dune	36	2	Dune	4	27	1	5878.515	403243.5	84335.71
Northern dunes	37	3	Dune	4	59	1	10973.43	403666.3	86262.08
Shell bay dunes	38	4	Dune	4	111	1	78455.08	403754.6	86154.26
South haven flats	39	5	Dune	4	90	1	6286.17	403451.5	86346.55
Zero ridge south	40	6	Dune	4	46	1	104029.1	403608.7	84623.99
Bramble bush bay	41	1	H_shore	5	94	1	131970.6	403101.9	86109.75
Brands creek	42	2	H_shore	5	92	1	26117.14	402276.8	84788.05

Dyke bay	43	3	H_shore	5	60	1	76795.11	402703.1	85840.35
Dyke bay saltmarsh	44	4	H_shore	5	37	1	6624.107	402531.3	85683.51
Gravel Spit	45	5	H_shore	5	38	1	4574.459	402924.7	85982.3
Plateau bay	46	6	H_shore	5	58	1	49603.62	402335.1	85642.19
Redhorn bay ex ciffs	47	7	H_shore	5	76	1	65331.81	402255.8	85251.07
Redhorn quay ex shore	48	8	H_shore	5	73	1	5514.588	402283.1	85493.83
Sandy point	49	9	H_shore	5	40	1	1170.44	402481	85708.04
Central marsh north	50	1	Marsh	6	80	1	131093.8	403488.1	85829.4

Central marsh south	51	2	Marsh	6	73	1	114065.2	403203.5	85228.98
Central tongue	52	3	Marsh	6	18	1	4295.939	403708.3	85316.46
East marsh	53	4	Marsh	6	59	1	64881.64	403228.7	84752.52
Eastern lake marsh	54	5	Marsh	6	51	1	89181.82	403394.1	85071.19
Little sea swamp	55	6	Marsh	6	57	1	35265.17	402857	84740.26
Lone dunes marsh	56	7	Marsh	6	24	1	1919.025	403203.6	84368.73
New pool marsh	57	8	Marsh	6	56	1	49369.14	403076	85404.74
Northern dunes marsh	58	9	Marsh	6	71	1	5918.71	403644.8	86198.01
Northern tongues	59	10	Marsh	6	32	1	7408.769	403991.6	85868.52
One Acre Pool Marsh	60	11	Marsh	6	44	1	22383.47	403204.4	85735.34

Pipley swamp	61	12	Marsh	6	98	1	57982.68	403011.1	83871.71
Saltings strip	62	13	Marsh	6	72	1	49044.66	403766.1	85581.13
Spur bog	63	14	Marsh	6	78	1	33773.25	402725.1	84294.74
Western Arm Marsh	64	15	Marsh	6	58	1	15544.56	402739.7	84998.22
Wood Marsh	65	16	Marsh	6	49	1	3016.789	402843.8	83925.32
Eastern lake	66	1	Aquatic	7	16	1	25373.45	403469.7	85047.66
Little sea central	67	2	Aquatic	7	33	1	86303.72	402994.9	84876.4
LS Northern one	68	3	Aquatic	7	20	1	6590.469	402984.4	85512.43
LS Northern two	69	4	Aquatic	7	21	1	58613.8	402879.7	85235.29
LS Southern one	70	5	Aquatic	7	38	1	108148.2	402969	84469
LS Southern two	71	6	Aquatic	7	48	1	41159.31	403082	84155.51

One acre pool main pool	72	7	Aquatic	7	21	1	4465.494	403237.4	85831.78
Pipley pools	73	8	Aquatic	7	61	1	9825.182	403250	83748.87
Western Arm	74	9	Aquatic	7	19	1	29835.04	402748.4	84844.74

The Models

$$SGL_i \sim \text{Bernoulli } (p_i)$$

$$\text{Logit } (p_i) = A_i^{VA} + B_i^{NV}\ B_i^{OR} + B_i^{AN} + B_i^{SY} + B_i^{OD} + Sp_{species\ i}$$

$$A_i^{VA} = \alpha + \alpha_{cmpt\ i}\ \sigma_{\alpha\ cmpt}$$

$$B_i^{NV} = \beta^{NV} + \beta_{cmpt\ i}^{NV}\ \sigma_{\beta\ cmpt}^{NV}$$

$$B_i^{OR} = \beta^{OR} + \beta_{cmpt\ i}^{OR}\ \sigma_{\beta\ cmpt}^{OR}$$

$$B_i^{AN} = \beta^{AN} + \beta_{cmpt\ i}^{AN}\ \sigma_{\beta\ cmpt}^{AN}$$

$$B_i^{SY} = \beta^{SY} + \beta_{cmpt\ i}^{SY}\ \sigma_{\beta\ cmpt}^{SY}$$

$$B_i^{OD} = \beta^{OD} + \beta_{cmpt\ i}^{OD}\ \sigma_{\beta\ cmpt}^{OD}$$

$$\begin{pmatrix} \alpha_{cmpt} \\ \beta_{cmpt}^{NV} \\ \beta_{cmpt}^{OR} \\ \beta_{cmpt}^{AN} \\ \beta_{cmpt}^{SY} \\ \beta_{cmpt}^{OD} \end{pmatrix} \sim \text{MVNormal } (0, S_{\ cmpt})$$

$$Sp_{species\ i} \sim \text{Normal } (0, \sigma_{species})$$

$$(\alpha, \beta^{NV}, \beta^{OR}, \beta^{AN}, \beta^{SY}, \beta^{OD}) \sim \text{Normal } (0, 5)$$

$$(\sigma_{\alpha\ cmpt}, \sigma_{\beta\ cmpt}^{NV}, \sigma_{\beta\ cmpt}^{OR}, \sigma_{\beta\ cmpt}^{AN}, \sigma_{\beta\ cmpt}^{SY}, \sigma_{\beta\ cmpt}^{OD}) \sim \text{HalfCauchy}(0, 2.5)$$

$$\sigma_{species} \sim \text{HalfCauchy}(0, 2.5)$$

Above is an algebraic representation of model M3.1 from chapter 3. The model is parameterised with an intercept A_i^{VA} which estimates the proportion of vascular plant species gains vs losses. A_i^{VA} varies by sampling compartment and is broken down into a mean (α) and compartment offset in the submodel ($A_i^{VA} = \alpha + \alpha_{cmpt\ i}\ \sigma_{\alpha\ cmpt}$), where $\sigma_{\alpha\ cmpt}$ provides an estimate of the variance among compartments. There are five sets of similarly varying slope parameters (B_i^{NV}, B_i^{OR}, B_i^{AN}, B_i^{SY} and B_i^{OD}), each of which estimates the difference in the proportion of species gains vs losses by compartment between the vascular plants and one of the remaining five focal taxa (non-vascular plants, Orthoptera, ants, hoverflies and Odonata). To construct intercept for any of these five taxa, we simply add the vascular plant intercept (A_i^{VA}) and the relevant slope value for the taxa of interest (eg. $A_i^{VA} + B_i^{SY}$ to construct intercepts for the hoverflies). To get a measure of pairwise congruencies in local changes (gains vs losses) between taxa across the peninsula, we construct posterior intercepts for each taxa and compute Pearson's correlations between them for each pair across the entire posteriors.

We now have pairwise distributions of correlations between taxa. However, we don't know what's causing these correlations; is it shared responses to environmental change, or possibly biotic interactions between taxa? We try to shed some light on the answer to this question by controlling for the effects of local changes in the environment on proportions of species gains vs losses, and recomputing the correlations. I present model M3.2 with environmental predictors in the R code used to fit the model, rather than expressing it algebraicly.

```
mFull_RDA__Ch2 <- map2stan(
 alist(
   # likeliood
   LG ~ dbinom(1,p),

   # linear models
   logit(p) <- (A + B_NV*NV + B_OR*OR + B_AN*AN + B_SY*SY + B_OD*OD) + Sp_offset[Species],

   A      <-    a +  a_Cmpt[Cmpt] +  a_Hab[Hab] + ba_F[Hab]*EIV_F + ba_L[Hab]*EIV_L + ba_R[Hab]*EIV_R + ba_S[Hab]*EIV_S,
   B_NV  <-  bnv  +  bnv_Cmpt[Cmpt]  +  bnv_Hab[Hab]  +  bnv_F[Hab]*EIV_F  +  bnv_L[Hab]*EIV_L  +  bnv_R[Hab]*EIV_R  +
bnv_S[Hab]*EIV_S,
   B_OR <- bor + bor_Cmpt[Cmpt] + bor_Hab[Hab] + bor_F[Hab]*EIV_F                                 + bor_R[Hab]*EIV_R,
   B_AN <- ban + ban_Cmpt[Cmpt] + ban_Hab[Hab] + ban_F[Hab]*EIV_F + ban_L[Hab]*EIV_L                                   +
ban_S[Hab]*EIV_S,
   B_SY  <- bsy + bsy_Cmpt[Cmpt] + bsy_Hab[Hab] + bsy_F[Hab]*EIV_F + bsy_L[Hab]*EIV_L,
   B_OD  <-  bod  +  bod_Cmpt[Cmpt]  +  bod_Hab[Hab]  +  bod_F[Hab]*EIV_F  +  bod_L[Hab]*EIV_L  +  bod_R[Hab]*EIV_R  +
bod_S[Hab]*EIV_S,

   # adaptive priors
   c(a_Cmpt,bnv_Cmpt,bor_Cmpt,ban_Cmpt,bsy_Cmpt,bod_Cmpt)[Cmpt] ~ dmvnormNC(sigma_Cmpt,Rho_Cmpt),
   c(a_Hab,bnv_Hab,bor_Hab,ban_Hab,bsy_Hab,bod_Hab,
     ba_F, bnv_F, bor_F, ban_F, bsy_F, bod_F,
     ba_L, bnv_L,        ban_L, bsy_L, bod_L,
     ba_R, bnv_R, bor_R,              bod_R,
     ba_S, bnv_S,        ban_S,       bod_S)[Hab] ~ dmvnormNC(sigma_Hab,Rho_Hab),
   Sp_offset[Species] ~ dnorm(0,sigma_Sp),

   # fixed priors
   c(a,bnv,bor,ban,bsy,bod) ~ dnorm(0,5),
   sigma_Cmpt ~ dcauchy(0,2.5),
   sigma_Hab ~ dcauchy(0,2.5),
   sigma_Sp ~ dcauchy(0,2.5),
   Rho_Cmpt ~ dlkjcorr(1),
   Rho_Hab ~ dlkjcorr(2)

 ) , data=df , iter=4000, warmup=1000, chains=4, cores=2)
```

Now the submodel for the vascular plant intercept is further broken down to include a variable offset for the habitat type a compartment belongs to, and varying slopes for mean changes per compartment in Ellenberg F, L, R, and S values (specifying wetness, light availability, pH, and salinity respectively). To get an estimate of the proportional species gains vs losses after controlling for these factors, we just add the mean and compartment offset ($\alpha + \alpha_{cmpt\ i}$). We similarly account for any systematic differences between the other taxa and the vascular plant attributable to these factors by adding them as predictors in the submodels for the slope parameters. We then recompute the posterior correlations having controlled for responses to these environmental changes (eg. correlation between vascular plants and hoverflies is the correlation between ($\alpha + \alpha_{cmpt\ i}$) and ($\alpha + \alpha_{cmpt\ i} + \beta^{SY} + \beta^{SY}_{cmpt\ i}$)).

Because the slope parameters are differences between the other taxa and the baseline (within the model) of the vascular plants, any shared signal in gains vs losses between vascular plants and another taxa which is caused by shared responses to environmental change will be contained within the intercept parameters. Once we strip out these shared effects, and any remaining systematic differences between vascular plants and another taxa, the residual correlations should be due to direct biotic interactions, and to shared responses to environmental change which was not included in the model.

Including varying habitat-level slope/intercept parameters allows us to account for these factors while not overloading the model with parameters.

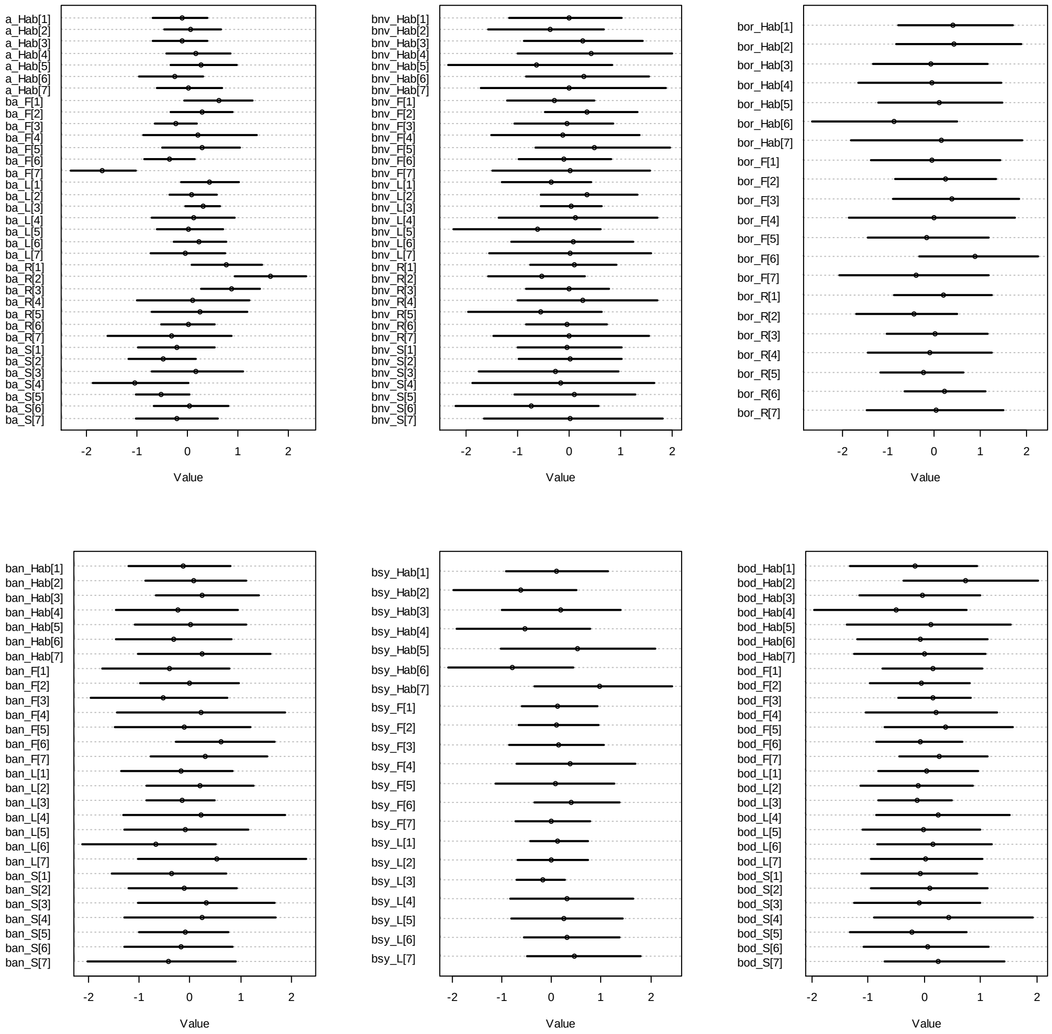

Figure 8.1 Parameter estimates from submodel predictors of model M3.2

Posterior predictive checks

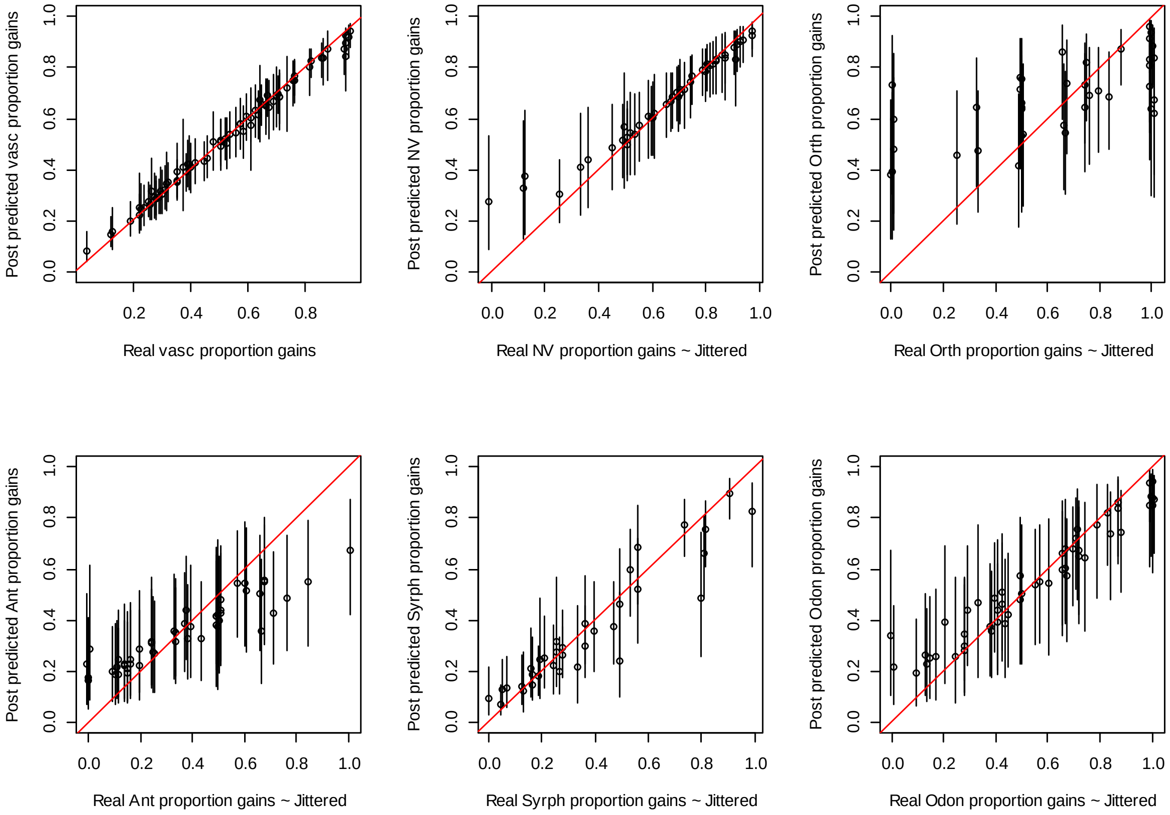

Figure 8.2 PPcheck for model m0 without the species offset.

All good and above board.

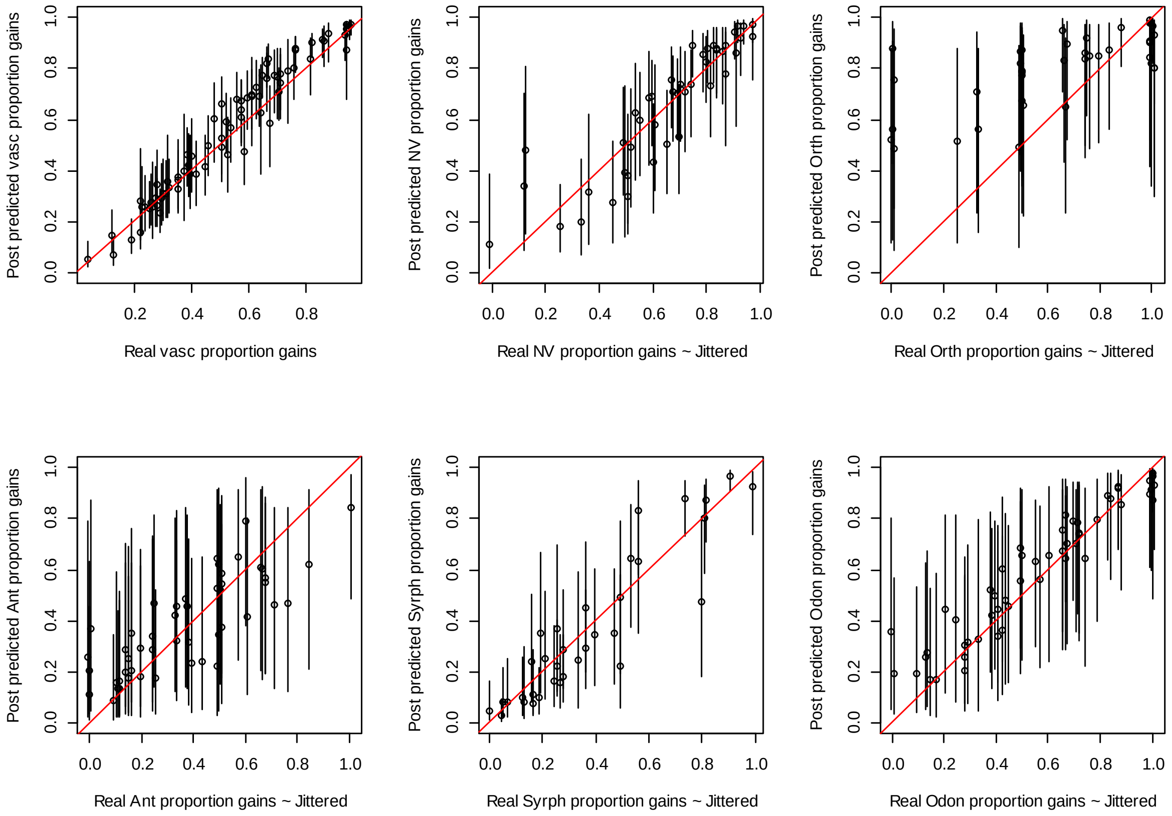

Figure 8.3 PPcheck for model M3.1.

Adding the species offset does introduce uncertainty into the compartment level estimates as we would expect – particularly for Orthoptera and ant groups. However, they are still mostly congruent with the raw proportions.

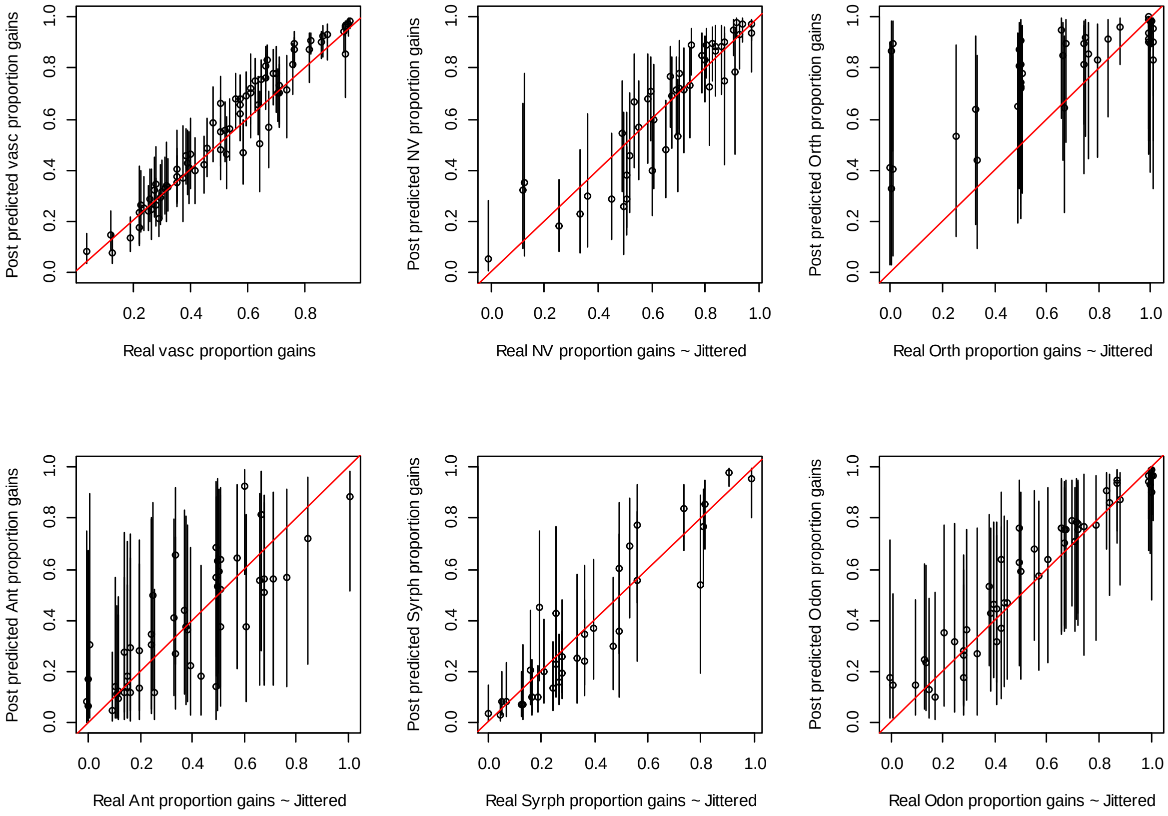

Figure 8.4 PPcheck for model M3.2 with environmental predictors.

Again, adding the submodel predictors causes a little more uncertainty in the compartment level estimates, but they are still mostly in agreement with the raw proportions.

Cross-taxon correlations data subset

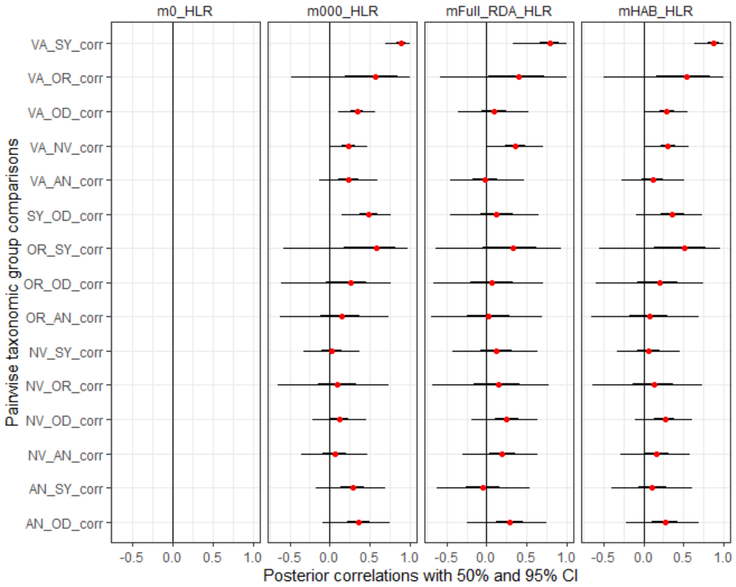

Figure 8.5 Cross-taxon correlations in proportional species gain vs losses (i.e. proportional species richness differences) computed for subset of data in which species were only included for each taxonomic group if they were recorded in 20% or more of the total (taxon specific) number of sampling compartments in the time-period in which that species was more widespread across compartments.

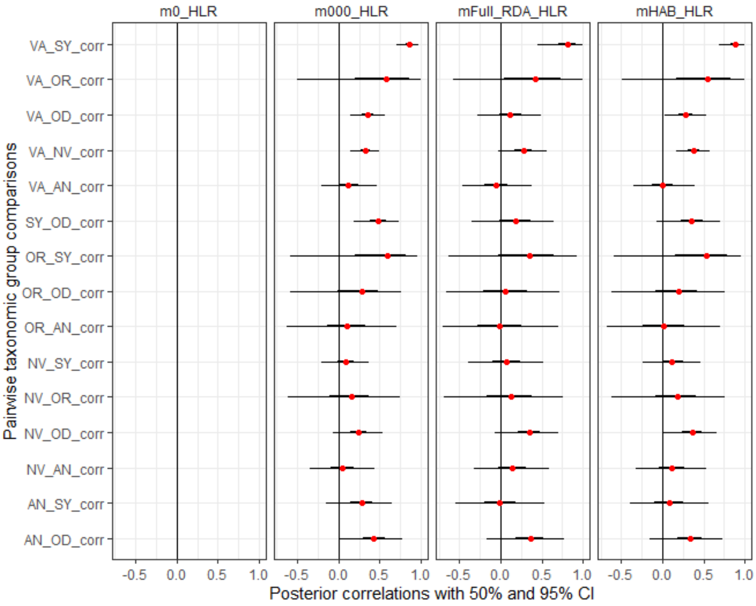

Figure 8.6 Cross-taxon correlations in proportional species gain vs losses for full dataset. The same as in main body of the text, but reproduced here for comparison.

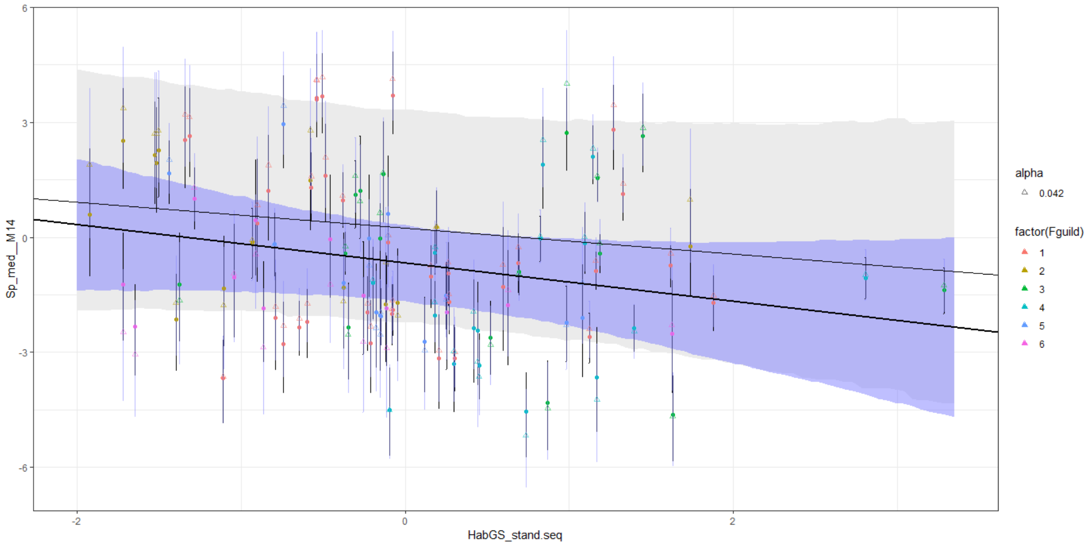

Figure 8.7 Effect of standardised number of habitats hoverfly species are associated with of the proportional gains vs losses between 1930s and 2010s. Blue interval is from model with just habitat gen/spe, grey interval is from full model.

Appendix 5. Spatial Autocorrelation

Spatial autocorrelation was tested for in R by computing Moran's I values on sampling compartment level proportional species gain vs losses for each taxa, and for model estimates of the same and compartment level model residuals. Autocorrelation was tested for on an adjacency matrix of compartments following (Brunsdon & Comber 2018). The adjacency matrix is a matrix indicating whether each sampling compartment pair share a boundary.

Min and max possible values of Moran's I, given W-matrix for compartments for each taxa are:

VA: [1] -1.082229 1.230397; NV:[1] -1.036326 1.104035; OR: [1] -1.031874 1.113671; AN: [1] -1.223380 1.278873; SY: [1] -1.154701 1.154701; OD: [1] -1.039250 1.133289

Table of Moran's I with associated p-values for mean species gains vs losses at sampling compartment level for Vascular plants (VA), Non-vascular plants (NV), Orthoptera (OR), Ants (AN), Hoverflies (SY) and Odonata (OD).

	VA	NV	OR	AN	SY	OD
Moran's I:	0.39	-0.156	0.123	0.149	0.23	-0.105
p-value:	< 0.005	0.85	0.15	0.09	0.06	0.79

Table of Moran's I with associated p-values for model estimates of proportional species gains vs losses at sampling compartment level for Vascular plants (VA), Non-vascular plants (NV), Orthoptera (OR), Ants (AN), Hoverflies (SY) and Odonata (OD). Models are m000 and mFULL from chapter 3 in the main body of the thesis.

Model		VA	NV	OR	AN	SY	OD
m000	*Moran's I:*	0.4	-0.145	0.234	0.176	0.39	-0.061
	p-value:	< 0.005	0.85	0.04	0.06	0.005	0.65
mFULL	*Moran's I:*	0.39	-0.15	0.242	0.212	0.412	-0.088
	p-value:	< 0.005	0.84	0.03	0.03	0.004	0.74

Table of Moran's I with associated p-values for model residuals for proportional species gains vs losses at sampling compartment level for Vascular plants (VA), Non-vascular plants (NV), Orthoptera (OR), Ants (AN), Hoverflies (SY) and Odonata (OD). Models are m000 and mFULL from chapter 3 in the main body of the thesis.

Model		VA	NV	OR	AN	SY	OD
m000	*Moran's I:*	0.08	-0.088	-0.078	0.169	-0.223	-0.105
	p-value:	0.13	0.71	0.64	0.06	0.88	0.79
mFULL	*Moran's I:*	0.187	-0.077	-0.074	0.179	-0.511	-0.06
	p-value:	0.009	0.67	0.63	0.05	0.99	0.65

Vascular plants, Ants and Hoverflies showed distinct patterns of autocorrelation in both compartment mean observations of proportional species gain vs losses, and model estimates of gains vs losses. However, statistically significant spatial autocorrelation was only apparent in model compartment level binned model residuals for vascular plants under the model (surprisingly) including habitat and EIV predicters.

Autocorrelated compartment means for model estimates may have contributed to pairwise correlations between taxa autocorrelation is present for both taxa out of the pair (REF: Legendre book). However, the underlying cause of spatial autocorrelations are unclear, and uncovering spatiotemporal correlations was a main aim of chapter 3 of this thesis.

In chapter 4, spatial autocorrelation may have contributed to the strength of the effect of plant species richness difference on the compartment level change in hoverfly species richness. However, spatial autocorrelation should not have affected any other parameters in the models for this chapter, as model m000 above was the starting point for hierarchical models in this chapter, and this model did not display any autocorrelation in the residuals.