Spatiotemporal patterns in population dynamics and consequences for ecosystem function

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Lisbeth Anna Hordley

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Preface

This thesis includes one published manuscript (Chapter 4):

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In this thesis Chapter 2 has also been submitted for publication as follows:

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Declaration

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

Lisbeth A. Hordley

For published and submitted chapters, author contributions are detailed below.

Chapter 2 – Developing a national indicator of functional connectivity:

LAH, OLP, JAT and THO designed the study. LAH conducted statistical analysis and GDP created scripts to calculate population synchrony. All authors contributed to writing the manuscript.

Chapter 4 – Diversity of response and effect traits provides complementary information about avian community dynamics linked to ecological function:

LAH, OLP, JAT and THO designed the study. LAH conducted statistical analysis. All authors contributed to the writing of the manuscript.

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Abstract

Biodiversity is declining across the globe, threatening ecosystem functioning, and the services that humans rely upon. Biodiversity monitoring schemes have provided a wealth of information on population changes across space and time and are used to advise and influence environmental legislation and policy. Despite the utilisation of monitoring data, there are still gaps in the application of this data in policy making and addressing unanswered questions. This thesis focuses on using long-term monitoring data and trait datasets to develop novel methodological techniques, and further understand the key drivers of population dynamics, and our ability to detect changes in community dynamics.

First, long-term population monitoring data are used to develop a novel technique to measure functional connectivity of butterflies and birds across the UK. Current methodologies to measure functional connectivity are constrained by time and data-availability. However, using a method based on correlations between species population dynamics offers a 'species-eyed view' of functional connectivity which can be easily updated. Second, the two key drivers of synchronised population dynamics, dispersal, and climate, are further investigated. After accounting for climate effects on population synchrony, temporal changes in population synchrony are associated with mobility-attributes of UK butterflies and birds. This represents an important contribution to the understanding of what drives spatiotemporal changes in population dynamics. For the next two chapters, the community dynamics of British birds is investigated, to determine how different functional trait approaches can affect our ability to detect community changes of functionally important birds. Extensive functional trait data alongside long-term monitoring data are used to show how different types of traits in metrics of functional diversity affect our ability to detect changes in community dynamics and ecosystem functioning. Furthermore, using traits that provide highly refined information alongside abundance data in measures of functional diversity increases our ability to predict community dynamics of functionally important birds.

This work highlights the use of long-term monitoring data and functional trait approaches to further understand changes in population dynamics, in particular to develop a new method to measure functional connectivity and linking changes in functional diversity to changes in community dynamics related to ecosystem functioning. In the final chapter, the limitations of the work are discussed along with the wide range of future applications.

Chapter 1. Introduction

1.1 Biodiversity and ecosystem functioning

There is overwhelming evidence that biodiversity is declining globally at unprecedented rates, with around 1 million animal and plant species now threatened with extinction, many within decades (IPBES, 2019). The picture is similar in the UK, where the abundance of UK species has, on average, declined by 13% since 1970 (State of Nature report, 2019). Changes in biodiversity can be attributed to anthropogenic drivers, including habitat loss and change, climate change, the introduction of invasive species, overexploitation, and pollution (Millennium Ecosystem Assessment, 2005). Increasing human impacts on the environment is not only driving declines in biodiversity, but also altering the structure and composition of biological communities by increasing rates of species invasions and species extinctions, at global and local scales (Hooper *et al.* 2005). Biodiversity is now known to be a major determinant of ecosystem dynamics and functioning (Tilman *et al.* 2014), as biodiversity enhances the ability for communities to capture resources, produce biomass, and recycle essential nutrients, and also contributes to ecosystem stability through time (Loreau & de Mazancourt 2013). Therefore, biodiversity loss could threaten the delivery of key ecosystem functions and services.

Ecosystem functions provided by biodiversity underpin the ecosystem services that humans rely upon. This includes provisioning services such as the supply of food and materials, supporting services including nutrient cycling and pollination, regulating services such as air and water quality regulation, and cultural services such as the recreational benefits gained from nature (Șekercioğlu *et al.* 2016). Birds are an important taxonomic group for providing all four types of ecosystem services. They are an important component of human diets (Moss & Bowers 2007) and are often hunted for consumption and recreation in developed countries (Bennett & Whitten 2003; Green & Elmberg 2014). Some species of birds contribute to regulating services as scavengers by consuming carcasses which helps regulate human disease (Șekercioğlu *et al.* 2016). Birds have also played an important part in our culture, through art, religion, and birdwatching. Finally, many birds contribute supporting services, as their foraging, seed dispersal, and pollination activities help to maintain ecosystems that humans rely upon (Sekercioglu 2006; Wenny *et al.* 2011). Butterflies also perform a range of ecosystem functions including the provision of food to higher trophic levels, as lepidopteran larvae are a key source of food for many bird species throughout chick development (Visser *et al.* 2006), and by providing pollination services through dispersing wildflower pollen (Courtney *et al.* 1982). Similar to birds, butterflies are also important culturally, whereby human well-being increases when time is spent in biodiverse and species-rich areas (Dallimer *et al.* 2012; Clark *et al.* 2014).

In order to safeguard biodiversity and the associated ecosystem services, the Convention on Biological Diversity (CBD) implemented the Strategic Plan for Biodiversity from 2011 – 2020 which consisted of 20 targets, named the Aichi Biodiversity Targets. Despite decades of conservation action, we did not meet any of the Aichi Targets in full (Buchanan *et al.* 2020). The post-2020 global biodiversity framework has the potential to address the loss and degradation of nature and attempt to "bend the curve" of biodiversity. As a result, there is great interest in monitoring the current state of biodiversity, how it has changed over time, and how this might impact the ecosystem functions that biodiversity provides.

1.2 Biodiversity monitoring

To help reduce biodiversity loss and the associated ecosystem services, we need well-informed, evidence-based decisions to help create and implement environmental policy. This relies upon there being available data on biodiversity across spatial and temporal scales. The UK has some of the longest running structured biodiversity monitoring schemes in the world. One of the first was the Common Birds Census (CBC), run by the British Trust for Ornithology (BTO) which ran from 1962 to 2000 to monitor population trends among widespread breeding birds, predominately in farmland and woodland habitats (Marchant 1990). This scheme has been superseded by the Breeding Bird Survey (BBS) which was launched in 1994 to overcome the spatial limitations of the CBC, which covers a wider geographical spread of UK bird populations and utilises a less intensive survey method (Harris *et al.* 2019). Another long-term monitoring scheme of a different taxonomic group is the UK Butterfly Monitoring Scheme (UKBMS) which has been ongoing since 1976 (Pollard & Yates 1993). The success of these schemes can be partly attributed to the use of members of the public volunteering their time to record species, and while there is a trade off in the accuracy of recordings in some instances due to observer error, this is outweighed by the geographical extent of these data, the level of spatial coverage, and the efficiency with which this data can be collected. These long-term monitoring schemes allow reliable estimates of trends in species abundances to be calculated (Newson *et al.* 2008; Pellet *et al.* 2012).

Trends in abundance across space and time can be used to assess progress towards national and international biodiversity targets set by the Convention on Biological Diversity (CBD). Despite decades of conservation action, the CBD Aichi Target 12 to halt species extinctions or reverse declines has not been achieved (Buchanan *et al.* 2020). The post-2020 global biodiversity framework aims to create targets that are measurable, and be more realistic, unambiguous, and scalable (Green *et al.* 2019). Global and national biodiversity indicators, produced using readily accessible data from long-term monitoring schemes, can allow assessment of the success and failure of interventions towards biodiversity targets (Mace *et al.* 2018). For example, the BBS data are used alongside other monitoring schemes for birds, to produce an indicator on the changes in abundance of breeding birds in farmland. This indicator can be used to understand the effectiveness of changes in farming management practices and interventions, such as agri-environment schemes, to increase farmland bird abundance, and therefore progress towards national biodiversity targets (Vickery *et al.* 2004; Walker *et al.* 2018).

It is clear that long-term monitoring schemes are crucial to aiding the recovery of biodiversity. Monitoring data can also be applied to answer ecological questions which can contribute to the conservation of populations and communities as a whole.

1.3 Population dynamics

Interactions between organisms and their environment result in changes in population dynamics, and these changes can be observed using long-term monitoring data. Understanding the causes of changes in species' population abundance is essential for effective policy development and conservation management and provides an understanding of how ecosystems may change with future climate change. There has been increasing recognition of the role that spatial context plays in population dynamics, shifting our perception from the dynamics of isolated populations to examining the dynamics of interconnected population dynamics.

1.3.1 Population synchrony

Spatial population dynamics can result in populations that vary together in population size. This phenomenon, termed population synchrony, was first described by Elton (1924) who demonstrated how the fluctuations in population sizes of snowshoe hares were spatially autocorrelated across North America due to the associations with its main predator, the

Canada lynx. The advance of long-term monitoring data which provides large quantities of spatially referenced time series data has allowed further analyses of spatial population dynamics. Population synchrony can be measured as the correlation in abundance between spatially separated populations over time and is known to be important for the long-term viability of metapopulations. Populations which are highly synchronised are more at risk of extinction (Heino *et al.* 1997), as all subpopulations will decline in abundance simultaneously reducing the ability for populations with high abundance to rescue those that go extinct. Understanding what mechanisms drive synchronous population dynamics therefore has practical implications for management and conservation.

There are three mechanisms which cause population synchrony. Firstly, synchronised population dynamics may be caused by shared environmental conditions between spatially separated sites, i.e. the ‘Moran effect’ (Moran 1953). Substantial theoretical (Ranta *et al.* 1995; Heino *et al.* 1997; Lande *et al.* 1999; Kendall *et al.* 2000; Ripa 2000) and empirical (Hanski & Woiwod 1993; Paradis *et al.* 1999; Ims & Andreassen 2000; Koenig 2002) work has supported environmentally driven spatial population synchrony, which declines with increasing distance between populations, partly due to spatial autocorrelation in climate (Hanski & Woiwod 1993; Roland & Matter 2007; Powney *et al.* 2011). Secondly, dispersal between spatially separated populations can bring them into synchrony through density-dependent emigration of individuals (Bjørnstad *et al.* 1999; Koenig 1999; Lande *et al.* 1999; Liebhold *et al.* 2004), with studies showing that species with high estimated dispersal capacities have greater levels of population synchrony (Sutcliffe *et al.* 1996; Paradis *et al.* 1999; Bellamy *et al.* 2003; Tittler *et al.* 2009). Finally, trophic interactions can give rise to spatial synchrony in prey or host populations due to the interactions between the predator or host (Bjørnstad *et al.* 1999; Ims & Andreassen 2000).

The two main drivers of population synchrony, climate and dispersal, are intertwined (Kendall *et al.* 2000). Future global warming is likely to cause direct changes to spatial population dynamics due to changes to the mean, variability, and spatial autocorrelation of the weather and environment (Koenig, 2002). Climate change could also impact population synchrony indirectly, through changes to dispersal and species interactions (Hansen *et al.* 2020). Therefore, patterns of synchrony from all three mechanisms are very similar and all may be acting simultaneously or in various combinations. Identifying which is the dominant force for a particular metapopulation in synchrony is one of the challenges in population dynamics. If we can disentangle the role of dispersal from environmental Moran effects, we may be able to obtain a signal of species' movement from temporal trends in population synchrony, which would be valuable for informing landscape-level conservation initiatives.

Fully understanding the effects of dispersal is crucial to applied ecology as human activities have led to increased habitat loss and fragmentation which can affect how species move through space and their ability for range expansion under climate change. Measuring the ability of individuals and populations to move between resource patches, i.e., functional connectivity, is crucial to understand the impact of anthropogenic land-use change on the viability of metapopulations (Hanski 1998; Tischendorf & Fahrig 2000).

1.3.2 Stability

The effect of biodiversity on the stability of natural systems is a central topic in ecology, as ecosystem stability suggests sustainability of species, communities, and ecosystem functioning. Early research demonstrated that more diverse communities enhanced ecosystem stability after observing that simplified communities are characterised by violent fluctuations in population density, thus decreasing stability (Odum 1953; MacArthur 1955; Elton 1958). This finding was further supported by experimental work in plant communities (Tilman & Downing 1994), and now there is substantial evidence that diversity increases stability at the community level (McCann 2000; Ives & Carpenter 2007; Pennekamp *et al.* 2018; Kéfi *et al.* 2019).

The commonly found positive correlation between diversity and stability is thought to be caused by three processes: overyielding, statistical averaging and compensatory dynamics. Overyielding occurs when there is higher ecosystem productivity (i.e. higher average total biomass) at higher diversity compared to monocultures (Tilman 1997; Hector *et al.* 1999; Loreau & Hector 2001; Cardinale *et al.* 2007). As traditional measures of stability are measured using the coefficient of variation (Schlapfer & Schmid 1999), a higher mean will decrease variability (Tilman 1999). Statistical averaging, also known as the portfolio effect, occurs because the relative fluctuations of a diverse community may be smaller than the relative fluctuation in the biomass of the constituent species (Doak *et al.* 1998). This leads to a lower coefficient of variance in a diverse community, compared to the average coefficient of variance of the individual species (Tilman *et al.* 1998). Finally, compensatory dynamics occurs where increase in abundance of one species is off set by the decline in abundance of another species, resulting in lower variability at the community level (Tilman 1999; Gonzalez & Loreau 2009; Loreau & de Mazancourt 2013). This asynchrony in population dynamics can be driven by competition for resources, predator-prey interactions, or asynchronous responses to environmental changes (Ives *et al.* 1999; Downing *et al.* 2008; Gonzalez & Loreau 2009). This latter process has been called the insurance hypothesis, where biodiversity insures ecosystems against declines in functioning due to a greater diversity of responses to environmental conditions in a community (Yachi & Loreau 1999).

As such, population dynamics and community stability are intricately linked to ecosystem functioning and the services they provide. Correlations between species' population dynamics can be utilised to determine whether functionally important species respond similarly to environmental conditions, and therefore inform upon the resilience of ecosystem functioning (Greenwell *et al.* 2019). Furthermore, the total number of individuals within a community (i.e., total community abundance) has been linked to the productivity of an ecosystem. This is predicted by the 'mass ratio hypothesis' (Grime 1998), where the most common or dominant species within a community use a larger proportion of resources and contribute more to ecosystem functioning (Smith & Knapp 2003; Kleijn *et al.* 2015; Winfree *et al.* 2015). In addition, dominant species can provide short-term resistance to reductions in ecosystems functions (Dangles & Malmqvist 2004).

1.4 Functional Diversity

There is now unequivocal evidence that biodiversity enhances the stability and magnitude of ecosystem functioning across variety of taxa (Hooper *et al.* 2005; Cardinale *et al.* 2011; Gaston *et al.* 2018; Delgado-Baquerizo *et al.* 2020). Understanding the effect of biodiversity loss on ecosystem functioning has resulted in a variety of methods to quantify biodiversity to improve our ability to capture changes in ecosystem functions (Hooper *et al.* 2005). Initial research into the biodiversity and ecosystem functioning (BEF) relationship experimentally manipulated species richness in grassland ecosystems and found that changes in species richness were strongly related to ecosystem processes such as nutrient availability (Naeem *et al.* 1994; Tilman & Downing 1994; Hector *et al.* 1999). However, there still remained a large proportion of variance in ecosystem functioning to be explained, which could not be captured by looking at species richness alone as it assumes that all species are equally distinct (Petchey & Gaston 2002). Instead of focussing on taxonomic diversity, measuring functional diversity, i.e., the number, type and distribution of functions performed by organisms within an ecosystem (Díaz & Cabido 2001), is widely recommended and its use has grown significantly for studies across a wide range of taxa (Zak *et al.* 1994; Stevens *et al.* 2003; Hooper *et al.* 2005; Cadotte *et al.* 2011; Cardinale *et al.* 2012).

1.4.1 Functional traits

In order to capture functional differences among species, ecologists use functional traits which are morphological, physiological or phenological characteristics measurable at the individual level and have an influence upon ecosystem functioning (Violle *et al.* 2007b). Early efforts to link species traits to ecosystem functioning have measured functional diversity by classifying species into functional groups based on the similarity of their traits, often according to expert opinion (Wedin & Tilman 1990; Hooper & Vitousek 1997; Tilman 1997; Hector *et al.* 1999). However, this approach has been criticised, as a single functional group is unlikely to capture to full extent of variation in functional traits within a community (Wright *et al.* 2006) and only a discrete metric of functional diversity is obtained (Petchey & Gaston 2006). More recently, quantitative methods have been developed which utilise information gained from multiple functional traits to produce a single continuous trait diversity index. The establishment of such indices has led to a more specific definition of functional diversity, which captures the value and range of those species and organismal traits that influence ecosystem functioning (Tilman 2001). The first of such indices defined functional diversity as the total branch length of a functional dendrogram, capturing the trait complementarity among species (Petchey & Gaston 2002). Various functional diversity metrics have since emerged by measuring the spread of species in multidimensional trait space (Walker *et al.* 1999; Mason *et al.* 2003; Petchey & Gaston 2006), however none of these indices were designed to use multiple traits and be weighted by species' relative abundance. Single-trait approaches are limited in the information they provide on functional diversity as multiple traits are required to characterise species resource niches (Mason *et al.* 2005). Furthermore, as more common species contribute more to ecosystem functioning (Grime 1998), functional diversity metrics can be weighted by abundance to reflect this. Villéger *et al.* (2008) produced a set of three complementary functional diversity indices, each capturing a different facet of functional diversity: functional richness (the volume of functional space occupied by a community), functional evenness (the regularity of the distribution of abundance within the volume), and functional divergence (the divergence in distribution of abundance in this volume). Finally, functional dispersion, which measures the mean distance in trait space of individual species to the centroid of all species, was developed to account for missing trait values and is unaffected by species richness (Laliberté & Legendre 2010). These trait-based indices have shown to be better predictors of ecosystem functioning compared to using species richness (Gagic *et al.* 2015) and therefore have been widely used in the literature to look at BEF relationships.

1.4.2 Methodological choices

A consistent message throughout the development of functional diversity indices is the importance of selecting the appropriate traits to predict ecosystem processes, and arguably this is more important than the choice of functional diversity measure (Petchey & Gaston 2006; Petchey *et al.* 2009). The success of trait-based methods relies on the selection of a sufficient number of informative functional traits (Hortal *et al.* 2015), as different traits are important for different ecosystem functions (Petchey & Gaston 2002). Possible methods to approach this issue include calculating functional diversity metrics with every combination of traits to test their explanatory power in predicting the ecosystem function of interest (Petchey *et al.* 2004) or calculating all possible functional spaces (Maire *et al.* 2015). These complete search methods outperform other trait selection methods which select a subset of traits to represent the variation of all traits highlighting the impact of trait choice in mechanistically linking functional traits to ecosystem functioning (Zhu *et al.* 2017).

The number of traits selected can also influence the values of functional diversity derived from multivariate indices (Maire *et al.* 2015; Legras *et al.* 2019) as this impacts the dimensionality of the trait space (Petchey & Gaston 2002). Recent studies have suggested that increasing the multidimensional trait space can more accurately predict trophic niches (Pigot *et al.* 2020) and capture phenotypic differences between species (Carscadden *et al.* 2017). Although higher dimensionality of trait space can reduce functional redundancy (Petchey & Gaston 2002), if such traits are highly correlated with each other, this reduces the ability to accurately identify species within trait space (Petchey *et al.* 2007; Calba *et al.* 2014; Laughlin 2014). Furthermore, the use of continuous traits over categorical or binary traits can also provide more in-depth information on species resource use, which affects the ability to detect true functional redundancy in a community (Kohli & Jarzyna 2021).

Finally, different types of traits provide information on different aspects of biodiversity related to ecosystem function (Tobias *et al.* 2020). Functional traits can be split into two categories: effect traits which determine the effect a species has on ecosystem functioning, and response traits which reflect species’ responses to environmental conditions (Lavorel &

Garnier 2002; Luck *et al.* 2012). This has allowed studies to specifically predict species' responses to environmental change using response traits (Azeria *et al.* 2011; Langlands *et al.* 2011). Grouping traits into these types has also resulted in a response-and-effect framework to be developed which incorporates both changes to communities as a result of their response to environmental change, and the effect of such changes on ecosystem function (Lavorel & Garnier 2002; Suding & Goldstein 2008). Some traits can be classified as both an effect and response trait (e.g. body size), and this can further increase the ability to predict the impact of environmental change on the delivery of ecosystem services (Lavorel & Garnier 2002; Suding *et al.* 2008).

1.4.3 Linking functional diversity to ecosystem functioning

Decades of research has made it evident that species functional traits are key to understanding the impact of environmental change on ecosystem functions and services (Cardinale *et al.* 2012). However, collecting many high-resolution traits is difficult due to practical limitations including cost and time and has resulted in taxonomic and spatial biases in trait datasets (Petchey & Gaston 2006; Pakeman 2014; Etard *et al.* 2020; Kohli & Jarzyna 2021). Despite such biases, trait-based methods have been widely used to provide an insight into the BEF relationship in both experimental and natural ecosystems across a wide range of taxonomic groups and spatiotemporal scales (Manning *et al.* 2019). Therefore, BEF research has the potential to influence policy and conservation management of 'real-world' ecosystems (Defra 2020c). Such trait-based methods can be used to understand the mechanisms underpinning stability of ecosystems to help make evidence-based conservation decisions (Oliver *et al.* 2015a). Many biodiversity conservation efforts have focussed on species only (Mace *et al.* 2003), however, the functional diversity of ecosystems is also at risk of declining due to anthropogenic pressures (Cadotte *et al.* 2011). Integrating functional ecology into conservation decision making can help reduce biodiversity loss and support the supply of multiple ecosystem services (Devictor *et al.* 2010; Manning *et al.* 2018, 2019).

1.5 Thesis overview

Long-term biological monitoring schemes of a wide variety of taxonomic groups have been vital in understanding how biodiversity has changed over time and been used to produce indicators of biodiversity change which have been pivotal in driving changes in policy and legislation. Furthermore, with the creation of large trait databases of well-studied taxonomic groups, we can utilise this breadth of information to further understand how biodiversity is changing, and what effect this could have on the provision of ecosystem functions.

The thesis aims to explore how population and community dynamics of functionally important species have changed across space and time under environmental change and how functional trait differences can help to understand these patterns. A common theme is the use of long-term monitoring data collected by volunteers as part of national recording schemes.

First, in Chapter 2, I develop an indicator of functional connectivity, utilising a new method based on population synchrony using long-term monitoring data from the UK Butterfly Monitoring Scheme (UKBMS), the Common Bird Census (CBC), and the Breeding Bird Survey (BBS). Previous indicators of functional connectivity are often very data intensive, restricted to small spatial scales, and require validation from independently collected data. However, this proposed indicator offers a 'species-eyed-view' of functional connectivity using a data-derived method based on widely available, annually updated species monitoring data. This work is currently an 'experimental indicator' being used by JNCC and Defra as part of the England Biodiversity Indicators (Defra 2020a).

In Chapter 3, I use the temporal trends in population synchrony calculated for butterflies and birds in Chapter 2 to determine whether we can untangle the two key drivers of population synchrony: climate and mobility. This chapter uses mobility-related traits to determine whether changes in synchrony over time are driven by more mobile species, after accounting for spatial autocorrelation in climate. This chapter adds to the growing body of literature that dispersal can synchronise populations not only across space, but also time. Furthermore, this provides evidence to support our use of population synchrony to measure functional connectivity in the UK.

I then ask whether our ability to detect changes in community dynamics over time depends on the type of traits used in metrics of functional diversity. In Chapter 4, I split bird species into their contribution to two ecosystem functions – seed dispersal and insect predation. I measure the stability and mean abundance of these functional guilds and investigate whether using effect or response traits affect our ability to observe these patterns. More specifically, I test the following hypotheses:

1. *Higher functional diversity measured using response traits will provide a more stable community abundance.*

2. *Higher functional diversity measured using effect traits will have a higher mean total community abundance.*

After finding that the choice of traits influences our ability to detect changes in community dynamics, I then seek to understand whether the resolution of data used also play a role. In Chapter 5, I test whether the resolution of trait and abundance data used to measure functional diversity affects our ability to predict community dynamics of functionally important birds. I hypothesise that more resolved data (i.e., a higher number of continuous functional traits and abundance data) used to measure functional diversity will explain more variation in community abundance.

Finally, in Chapter 6, I discuss the conclusions that can be drawn from this body of work, identify its strengths and weaknesses, and suggestions for future research.

Chapter 2. Developing a national indicator of functional connectivity

2.1 Abstract

Habitat loss is a significant driver of biodiversity loss, causing fragmentation into small, isolated patches of suitable land cover. This reduces the permeability of landscapes to the movement of individuals and reduces the likelihood of metapopulation persistence. Quantifying functional connectivity, the ability of a focal species to move between resource patches, is therefore essential for conservation management. There is substantial evidence supporting a technique based on 'population synchrony'- the degree of correlation in time-series of annual population growth rates between different long-term monitoring sites, to provide a measure of functional connectivity. However, synchronised population dynamics are not only driven by the movement of individuals between sites, but also shared environmental conditions which must be accounted for. Here, we use species survey data from over four decades to investigate average levels and temporal trends in population synchrony for 58 British bird and butterfly species. We first show that population synchrony is significantly associated with synchrony in some seasonal climatic variables. Once we accounted for spatiotemporal climatic patterns, we found that synchrony in butterflies declined over time by 71% between 1985 and 2000 but increased by 64% in recent years. Synchrony in birds showed some decline between 1999 and 2005, after which there appears to being recovery, however most species (74%) show no significant overall change in synchrony. Our proposed indicator provides a 'species-eye-view' of functional connectivity using widely available abundance data. Developing such indicators of functional connectivity, which can be updated annually, is crucial to improve the effectiveness of land management strategies for conservation under increasing environmental change.

2.2 Introduction

Habitat loss and fragmentation is a key concern of conservation policy both in the UK and globally, as it is implicated as the main driver of biodiversity loss in numerous taxa across a variety of regions (Fahrig 2003; Butchart *et al.* 2010; Pimm *et al.* 2014). Despite decades of conservation action, the Convention on Biological Diversity (CBD) Aichi Target 12 has not achieved its target to halt species extinctions or reverse declines (Buchanan *et al.* 2020). Habitat fragmentation, driven by anthropogenic land-use change, decreases the amount of available habitat and increases ecological isolation between patches. This can result in an increased extinction risk and a reduction in the exchange of individuals among fragmented populations (Hanski 1998). Therefore, functional connectivity, i.e. the ability of individuals and populations to move between resource patches in response to landscape elements, is crucial for managing and conserving viable metapopulations (Hanski 1998; Tischendorf & Fahrig 2000). Dispersal across landscapes is also essential for range expansion under climate change and the maintenance of genetic diversity (Hanski & Gilpin 1991; Hanski 1998).

Measuring levels of functional connectivity is vital for monitoring and predicting the effects of climate change and increasing habitat fragmentation on population persistence. Traditional approaches to calculate functional connectivity have focussed on measuring dispersal. Empirical movement data has been collected using mark-release-recapture (MRR) methods (Sutcliffe *et al.* 1997, 2003; Roland *et al.* 2000), by radio-tracking individuals (Sutcliffe & Thomas 1996; Rubenstein & Hobson 2004), or more recently, by using landscape genetics to measure the genetic similarity of populations (Schwartz *et al.* 2002; Clegg *et al.* 2003; Fenderson *et al.* 2020). However, these techniques are expensive, time consuming and labour intensive, and can therefore only be carried out over small spatial scales and/or short time periods (e.g. Finch et al., 2020). Other models of functional connectivity are mechanistic and built from sound theoretical understanding of dispersal capabilities (e.g. Watts & Handley 2010; Bocedi *et al.* 2014; Merrick & Koprowski 2017), but are rarely validated using empirical data (Laliberté & St-Laurent 2020). For example, a previous indicator of functional connectivity for the UK used metrics based on land cover combined with expert opinion of species' habitat associations and movement capacity (Watts & Handley 2010). This approach has limitations in that land cover data are not updated frequently and there is substantial uncertainty in estimating species' movement capacities across different land cover types (Watts *et al.* 2008). It is therefore ideal for indicators of functional connectivity to be data-driven and assessed from a species' point of view to robustly inform conservation policy.

An alternative method to estimate functional connectivity has been proposed based on a measure of population synchrony — the correlations in time series of annual population growth rates between different locations — using long-term species monitoring data (Powney *et al.* 2011, 2012; Oliver *et al.* 2017). This is because the movement of individuals between sites is known to lead to increased synchrony in population dynamics (Hanski 1998; e.g. Ranta *et al.* 2008). Density-dependent emigration of individuals can link populations, leading to increased levels of population synchrony (Fig. 2.1). Empirical evidence has shown that population dynamics in different locations are more synchronised for species with high estimated dispersal ability (as measured using mark-release-recapture, Paradis *et al.* 1999; Bellamy *et al.* 2003; expert opinion, Sutcliffe *et al.* 1996; or using dispersal-related traits as a proxy for dispersal ability, Tittler *et al.* 2009). Additional research has found correlations between population synchrony and landscape suitability (Powney *et al.* 2011, 2012), demonstrating the sensitivity of population synchrony to the movement of individuals.

However, population synchrony can also be driven by shared environmental conditions, i.e. the ‘Moran effect’ (Moran 1953; Koenig 2002), which declines with increasing distance between populations, partly due to spatial autocorrelation in climatic conditions (Hanski & Woiwod 1993; Roland & Matter 2007; Powney *et al.* 2011). Additional research has shown that populations are more synchronised if they occupy similar habitat types (Powney *et al.* 2010, 2011) or are situated at geographic range margins (Powney *et al.* 2010; Mills *et al.* 2017), potentially driven by increased climatic constraints on marginal populations reducing the availability of suitable microhabitats (Powney *et al.* 2010; Oliver *et al.* 2014). To explain changes in population synchrony over time, several studies have concluded that climate is a major driver of temporal trends (Sheppard *et al.* 2016; Shestakova *et al.* 2016; Black *et al.* 2018; Dallas *et al.* 2020; but see Cayuela *et al.* 2020). For example, climate change could be driving an increased frequency of extreme weather events, leading to greater synchronised population dynamics (Black *et al.* 2018b). In addition, there may be temporal trends in the degree of spatial autocorrelation in climate (Post & Forchhammer 2004).

To obtain a better signal of dispersal, one would need to account for the Moran effect in estimates of population synchrony. After accounting for some climate-related factors (including distance between sites, habitat similarity, shared climate, and position in geographic range), recent evidence has shown that residual synchrony reflects actual movements of individuals measured using mark-release-recapture (Oliver *et al.* 2017). Thus, evidence is accumulating to suggest that, if climate can be sufficiently taken into account, the movement of individuals has a key role in promoting population synchrony in population dynamics across space (Oliver *et al.* 2017).

To further develop and operationalise the use of population synchrony as an indicator of functional connectivity, we calculate temporal trends in population synchrony for 58 British birds and butterflies using long-term monitoring datasets from 1980-2016 for a total of 3,306 sites across Great Britain. We use data from three monitoring schemes: the UK Butterfly

Monitoring Scheme (hereafter UKBMS), the Common Birds Census (hereafter CBC), and the Breeding Bird Survey (hereafter BBS). We develop new approaches to account for spatiotemporal climatic patterns that drive correlated population dynamics, i.e. a dynamic Moran effect. After accounting for these effects of climate, we produce a residual temporal trend in population synchrony that reveals changes in functional connectivity over time.

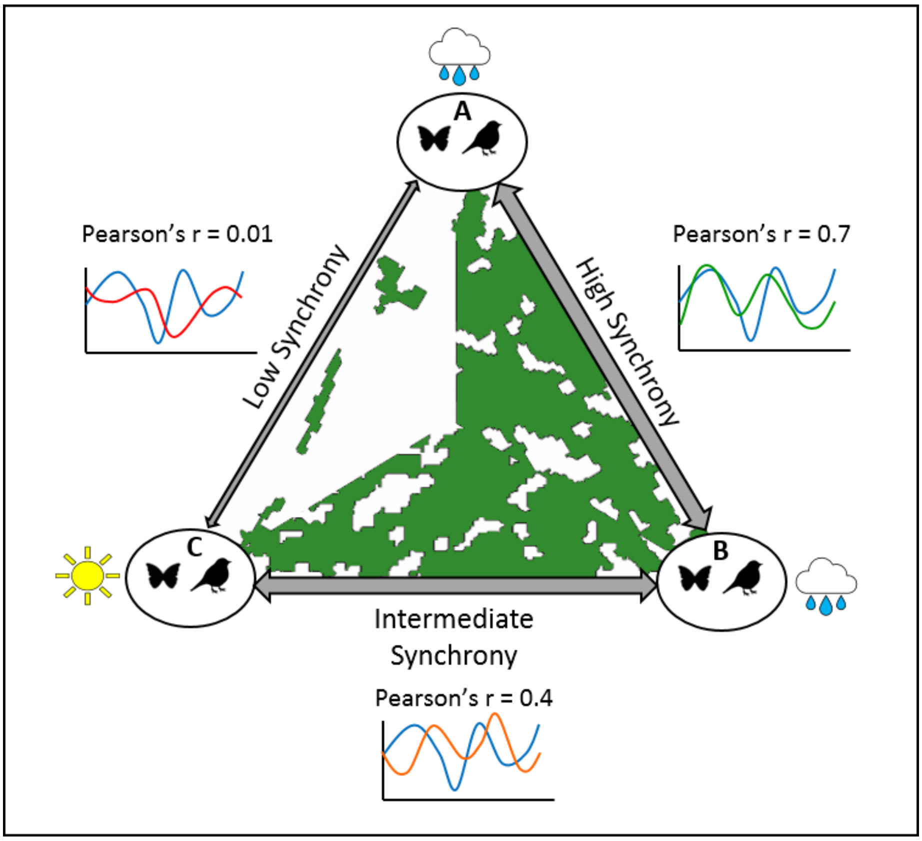

Figure 2.1. Schematic of factors which influence population synchrony. Sites A and B share the same climate and have a highly permeable landscape matrix between them (green shaded areas), allowing greater movement of individuals. These sites therefore have high synchrony. Sites B and C also have movement of individuals, but do not share the same climate, and have intermediate levels of synchrony. Finally, sites A and C have different climatic conditions and the hostile matrix of habitat prevents movement of individuals. Therefore, these sites have low levels of synchrony. Pearson's r values were chosen to reflect synchrony values for high, low, and intermediate synchrony.

2.3 Methods

2.3.1 Data collation

Butterfly data were derived from the United Kingdom Butterfly Monitoring Scheme (UKBMS) (Pollard & Yates 1993). UKBMS transects are walked by trained volunteers who survey 5m-wide strip transects for 26 weeks between April and September recording all butterflies observed. Further details can be found in Pollard and Yates (1993) and in Rothery and Roy (2001). An index of abundance for each butterfly species for each transect, each year from 1980-2016, was extracted from the UKBMS database. To ensure adequate data for analysis, resident butterfly species which had at least 75% of years with 50 sites or more sampled per year were included in the analysis.

Woodland bird abundance data were derived from two datasets, the Common Birds Census (CBC) and the Breeding Bird Survey (BBS). The CBC monitoring scheme monitored population trends for British breeding birds from 1962 until 2000 (Marchant 1990). Volunteer observers undertook repeated surveys between 8 and 10 times a year between late March and early July, recording all species seen or heard at each site. The BBS has monitored birds since 1994, where two 1km transects are visited twice a year, once between April and mid-May (early visit), and once between mid-May and the end of June (late visit) and all birds seen or heard are recorded (Harris *et al.* 2018). The total number of adult birds of each species for each site and each visit are calculated for each year. We obtained the maximum number of adult birds across all visits at each site for the years 1980-2000 from the CBC and 1994-2016 from the BBS. Species which had at least 75% of years with 50 sites or more sampled per year were included in the analysis.

In addition to interannual fluctuations in population size, raw abundance values also reflect long-term temporal trends arising from drivers such as land use and climate change, therefore we used between-year rates of change to focus on interannual population synchrony (Bjørnstad *et al.* 1999). We converted annual abundance values into rate of change as follows: $logN_t - logN_{t-1}$, where N_t is the abundance index estimate in time t (Powney *et al.* 2010). We added one to all population counts prior to the growth rate calculation to avoid taking the log of zero.

2.3.2 Population synchrony

For each species, population synchrony between pairs of monitoring sites was estimated as the Pearson's correlation coefficient of yearly population growth rates. To assess temporal trends in population synchrony, we repeatedly calculated population synchrony using a 10-year moving window (Bjørnstad *et al.* 1999). A 10-year moving window was selected to balance the need for a reasonable-length time series to estimate population synchrony versus the number of separate windows where we could calculate population synchrony. The following pair-wise site combinations were excluded from the analysis: i) for either site, less than 7 years of growth rates in common to ensure data quality, ii) for either site with a chain of zero growth rates followed by positive growth rates, as this can inflate synchrony values and increase Type I errors, and iii) site combinations that were more than 100km apart. Although evidence has shown synchrony remains positively associated with landscape suitability for sites up to 200km apart (Powney *et al.* 2011), we selected an upper distance limit of 100km for computational feasibility. Additionally, due to computational limitations, synchrony was only calculated on BBS sites with at least 10 years of data, and a maximum of 10,000 random pairs of sites. This represents a subset of sites for species with large amounts of data (ranging from 3% to 98% of total available site comparisons with a median of 14%). We repeated this process five times to confirm that each subset adequately represented the whole dataset (Figure A1). The resulting dataset had population synchrony values for 32 butterflies from 701 sites between 1980-2016, 26 birds from 106 sites between 1980-2000, and 24 birds from 2,499 sites between 1994-2016 (Table A1-A3).

2.3.3 Climate synchrony

To determine whether temporal trends in population synchrony are driven by patterns in climatic synchrony over time, we measured synchrony of mean temperature and total precipitation for each season (i.e. eight variables) using 5km gridded climate data from Met Office *et al.* (2017). We converted coordinates from the sites where we measured species population synchrony from 1km to 5km grid squares and matched these to climate data for each of the three datasets. Climate synchrony was calculated using the same method as population synchrony, i.e. calculating a Pearson's correlation metric for each climate variable between each pair of monitoring sites for grid squares using a 10-year moving window. The resulting dataset had climate synchrony values for 4 seasons from 686 UKBMS sites from 1980-2016, 106 CBC sites from 1980-2000 and 2490 BBS sites from 1994-2016 (Figure A2).

Samples sizes are very slightly lower due to a small number of species monitoring sites falling within the same 5km grid square.

2.3.4 Additional control variables

To control for other known drivers of population synchrony, three attributes were calculated for each pair of sites, in each dataset. First, distance was calculated as the Euclidean distance (km) between each pair of sites. Second, northerliness was calculated as the mean Northing (km from Ordnance Survey National Grid) between each pair of sites. Finally, we used a Renkonen's percentage similarity index to calculate habitat similarity of a 500m buffer surrounding each focal pair of sites (Renkonen 1938; Jost *et al.* 2011). The index was bound between 0 and 1, with a value of 1 for two sites surrounded by the same habitat composition, and 0 being completely distinct compositions. Habitat data were extracted from the CEH Land Cover Map 2007 (Morton *et al.* 2011) and aggregated to the broad habitat level (10 habitat biotopes in total). This landcover map represents a roughly intermediate point in our indicator time series, and UK biotopes have not changed commonly or substantially enough for there to be frequent substantial differences in habitat composition between maps (plus, there are issues with comparability between maps due to changes in remote sensing and processing methodology) (Carey *et al.* 2008). Sites for CBC were primarily woodland sites with woodland type recorded by trained volunteers as a categorical variable (four types), therefore habitat similarity was calculated as a binary variable, with 1 representing a pair of sites with the same woodland type and 0 representing a pair of sites with different woodland types.

2.3.5 Trends in abundance

Changes in synchrony over time could be reflected in changes in abundance due to 'propagule pressure' (emigration of individuals) of highly abundant species facilitating the spread of populations, and therefore increasing population synchrony. To calculate the change in abundance for butterflies, we used the UKBMS Collated Index data which is a national annual index for each species for each year derived using a statistical model (Moss and Pollard 1993, Rothery and Roy 2001). We compared mean abundance using a t-test between two independent 10-year windows: 1980-1989 and 1995-2004, representing the change in abundance for the first two decades, and between 1995-2004 and 2007-2016 for the latter two decades for each species. For birds, we used the joint CBC/BBS population trend data to compare mean abundance using a t-test between 1980-1989 and 1991-2000, representing the time period of change for CBC data, and between 1994-2003 and 2007-2016, representing the time period of change for BBS data. Each species was classified as either increasing, decreasing, or showing no change in abundance over time.

2.3.6 Statistical analysis

All statistical analysis was carried out using R 3.5.0 (R Core Team 2018).

Accounting for climatic synchrony

We first sought to account for variation in population synchrony that could be attributed to climate synchrony, not to infer which climate variables were important. We found no evidence for collinearity between each climate synchrony variable for each dataset. We fitted a mixed effects model using the *lme4* package (Bates *et al.* 2015) to each of the three monitoring datasets separately ('all species models'). Each model contained population synchrony values for every pair-wise site comparison for each species as the response variable, the mid-year of each moving window as a categorical fixed effect, and each of the eight climate synchrony variables as continuous fixed effects. Species and pair ID of the sites were included as random intercepts to account for repeated measures and the number and identity of monitoring sites varying through time. Any climate variable with a significant relationship with population synchrony ($p<0.05$) was included as a covariate in future analyses to account for climatic effects. We note that this approach could be conservative as we may be less likely to detect other patterns in population synchrony than if we had attempted to avoid any possible overfitting.

Secondly, we investigated for evidence of increasing variance in climate over time over the study period. We used an F-test to determine whether the variation in seasonal mean temperature and total precipitation for each season differed between 1985-2000 and 2000-2012.

Temporal trends in population synchrony

To estimate a temporal trend in population synchrony for all birds or all butterflies, while accounting for known drivers of synchrony, we ran modified versions of the 'all species models' for each dataset by including distance, habitat similarity, mean northerliness, and the significant climate synchrony variable (unique for each dataset) as continuous fixed effects. All fixed effects were standardised to zero mean and one standard deviation. The coefficients for each mid-year and their associated standard errors were extracted from the model and are used as our index of population synchrony and associated uncertainty for each 10-year moving window. Population synchrony values for the first year were standardised at 100.

To assess how individual species were changing in population synchrony over time, we refitted the mixed effects model for each species within each dataset separately (‘single-species models’). We used only two mid-year values as fixed categorical effects which were chosen to ensure there was no overlap in the 10-year moving window (i.e. they represent independent input data) and to match the time periods for species change in abundance. For butterflies, we examined change between two 10-year periods with mid-years of 1985 and 2000, and subsequently between two 10-year periods with mid-years of 2000 and 2012. For CBC birds we examined change between two 10-year periods with mid-years of 1985 and 1996 and for BBS birds between two 10-year time periods with mid-years of 1999 and 2012. For each species, the coefficients and associated p-values for each mid-year were extracted to determine whether each species had experienced an increase or decrease in population synchrony between the two comparison periods. Some species had insufficient data for the mixed effects model to run and could not be analysed individually (Table A1-A3). Since synchrony measures of pair-wise sites are not independent, to obtain p-values we ran 1,000 permutation tests (e.g. see Powney et al. 2012) on each species to determine the significance of change in synchrony between the two comparison years. At each permutation, the predictor variable (year) was randomised, and a linear mixed effects model fitted, and the F-values extracted. We plotted the frequency distribution of the F-values and calculated the p-values for each predictor variable based on the position of the observed vs. simulated values (e.g. a value in the top 5% of the F-value frequency distribution would have a significant p-value of <0.05).

All models are described using mathematical notation in Supplementary Material A1.

Trends in abundance and population synchrony

To determine whether changes in population synchrony over time are explained by trends in abundance, we used chi-squared tests to test for a significant association between the change in synchrony and change in abundance categories over time.

2.4 Results

2.4.1 Climate accounts for variation in population synchrony

We selected which climate synchrony variables explained a significant amount of variation in population synchrony for each dataset. For UKBMS, we selected all eight climate synchrony variables ($R^2 = 0.00035$) (Table A4). For CBC birds, only summer temperature was included ($R^2 = 0.00024$) and for BBS birds, spring, autumn, and winter rainfall were selected ($R^2 = 0.000014$) (Table A4). These variables were included in all future models as fixed effects to account for the relationship between climate and population synchrony. We found no significant results to suggest that variation in seasonal mean temperature and rainfall has differed between 1985-2000 and 2000-2012 (Table A5).

2.4.2 Overall trends in population synchrony for birds and butterflies

The temporal trend in population synchrony for butterflies declined until 2004, thereafter it rapidly increased (Fig. 2.2a). This trend was reflected across the 32 butterfly species studied, with 71% of species declining in synchrony between 1985 and 2000, and 64% increasing in synchrony between 2000 and 2012 (Fig. 2.2d). Synchrony in birds was stable between 1985 and 1996 (Fig. 2.2b) with most species (74%) showing no trend in synchrony. Although synchrony values look identical between 1985 and 1996, there is variation in synchrony from 99.6 – 100.4. From 1999 onwards, birds declined in synchrony until 2005 where they appeared to be showing some signs of recovery (Fig. 2.2c). However, 74% of species showed no change in synchrony between 1999 and 2012 (Fig. 2.2e).

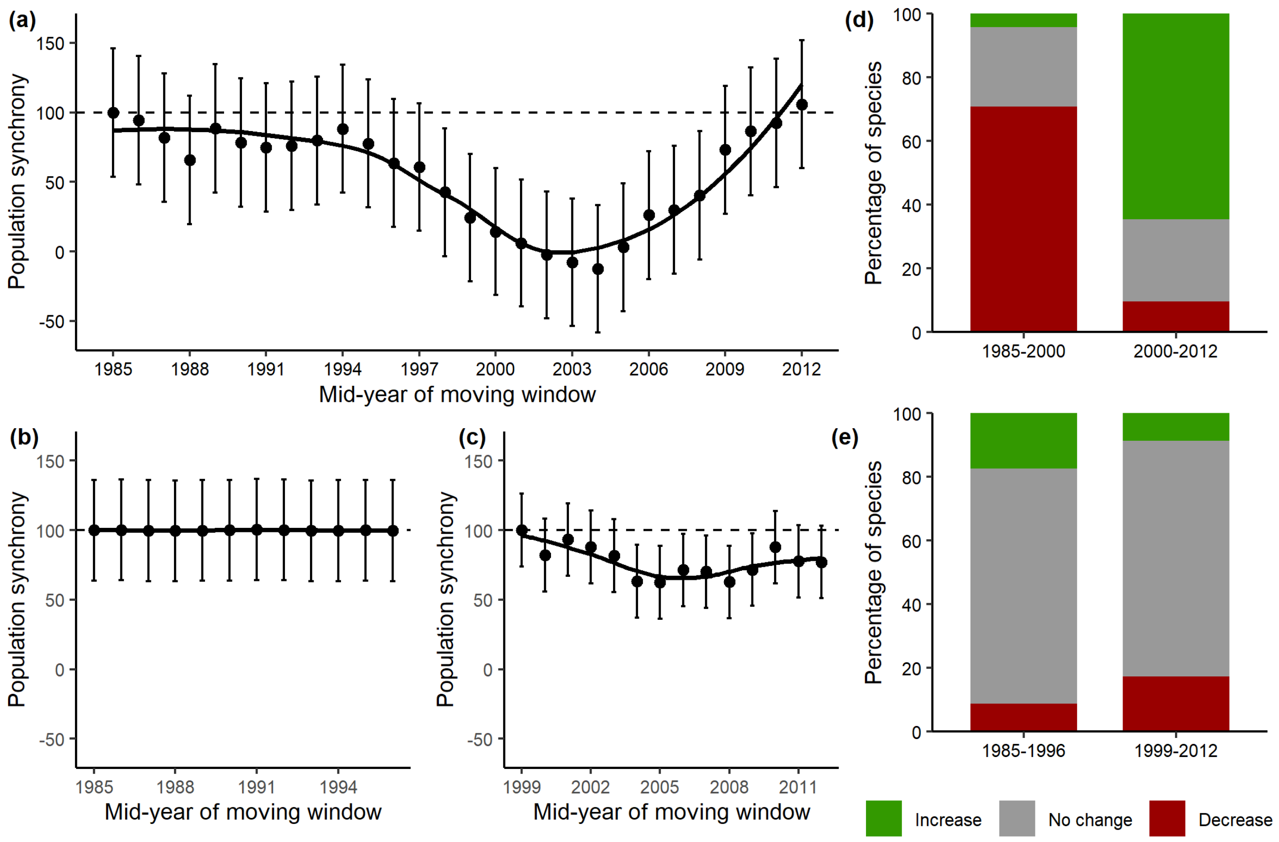

Figure 2.2. The temporal trend in population synchrony fitted using a LOESS regression function with standard error bars for (a) butterflies between 1985 and 2012, (b) CBC birds between 1985 and 1996, and (c) BBS birds between 1999 and 2012. Population synchrony scores were standardised, so the first mid-year was set to 100. Bar charts show the percentage of species which have either statistically significantly increased, decreased or remain unchanged in population synchrony between (d) 1985-2000 and 2000-2012 for butterflies (n=24 and n=31 species respectively) and (e) 1985-1996 for CBC (n=23 species) and 1999-2012 for BBS (n=23 species).

2.4.3 Control variables affecting population synchrony

For all three control variables in our mixed effects model, our hypotheses were supported when tested for butterflies. We found that more northerly pairs of sites, those closer together and those with similar habitat types had higher levels of population synchrony (Fig. 2.3). For birds, we found only BBS sites which have similar habitat type to have higher average synchrony (Fig. 2.3). These results remained significant after running 1,000 permutation tests (Table A6).

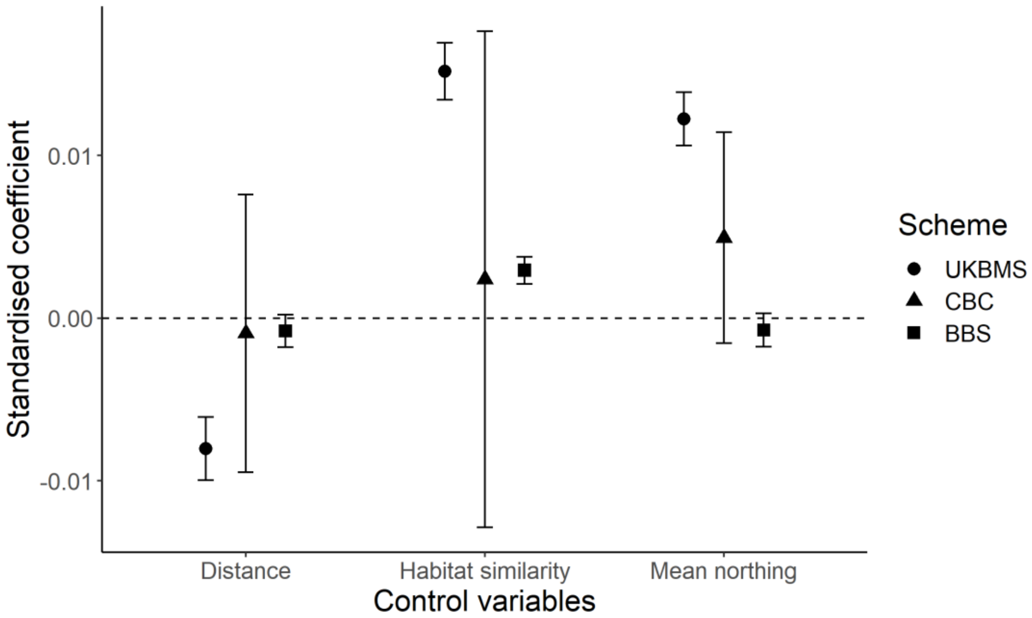

Figure 2.3. Standardised regression coefficients from mixed effects models with average synchrony as the response variable and control variables as fixed effects. Symbols mark the regression coefficients for each fixed effect and error bars mark the 95% confidence intervals. A positive coefficient indicates that a higher level of a given control variable (e.g. greater habitat similarity) is associated with greater synchrony in population dynamics between sites for that species.

2.4.4 Trends in abundance and population synchrony

We found no significant association between the categories of abundance change and population synchrony change for butterflies between 1985-2000 χ^2 = 2.92, P = 0.47) and between 2000-2012 (χ^2 = 5.90 P = 0.19), and for CBC birds (χ^2 = 2.51 P = 0.81), and BBS birds (χ^2 = 1.7 P = 0.80).

2.5 Discussion

The proposed indicator presented based on a population synchrony offers a ‘species-eyed-view’ of functional connectivity using a data-derived method based on widely available, annually updated species monitoring data. We found patterns in population synchrony clearly associated with synchrony in temperature and rainfall. Once these variables were accounted for, we demonstrate the temporal trends in residual population synchrony for UK birds and butterflies, suggesting that functional connectivity is changing over time.

Successful biodiversity indicators summarise complex ecological datasets into robust measures that can be used to assess trends over time and are used to assess progress towards meeting national and international goals and targets and help inform governmental policy (Butchart *et al.* 2010; Costelloe *et al.* 2016; McQuatters-Gollop *et al.* 2019). Developing an indicator of functional connectivity involves a trade-off between the data requirements and level of information produced (Calabrese & Fagan 2004). Basic measures of structural connectivity, for example average nearest neighbour distances of biotope types deemed suitable habitat, do not require extensive data, but they only produce a simple estimate of connectivity that, for example, ignores the differing resistance of intermediate landcover types (Watts and Handley, 2010). Complex mechanistic models can produce very detailed estimates of connectivity (e.g. Watts & Handley 2010; Bocedi *et al.* 2014; Merrick & Koprowski 2017), but are very data intensive and require validation from independently collected data (Laliberté & St-Laurent 2020). Similarly, direct observations of species' movement, for example from mark-release-recapture, provide more realistic estimates of connectivity but are very data-intensive and often limited to small spatial scales (Calabrese & Fagan 2004).

Our proposed indicator utilises widely available abundance data to calculate a temporal trend in population synchrony, which may provide an estimate of connectivity. Empirical evidence has shown correlations between population synchrony and the distance by which populations were separated by hostile land cover types (Roland & Matter 2007) and the coverage of quality habitat types in the intervening landscapes (Powney *et al.* 2011). Furthermore, the distance along woodland edges has shown to better predictor of movement than Euclidean distance, which was consistent to data collected using mark-release-recapture (Powney *et al.* 2012). Additionally, higher population synchrony has been found between patches with higher frequency of movements between them, obtained from mark-release-recapture of a butterfly species (Oliver *et al.* 2017). This empirical evidence demonstrates that population synchrony does reflect movement frequencies rather than being solely driven by shared climatic conditions or connectivity of interacting species.

However, if we seek to track connectivity using population synchrony, we need to account for climate as a confounding variable. Previous research has shown parallel increases in population synchrony and environmental synchrony, suggesting a potential role of the Moran effect in driving shared population dynamics over time (Koenig & Liebhold 2016; Sheppard *et al.* 2016; Shestakova *et al.* 2016; Kahilainen *et al.* 2018). Here, we show that population synchrony is significantly associated with synchrony in some seasonal climatic variables. For butterflies, each of the eight climate variables tested were individually associated with population synchrony, whereas for the BBS dataset, only three rainfall variables were significant and for CBC birds only summer temperature (Table A4). This provides convincing evidence that synchrony in temperature and rainfall play a role in driving shared population dynamics (Koenig 2002; Post & Forchhammer 2004; Koenig & Liebhold 2016; Sheppard *et al.* 2016). Our results also confirm that sites which are closer together, share similar habitat, and are situated closer to species' range margin have higher mean synchrony values (Sutcliffe *et al.* 1996; Roland & Matter 2007; Powney *et al.* 2010). Increased variation in climate can cause extreme population crashes (Palmer *et al.* 2017) and drive more synchronised populations (Pomara & Zuckerberg 2017; Black *et al.* 2018b). However, we found no evidence for significant changes in climate variability over time in our UK dataset (Table A5), suggesting that it is unlikely to be driving trends in shared population dynamics in our current dataset.

Changes in density-dependent emigration due to propagule pressure can facilitate the spread of individuals (Hanski 1998). This has been shown to drive more synchronous population dynamics in birds (Paradis *et al.* 1999, 2000; Bellamy *et al.* 2003) and could explain the changes in temporal synchrony we find here. However, we found no overall association between the trend in abundance and trend in population synchrony in our three datasets. Despite this, 15 butterfly species (out of 24 species) in our study show a 'u-shaped' pattern in synchrony over time, with a decline between 1985-2000 and increase between 2000-2012. This suggests that functional connectivity for butterflies may be changing over time in the UK, which could be driven by structural factors in the landscape, for example, geographical barriers and habitat restoration. Many of these species which show a u-shaped pattern in temporal synchrony are wider countryside species and/or associated with garden and hedgerow habitats (Asher *et al.* 2001) and could be impacted by wider landscape changes. A major push for the uptake of English agri-environment schemes through the Entry and Higher Level Stewardship schemes began in 2005, which is where we also see the inflection point in butterfly functional connectivity trends. The schemes were designed to reduce the negative impacts of agricultural intensification by providing support to farmers for environmentally friendly management (Food and Environment Research Agency 2013). They led to increased height and width of hedgerows (Food and Environment Research Agency 2013) and therefore have allowed these habitats to support higher butterfly population densities (Food and

Environment Research Agency 2014). Furthermore, farms which adopted additional wildlife-friendly management supported 50% higher butterfly species richness compared to farms meeting the minimum requirements (Hardman *et al.* 2016). Therefore, it is possible that the introduction of agri-environment schemes explains the upturn in butterfly population synchrony/connectivity in the mid-2000s. In contrast, woodland bird population synchrony remained stable over time, with most species showing no change in synchrony. Woodland cover across the UK has increased from 9% in 1980 to 13.1% in 2018 (in England, this has increased from 7.3% in 1980 to 10% in 2018) (Forestry Commission 2018). Hence, woodland cover change has not been marked, yet may possibly have contributed to the increase in connectivity for four bird species between 1985 and 1996 and two species between 1999 and 2012. Although woodland creation has been shown to help recovery of generalist woodland birds, there is often a time-lag of several years while trees mature before species respond to changes in the habitat (Watts *et al.* 2020). This could explain a more recent recovery in woodland bird connectivity from 2005 onwards. The UK is planning to increase forestry substantially by at least 30,000ha per year cover under the net-zero 2050 target to reduce carbon emissions (Committee on Climate Change 2020; Defra 2020b). Increasing the size and quality of habitat patches can increase the abundance of source populations (Hodgson *et al.* 2011), which plays an important role in promoting connectivity across the landscape (Robertson *et al.* 2018) and could lead to further recovery of woodland bird populations.

In addition to changes in landscape structure affecting source population size and improving landscape permeability, functional connectivity might also be explained by changes in individual movement capacity. However, although there is evidence of evolution in movement capacity related to physiological changes (e.g. wing-thorax ratio, see Simmons and Thomas 2004; and Hughes et al. 2007), there is no reported evidence of increased movement capacity over time. In fact, some evidence suggests that at high-latitudes insects may be getting smaller over time (Bowden *et al.* 2015). Therefore, we anticipate our UK results most likely due to changing structural connectivity related to changes in the landscape character, which could be mediated through habitat management (Hanski 1998).

Increasing synchrony has been suggested to be a ‘double-edged sword’, where it is associated with increased extinction risk (Heino *et al.* 1997). But in practice, absolute levels of symphony are low enough that synchronous extinction seems unlikely (e.g. in our data absolute Pearson correlations have low median values of 0.3, 0.1, and 0.03 for UKBMS, CBC, and BBS datasets respectively). Also, studies considering the association between synchrony and extinction often fail to consider that synchrony is not the driving factor: where populations are highly synchronised (e.g. at range edges; Mills *et al.* 2017) then weather is the driving factor causing population declines and synchrony is simply the shared response to this driver. Hence, increasing population synchrony arising from enhanced landscape connectivity is unlikely to increase extinction risk, but, instead, can actually make meta-populations more robust, as confirmed by substantial theoretical and empirical work (Hanski 1998).

Our approach of measuring functional connectivity has some limitations. Firstly, measuring cross-correlations between pairs of sites requires a large amount long-term site-based monitoring data to capture the picture of population synchrony across a large spatial scale. To maximise our site data, we include sites which are newly added to the monitoring schemes. However, we included a random effect for site pair ID to account for the identity of monitoring sites varying through time, and therefore allowing utilisation of data from newly added sites. Secondly, although we find evidence that spatial autocorrelation in climate is driving temporal trends in population synchrony, as per previous research (Sheppard *et al.* 2016; Shestakova *et al.* 2016; Black *et al.* 2018; Dallas *et al.* 2020), it is possible that there are other climate variables influencing population synchrony which we have not accounted for. For example, previous research has shown that the number of frost nights can cause declines in the population abundance of wrens (Bellamy *et al.* 2003). However, researchers found the same relationship using mean winter temperature as an explanatory variable, as this measure is highly correlated with the number of frost days. Future analysis could use a species-specific approach tailoring specific climate variables (both type of variable and the time window of measurement) to each species, but we expect it would produce broadly similar results as we have here as it is likely that our seasonal temperature and rainfall variables are correlated with species-specific climate variables.

In conclusion, our proposed indicator based on population synchrony offers a data-driven approach to measuring functional connectivity using widely available abundance data which can be updated annually. Although population synchrony is driven by shared environmental conditions, once accounted for, residual population synchrony has been shown to reflect the movement of individuals. This suggests that the temporal trend in population synchrony can be a useful conservation metric for tracking functional connectivity which can be updated annually. Further research linking species' movement capacity with temporal trends in population synchrony would add further evidence to the use of this indicator in facilitating more targeted landscape conservation management.

Chapter 3. Disentangling how climate and dispersal drive temporal trends in population synchrony

3.1 Abstract

Synchronised population dynamics are driven by a combination of shared environmental conditions and the movements of individuals between sites. Untangling the drivers of population synchrony requires investigation of how populations are correlated across space and time in relation to climate and mobility-related attributes. Here, we use species survey data and from over four decades to investigate average levels and temporal trends in population synchrony for 58 British bird and butterfly species. We first show that population synchrony is significantly associated with synchrony in some seasonal climatic variables. Once we accounted for spatiotemporal climatic patterns, we could determine whether temporal trends in population synchrony were related to mobility-related attributes. We tested this through an interspecies comparison using three mobility-related attributes: biotope specialism, estimated species mobility, and local abundance change, which is known to affect emigration rate. We show that temporal trends in population synchrony were most marked for butterfly species that had changed in their mean abundance, and for bird species with high estimated mobility. Population synchrony was also often strongly related to distance between sites reflecting both the effects of shared climate and movement frequency. Our results reveal a consistent effect of mobility attributes and abundance patterns on population synchrony over time, after accounting for climate as a confounding effect, therefore adding to the growing body of literature that dispersal can synchronise populations across space and time.

3.2 Introduction

Population synchrony, measured as the correlation in abundance between spatially separated populations over time, is exhibited in many taxonomic groups including insects (Sutcliffe *et al.* 1996), fish (Cheal *et al.* 2007), birds (Paradis *et al.* 2000; Bellamy *et al.* 2003; Kerlin *et al.* 2007), plants (Kiviniemi & Löfgren 2009), and mammals (Swanson & Johnson 1999). Synchronous population dynamics can be driven by a variety of factors, including dispersal (Ripa 2000), environmental factors (Moran 1953; Ranta *et al.* 1997), and trophic interactions (Ims & Andreassen 2000). Spatial synchrony is thought to be important for the long-term viability of metapopulations as synchronised population dynamics prevent poorly performing populations being rescued by populations increasing in abundance, and increasing the risk of extinction (Heino *et al.* 1997). Therefore, it is crucial to measure how spatial population synchrony is changing across time, as well as whether such changes can be attributed to the two key drivers, dispersal, and climate.

Previous research has shown theoretical and empirical support that shared environmental conditions as the driver of population synchrony, i.e. the ‘Moran effect’ (Moran 1953; Koenig 2002), which declines with increasing distance between populations, partly due to spatial autocorrelation in climatic conditions (Hanski & Woiwod 1993; Roland & Matter 2007; Powney *et al.* 2011). Additional research has shown that populations are more synchronised if they occupy similar habitat types (Powney *et al.* 2010, 2011) or are situated at geographic range margins (Powney *et al.* 2010; Mills *et al.* 2017), which can lead to increased climatic constraints on marginal populations, reducing the availability of suitable microhabitats (Powney *et al.* 2010; Oliver *et al.* 2014). To explain changes in population synchrony over time, several studies have concluded that climate is a major driver of temporal trends (Sheppard *et al.* 2016; Shestakova *et al.* 2016; Black *et al.* 2018b; Hansen *et al.* 2020). For example, climate change could be driving an increased frequency of extreme weather events, leading to greater synchronised population dynamics (Black *et al.* 2018b). In addition, there may be temporal trends in the degree of spatial autocorrelation in climate (Post & Forchhammer 2004).

There is also significant evidence that the movement of individuals between populations also leads to increased synchrony in population dynamics (Hanski 1998, e.g. Ranta et al. 2008). Density-dependent emigration of individuals can link populations, leading to fluctuations in population synchrony (Ranta *et al.* 1995). Empirical evidence has shown that population dynamics in different locations are more synchronised for species with high estimated dispersal ability (as measured using mark-release-recapture, Paradis *et al.* 1999; Bellamy *et al.* 2003; expert opinion, Sutcliffe *et al.* 1996; or using dispersal-related traits as a proxy for dispersal ability, Tittler *et al.* 2009). More abundant species also often have higher levels of population synchrony (Paradis *et al.* 1999, 2000; Bellamy *et al.* 2003), due to higher ‘propagule pressure’ (emigration of individuals) facilitating the spread of populations (Hanski 1998). We would therefore expect biotype generalist species who use a broad range of habitat types to have high levels of average population synchrony. Additional research has found correlations between population synchrony and landscape suitability (Powney *et al.* 2011, 2012), demonstrating the sensitivity of population synchrony to the movement of individuals. Recent evidence has also shown that residual synchrony reflects actual movements of individuals measured using mark-release-recapture (Oliver *et al.* 2017).

Few studies have attempted to disentangle the role of dispersal from environmental effects. Kendall et al. (2000) found strong interactions between dispersal and the correlated environment which cause greater synchrony between populations. Climate can have direct impacts on population synchrony as described above, but can also influence synchrony indirectly through climate induced changes in dispersal (Hansen *et al.* 2020). However, there has been no attempt to disentangle dispersal and climate and determine whether dispersal is driving temporal trends in population synchrony after accounting for the direct impact of the Moran effect.

To investigate this, we calculated both average levels, and temporal trends, in population synchrony for 58 British birds and butterflies using long-term monitoring datasets from 1980-2016 for a total of 3,306 sites across Great Britain. We use data from three monitoring schemes: the UK Butterfly Monitoring Scheme (hereafter UKBMS), the Common Birds Census (hereafter CBC), and the Breeding Bird Survey (hereafter BBS). We develop approaches to account for spatiotemporal climatic patterns that drive correlated population dynamics, i.e., the Moran effect. After accounting for these effects of climate, we produce a residual temporal trend in population synchrony that we hypothesise is related to changes in inter-site movement frequency. This is then tested through an interspecies comparison where we predict that certain types of species differ in average and temporal levels of population synchrony. Namely, using three movement-related species attributes: specialism, mobility, and population abundance, we predict that generalist species, with higher mobility and higher mean abundance will have higher average levels of population synchrony and show greater changes in synchrony over time (Table 3.1).

Table 3.1 Table of hypotheses for species attributes and control variables in relation to both average levels and temporal trends in synchrony. Ticks and dashes represent whether the hypothesis was supported or rejected respectively, and crosses indicate that the opposite result was found. Brackets indicate an accepted hypothesis for one time period.

Explanatory variable	**Response variable**	**Hypothesis**	**Shown by previous authors**	**Butterflies**	**Birds**	
					CBC	**BBS**
Biotype specialism	Average synchrony	Generalists have higher levels of average synchrony		–	–	–
	Change in synchrony			✓	✓	✓
Mobility	Average synchrony	More mobile species have higher average levels of synchrony	Bellamy et al., 2003 Paradis et al., 1999 Sutcliffe et al., 1996	✓	–	–
	Change in synchrony			(✓)	–	✓
Abundance	Average synchrony	More common species have higher average levels of synchrony	Bellamy et al., 2003 Paradis et al., 1999 Paradis et al., 2000	–	✓	–
	Change in synchrony	Species increasing in abundance also increase in synchrony over time		(✓)	–	–

3.3 Methods

3.3.1 Data collation

Butterfly data were derived from the United Kingdom Butterfly Monitoring Scheme (UKBMS) (Pollard & Yates 1993). UKBMS transects are walked by trained volunteers who survey 5m-wide strip transects for 26 weeks between April and September recording all butterflies observed. Further details can be found in Pollard and Yates (1993) and in Rothery and Roy (2001). An index of abundance for each butterfly species for each transect, each year from 1980-2016, was extracted from the UKBMS database. To ensure adequate data for analysis, resident butterfly species which had at least 75% of years with 50 sites or more sampled per year were included in the analysis.

Woodland bird abundance data were derived from two datasets, the Common Birds Census (CBC) and the Breeding Bird Survey (BBS). The CBC monitoring scheme monitored population trends for British breeding birds from 1962 until 2000 (Marchant 1990). Volunteer observers undertook repeated surveys between 8 and 10 times a year between late March and early July, recording all species seen or heard at each site. The BBS has monitored birds since 1994, where two 1km transects are visited twice a year, once between April and mid-May (early visit), and once between mid-May and the end of June (late visit) and all birds seen or heard are recorded (Harris *et al.* 2018). The total number of adult birds of each species for each site and each visit are calculated for each year. We obtained the maximum number of adult birds across all visits at each site for the years 1980-2000 from the CBC and 1994-2016 from the BBS. Species which had at least 75% of years with 50 sites or more sampled per year were included in the analysis.

In addition to interannual fluctuations in population size, raw abundance values also reflect long-term temporal trends arising from drivers such as land use and climate change, therefore we used rates of change to focus on interannual population synchrony (Bjørnstad *et al.* 1999). We converted annual abundance values into rate of change as follows: $logN_t - logN_{t-1}$, where N_t is the abundance index estimate in time t (Powney *et al.* 2010). We added one to all population counts prior to the growth rate calculation to avoid taking the log of zero.

3.3.2 Population synchrony

For each species, population synchrony between pairs of monitoring sites was estimated as the Pearson's correlation coefficient of yearly population growth rates. To assess temporal trends in population synchrony, we repeatedly calculated population synchrony using a 10-year moving window (Bjørnstad *et al.* 1999). A 10-year moving window was selected to balance the need for a reasonable-length time series to estimate population synchrony versus the number of separate windows where we could calculate population synchrony. The following pair-wise site combinations were excluded from the analysis: i) for either site, less than 7 years of growth rates in common to ensure data quality, ii) for either site with a chain of zero growth rates followed by positive growth rates, as this can inflate synchrony values and increase Type I errors, and iii) site combinations that were more than 100km apart. Although evidence has shown synchrony remains positively associated with landscape suitability for sites up to 200km apart (Powney *et al.* 2011), we selected an upper distance limit of 100km for computational feasibility. Additionally, due to computational limitations, synchrony was only calculated on BBS sites with at least 10 years of data, and a maximum of 10,000 random pairs of sites. This represents a subset of sites for species with large amounts of data (ranging from 3% to 98% of total available site comparisons with a median of 14%). We repeated this process five times to confirm that each subset adequately represented the whole dataset (Figure B1). The resulting dataset had population synchrony values for 32 butterflies from 701 sites between 1980-2016, 26 birds from 106 sites between 1980-2000, and 24 birds from 2,499 sites between 1994-2016 (Table B1-B3).

3.3.3 Climate synchrony

To determine whether temporal trends in population synchrony are driven by patterns in climatic synchrony over time, we measured synchrony of mean temperature and mean precipitation for each season (i.e. eight variables) using 5km gridded climate data from (Met Office *et al.* 2017). We converted population synchrony sites from 1km to 5km grid squares and matched these to climate data for each of the three datasets. Synchrony was calculated using the same method as population synchrony, i.e., calculating a Pearson's correlation metric for each climate variable between each pair of monitoring sites for grid squares using a 10-year moving window. The resulting dataset had climate synchrony values for 4 seasons from 686 UKBMS sites from 1980-2016, 106 CBC sites from 1980-2000 and 2490 BBS sites from 1994-2016 (Figure B2).

3.3.4 Control variables

To control for known drivers of population synchrony, three attributes were calculated for each pair of sites, in each dataset. First, distance was calculated as the Euclidean distance (km) between each pair of sites. Second, northerliness was calculated as the mean Northing (km from Ordnance Survey National Grid) between each pair of sites. Finally, we used a Renkonen's percentage similarity index to calculate habitat similarity of a 500m buffer surrounding each focal pair of sites (Renkonen 1938; Jost *et al.* 2011). The index was bound between 0 and 1, with a value of 1 for two sites surrounded by the same habitat composition, and 0 being completely distinct compositions. Habitat data were extracted from the CEH Land Cover Map 2007 (Morton *et al.* 2011) and aggregated to the broad habitat level (10 habitat biotopes in total). Sites for CBC were primarily woodland sites with woodland type recorded as a categorical variable (four types), therefore habitat similarity was calculated as a binary variable, with 1 representing a pair of sites with the same woodland type and 0 representing a pair of sites with different woodland types.

3.3.5 Species attributes

We selected three species attributes: biotype specialisation, mobility, and abundance, to relate to levels of population synchrony. For biotype specialisation, butterflies were split into either wider countryside or habitat specialist species (Asher *et al.* 2001) and birds were classified into either woodland generalists or specialists (Defra 2017). Mobility ranks for butterflies were obtained from (Wilson *et al.* 2004) and breeding dispersal distances for birds were taken from (Paradis *et al.* 1998). We obtained two measures of abundance: average abundance and change in abundance over time. Our measure of average abundance for butterflies uses the Wider Countryside Butterfly Survey (WCBS) (Brereton *et al.* 2011) which has run since 2009 where volunteers visit sites 2-4 times a year counting along two parallel 1km transects. For our measure of average butterfly abundance, we calculated the mean abundance for each species between 2009-2016. For birds, we used national population estimates from (Musgrove *et al.* 2013). The change in abundance for butterflies uses the UKBMS Collated Index data which is a national annual index for each species for each year derived using a statistical model (Moss & Pollard 1993; Rothery & Roy 2001). We calculated the mean difference in abundance between two independent 10-year windows: 1980-1989 and 1995-2004 to represent the change in abundance for the first two decades, and between 1995-2004 and 2007-2016 for the latter two decades for each species. For the CBC, we calculated mean difference in abundance between 1980-1989 and 1991-2000 for each species. For the BBS, we calculated mean difference in abundance between 1994-2003 and 2007-2016 for each species. All species were firstly classified as either increasing or decreasing in abundance over time regardless of significance. Secondly, we used a t-test to determine whether species had significantly increased or decreased in abundance and removed species from the analysis which showed no significant change in abundance over time. The analysis was run on both non-significant abundance changes and significant abundance changes. Attribute data was missing for some species, see Supplementary Material tables B1, B2 and B3 for a list of all species and associated attributes.

3.3.6 Statistical analysis

All statistical analysis was carried out using R 3.5.0 (R Core Team 2018).

Accounting for climatic synchrony

Initially, we sought to account for variation in population synchrony that could be attributed to climate synchrony, not to infer which climate variables were important. We found no evidence for collinearity between each climate synchrony variable for each dataset. We fitted a mixed effects model using the *lme4* package (Bates *et al.* 2015) to each of the three monitoring datasets separately (‘all species models’). Each model contained population synchrony values for every pair-wise site comparison for each species as the response variable, the mid-year of each moving window as a categorical fixed effect, and each of the eight climate synchrony variables as continuous fixed effects. Species and pair ID of the sites were included as random intercepts to account for repeated measures and the number and identity of monitoring sites varying through time. Any climate variable with a significant relationship with population synchrony ($p<0.05$) was included as a covariate in future analyses to account for climatic effects. We note that this approach could be conservative as we may be less likely to detect other patterns in population synchrony than if we had attempted to avoid any possible overfitting.

Secondly, we investigated for evidence of increasing variance in climate over time over the study period. We used an F-test to determine whether the variation in seasonal mean temperature and total precipitation for each season differed between 1985-2000 and 2000-2012.

Population synchrony and species attributes

To understand whether each species attributes could explain differences in population synchrony between species, we fitted a variant of the all species model for each dataset, by including distance, habitat similarity, mean northerliness, and the significant climate synchrony variable (unique for each dataset) as continuous fixed effects to account for known drivers of population synchrony. Each attribute was included as an additional fixed effect and placed into three separate models, one for each attribute (biotope specialism as a fixed categorical effect and mobility and average abundance as fixed continuous effects). All continuous fixed effects were standardised to zero mean and one standard deviation. To ensure that population synchrony was not being driven by phylogenetic relatedness, we tested for an additional effect of family and genus in the all-species models for each dataset. We did not find a significant result for butterflies or BBS birds, but family was significant for CBC birds. Hence this variable was added as a random effect unless we obtained singular fit errors where we removed the family random effect and found no qualitative difference in results between the two models. We also included an interaction between the mid-year of the moving window and each species attribute in separate models for each attribute. This determined whether certain types of species were increasing or decreasing in population synchrony between two non-overlapping 10-year periods. This was repeated using abundance change categories obtained from both the non-significant abundance changes and significant abundance changes over time. Since synchrony measures of pair-wise sites are not independent, to obtain p-values we ran 1,000 permutation tests (e.g. see Powney et al. 2012) on each species to determine the significance of change in synchrony between the two comparison years. At each permutation, the predictor variable (species attribute) was randomised, and a linear mixed effects model fitted, and the F-values extracted. We plotted the frequency distribution of the F-values and calculated the p-values for each predictor variable based on the position of the observed vs. simulated values (e.g. a value in the top 5% of the F-value frequency distribution would have a significant p-value of <0.05).

All models are described using mathematical notation in Supplementary Material B1.

3.4 Results

3.4.1 Climate accounts for variation in population synchrony

We selected which climate synchrony variables explained a significant amount of variation in population synchrony for each dataset. For UKBMS, we selected all eight climate synchrony variables ($R^2 = 0.00035$) (Table B4). For CBC birds, only summer temperature was included ($R^2 = 0.00024$) and for BBS birds, spring, autumn, and winter rainfall were selected ($R^2 = 0.000014$) (Table B4). These variables were included in all future models as fixed effects to account for the relationship between climate and population synchrony. We found no significant results to suggest that variation in seasonal mean temperature and rainfall has differed between 1985-2000 and 2000-2012 (Table B5).

3.4.2 Associations with species attributes

With regards to biotope specialism, we did not find any significant relationship with average levels of synchrony for butterflies or birds (Figure 3.1). For butterflies we found a significant result of specialism on the temporal trend in synchrony, with generalists showing a greater decline in synchrony between 1985 and 2000 compared to specialists (Fig. 3.2a) and showing the greatest recovery in synchrony between 2000 and 2012 (Table B6). For BBS birds, we found that generalist birds show a slightly steeper decline in synchrony compared to specialists under the BBS dataset (Table B8), however this result was non-significant when permutation tests were run (Table B9). In comparison, CBC specialist species increase in synchrony between 1985 and 1996, whereas generalists show no change (Table B7).

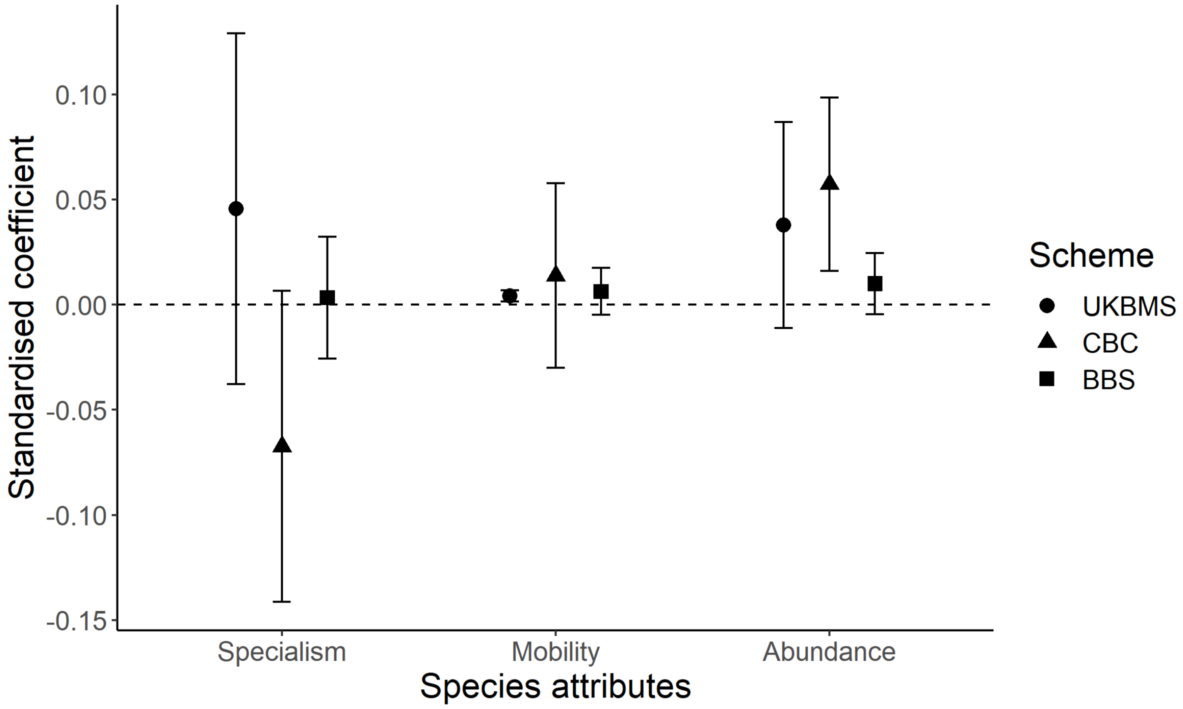

Figure 3.1. Standardised regression coefficients from mixed effects models with average synchrony as the response variable and species attributes as fixed effects. Symbols mark the regression coefficients for each fixed effect and error bars mark the 95% confidence intervals. A positive coefficient indicates that a higher level of a given species attribute (e.g., higher mean species abundance) is associated with greater synchrony in population dynamics between sites for that species.

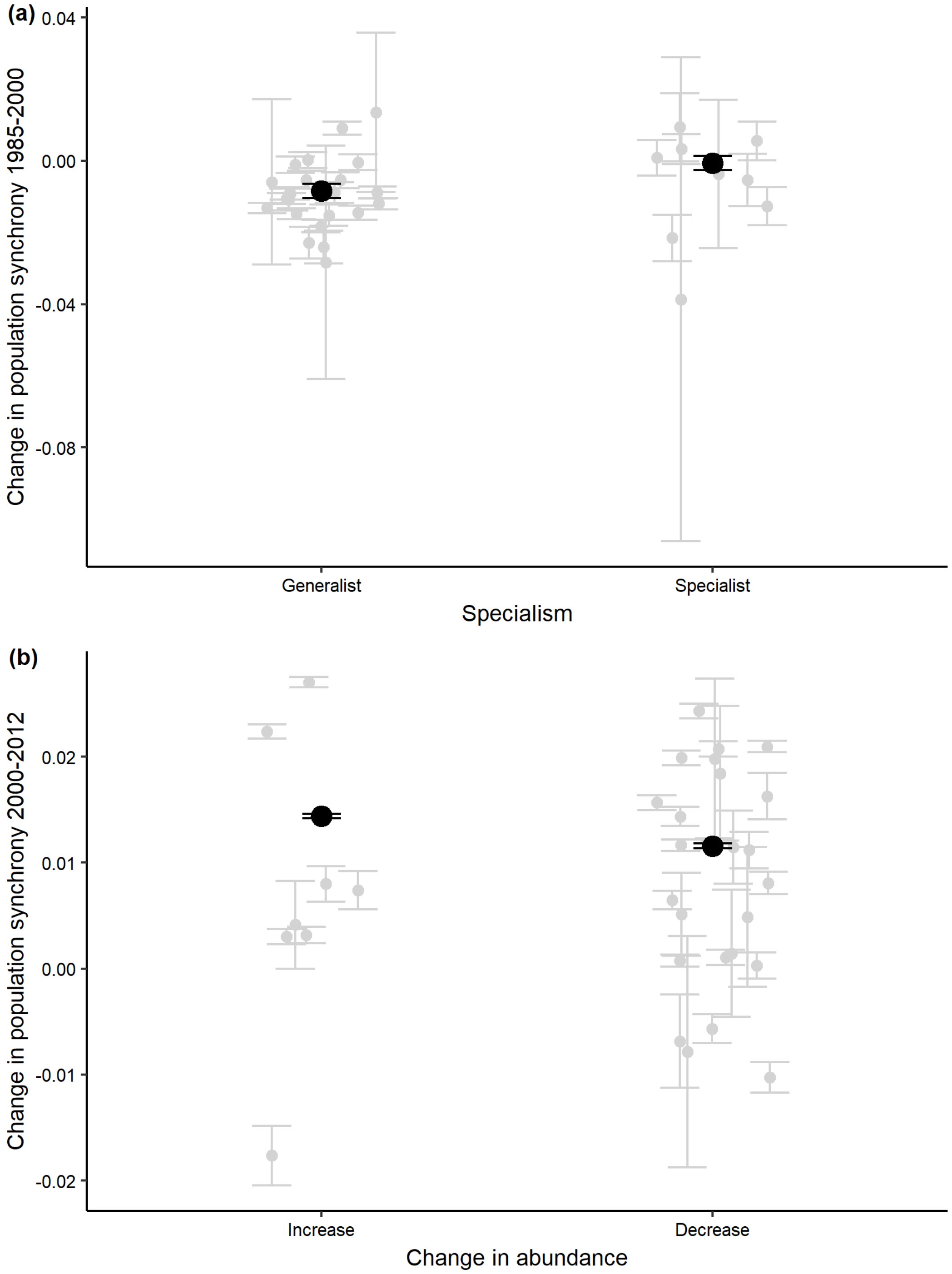

Figure 3.2. The change in population synchrony over time for butterflies in relation to (a) biotype specialism and (b) change in abundance. Grey points represent each species raw data with standard error bars, and black points represent the slope (i.e. change in synchrony over time) from the mixed effects models with their associated standard errors. Grey points were scattered randomly with a small deviation to increase clarity.

With regards to estimated mobility of species, our analysis also showed that butterfly species which are more mobile have higher average levels of synchrony (Fig. 3.1). Average synchrony for birds was not related to dispersal ability (Fig. 3.1), however birds which have a high dispersal distance show marked increases in synchrony over time (in the BBS dataset), whereas those with low dispersal ability have declined (Fig. 3.3). The recovery in synchrony between 2000 and 2012 was best for butterflies with high mobility (Table B6).

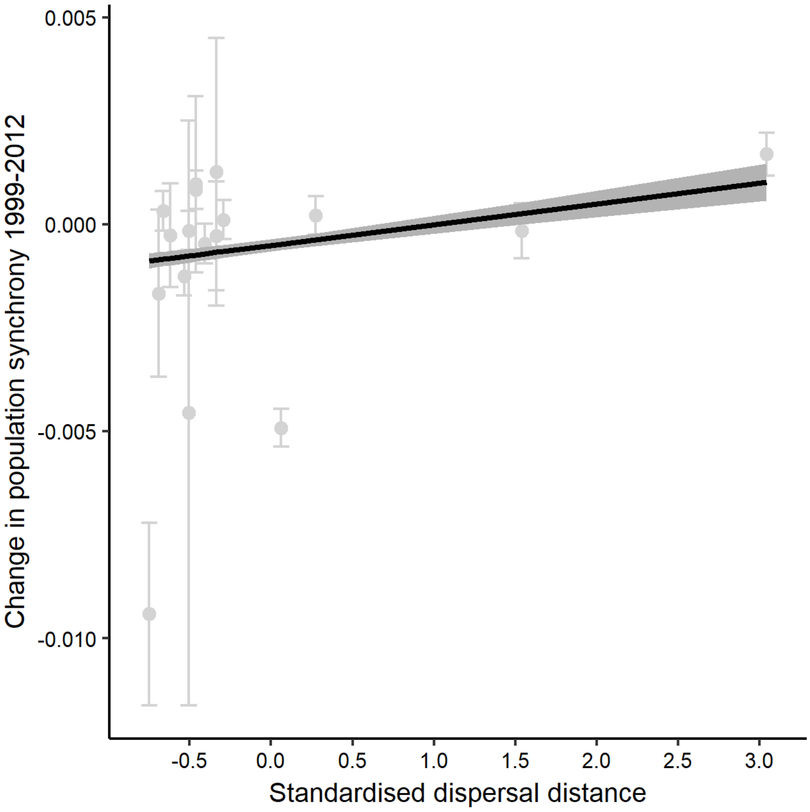

Figure 3.3. Change in population synchrony over time for BBS birds in relation to dispersal distance (standardised with a mean of zero and standard deviation of one). Grey points represent each species raw data with standard error bars, and solid line represent the slope (i.e. change in synchrony over time) for each dispersal distance from the mixed effects models with their associated standard error. Points on the x-axis were scattered randomly with a small deviation to increase clarity.

In relation to mean abundance of species, we found that more common CBC birds had higher average levels of population synchrony, but we did not find any significant effects for BBS birds or butterflies (Fig. 3.1). However, between 2000 and 2012, butterflies which increased in abundance also increased in population synchrony more rapidly than those which declined in abundance (Fig. 3.2b). We did not find any significant results for birds (Table B7 & B8). When only using species with significant changes in abundance over time, we found that butterflies that had significantly increased in abundance over time had increased in synchrony over time between 1985 and 2000 but declined in synchrony between 2000 and 2012 (Figure B3), opposite to the result when non-significant abundance changes are included. For CBC birds, species with significant increases in abundance over time also increased in population synchrony faster than those showing significant decreased in abundance (Figure B4), however this result was marginally significant (Table B7). We found no significant result for BBS using significant changes in abundance over time (Table B8). However, our sample size for significant changes in abundance was smaller (n=9 for butterflies between 1985 and 2000, n=10 for butterflies between 2000 and 2012, n=20 for CBC birds, and n=17 for BBS birds).

3.5 Discussion

We present the first evidence to disentangle the relative role of dispersal in population synchrony trends while accounting for climatic effects, for multiple species over time. We found patterns in population synchrony clearly associated with synchrony in temperature and rainfall. However, once these variables were accounted for, we found several clear relationships between population synchrony and mobility-related attributes.

Previous research has shown parallel increases in population synchrony and environmental synchrony, suggesting a potential role of the Moran effect in driving shared population dynamics over time (Koenig & Liebhold 2016; Sheppard *et al.* 2016; Shestakova *et al.* 2016; Kahilainen *et al.* 2018). Here, we show that population synchrony is significantly associated with synchrony in some seasonal climatic variables. For butterflies, each of the eight climate variables tested were individually associated with population synchrony, whereas for the BBS dataset, only three rainfall variables were significant and for CBC birds only summer temperature (Table B4). This provides convincing evidence that synchrony in temperature and rainfall play a role in driving shared population dynamics (Koenig 2002; Post & Forchhammer 2004; Koenig & Liebhold 2016; Sheppard *et al.* 2016). Previous studies have shown that monitoring sites which are closer together, share similar habitat, and are situated closer to species' range margin have higher mean synchrony values (Sutcliffe et al. 1996, Roland and Matter 2007, Powney et al. 2010; Hordley et al., in prep.). Increased variation in climate can cause extreme population crashes (Palmer *et al.* 2017) and drive more synchronised populations (Pomara & Zuckerberg 2017; Black *et al.* 2018b). However, we found no evidence for in changes in climate variability over time (Table B5), suggesting that climate extremes are unlikely to be driving trends in shared population dynamics in our current dataset.

Once synchrony in temperature and rainfall was accounted for, generalist butterflies showed the greatest changes in population synchrony over time, demonstrating the greatest decline in synchrony in the first two decades of our data, followed by the most rapid recovery in the latter two decades (Table B6). Generalist butterflies have increased their geographic distribution in recent years (Warren *et al.* 2001) and may be responsive to changes in the wider landscape because their host plants occur more widely. For example, landscape context up to 10km around sites has been shown to be important in influencing the population dynamics of generalist butterflies, whilst specialist species respond to more localised aspects of landscape structure (Oliver *et al.* 2010). As such, generalist butterflies tend to be more mobile, suggesting that changes in population synchrony for generalist butterflies is due to their greater ability to move across the landscape. In contrast, we found that specialist birds showed a different pattern, with increases in synchrony across the latter two decades of our study (Table B7). Most specialist bird species in our study are also migrants, which spend winter months in Europe and Africa (e.g. blackcap and chiffchaff) (Hewson & Noble 2009). Migrant species have also been shown to disperse further than resident species (Paradis *et al.* 1998), hence could show greater increases in population synchrony over time as population synchrony is being driven by movement through migration, as opposed to local movements.

Regarding the mobility of species, we find that more mobile butterflies have higher average levels of population synchrony, providing further evidence that dispersal is a key driver of shared population dynamics (Sutcliffe *et al.* 1996; Paradis *et al.* 1999, 2000; Bellamy *et al.* 2003; Chevalier *et al.* 2014). We also found that birds with higher dispersal distance have increased in synchrony across the latter two decades, whereas species with a lower dispersal distance have declined in synchrony (Fig. 3.3). This could be a context-dependent response to environmental factors, where the landscape structure and/or climate conditions benefit more mobile species but hinder less mobile species. In addition, recovery of synchrony in butterflies was most marked in more mobile butterflies during the latter decade of our study, a similar result to those found for generalist butterflies (Table B6).

Regarding the abundance of species, we found that more common birds show higher levels of average synchrony (Paradis *et al.* 1999, 2000; Bellamy *et al.* 2003). Additionally, we found that butterflies which have increased in abundance over time have shown strong increases in population synchrony during the latter decade of our study (Fig. 3.2b). This is consistent with the explanation that changes in density-dependent emigration can facilitate the spread of individuals (Hanski 1998; Roland *et al.* 2000). This potentially offers an avenue for in-situ conservation to enable connectivity between habitat patches (Hodgson *et al.* 2011).

After accounting for synchrony in temperature and rainfall, our results are consistent with the view that changes in population synchrony are influenced by mobility-related attributes (Table 3.1). But the strength of density regulation between populations can affect how well dispersal contributes to population synchrony (Lande *et al.* 1999; Hansen *et al.* 2020). If populations are weakly regulated by density, dispersal can increase the scale of population synchrony even if individual dispersal is low (Lande *et al.* 1999). Hence understanding the strength of density dependence can help further examine the role of dispersal in synchronising population dynamics. Furthermore, although we account for the direct impact of climate on population synchrony, climate could be indirectly driving synchronised population dynamics by altering dispersal rates, or by influencing habitat fragmentation which can disrupt dispersal patterns (Hansen *et al.* 2020). It should also be considered that a number of expected patterns showed non-significant results, which could be due to low statistical power where a large number of interacting factors affect population dynamics causing lower effect sizes.

We found a greater number of significant results overall for butterflies compared to birds. This could be explained by CBC having many fewer sites in total and only 8-10 visits per year, and BBS having only two site visits per year with over three times the number of sites compared to UKBMS sites. Fewer site visits per year leads to higher uncertainty around annual indices of population size, making patterns of local abundance and synchrony much harder to detect. Although we find several significant results, our effect sizes are low (Table B6-B8). This could be due to some climate variables being unaccounted for that are be driving species population synchrony patterns. However, seasonal temperature and rainfall have been shown to capture other climate variables, for example, the decline of wren populations with the number of frost nights can also be captured using mean winter temperature (Bellamy *et al.* 2003). Therefore, we are likely to have similar results as we have here using seasonal temperature and rainfall variables if we used species-specific climate variables.

In conclusion, our exploratory analyses reveal a consistent effect of mobility-related attributes and abundance patterns on population synchrony over time, after accounting for seasonal temperature and rainfall as a confounding effect. This contributes to our understanding of the mechanisms driving population synchrony, adding to the growing body of literature that dispersal can synchronise populations, although accounting for additional drivers such as shared environmental conditions is key.

Chapter 4. Diversity of response and effect traits provides complementary information about avian community dynamics linked to ecological function

4.1 Abstract

Functional diversity metrics based on species traits are widely used to investigate ecosystem functioning. In theory, such metrics have different implications depending on whether they are calculated from traits mediating responses to environmental change (response traits) or those regulating function (effect traits), yet trait choice in diversity metrics is rarely scrutinized. Here, we compile effect and response traits for British bird species supplying two key ecological services – seed dispersal and insect predation – to assess the relationship between functional diversity and both mean and stability of community abundance over time. As predicted, functional diversity correlates with stability in community abundance of seed dispersers when calculated using response traits. However, we found a negative relationship between functional diversity and mean community abundance of seed dispersers when calculated using effect traits. Subsequently, when combining all traits together, we found inconsistent results with functional diversity correlating with reduced stability in insectivores, but greater stability in seed dispersers. Our findings suggest that trait choice should be considered more carefully when applying such metrics in ecosystem management.

4.2 Introduction

Ecosystem services, and the functions underpinning them, are crucial for human survival (Millennium Ecosystem Assessment, 2005). There is now unequivocal evidence that biodiversity enhances the provision of ecosystem functions (Loreau *et al.* 2001; Hooper *et al.* 2005; Tilman *et al.* 2014; Delgado-Baquerizo *et al.* 2020), and due to human activity we are losing biodiversity, thus threatening the delivery of ecosystem functions across the globe (Cardinale *et al.* 2012; IPBES 2019). Initial research into the relationship between biodiversity and ecosystem function used basic measures such as species richness, which provide relatively crude information about the differences between species and their ecological functions (Díaz & Cabido 2001). To provide further insight, ecologists now more commonly estimate the extent of functional differences in a community (i.e. functional diversity) using functional traits that reflect differences in species' resource use as well as their responses to environmental change (Hooper *et al.* 2005; Violle *et al.* 2007b; Cadotte *et* *al.* 2011). Previous analyses have shown that such measures of functional trait diversity perform better than species richness in predicting key aspects of ecosystem function (Gagic *et al.* 2015). However, the trait-based approach is sensitive to a number of methodological details, including the number and type of traits available for each species.

The choice of traits is a key factor in particular because it can influence the ability of functional diversity estimates to predict ecosystem processes (Petchey & Gaston 2006; Petchey *et al.* 2009; Lefcheck *et al.* 2015; Maire *et al.* 2015). Different combinations of traits affect the strength of association between functional diversity indices and basic ecosystem properties such as species richness (Zhu *et al.* 2017). Furthermore, different categories of traits may provide insight into contrasting aspects of biodiversity related to ecosystem function (Tobias *et al.* 2020). For example, ecologists investigating the impacts of environmental change increasingly use traits that reflect species' responses to environmental conditions (i.e. 'response traits') for example traits relating to species' reproductive effect (Luck *et al.* 2012). On the other hand, to understand the relationship between functional diversity and ecosystem functioning, ecologists use traits that determine the effect a species has on ecosystem functioning (i.e. 'effect traits'), for example bill morphology (Luck *et al.* 2012). However some features act simultaneously as an effect and response trait (e.g. body size, Luck *et al.* 2012; Díaz *et al.* 2013). Since multivariate functional diversity metrics routinely combine response and effect traits to produce a single index (Gagic *et al.* 2015), it is not clear whether additional information could be obtained from calculating response and effect trait diversity separately.

From ecological theory, we would expect communities with a high diversity of response traits to have more stable ecological function, based on the insurance hypothesis where greater response diversity buffers ecosystems against the loss of function caused by environmental change (Yachi & Loreau 1999). Communities with high response diversity will have a more diverse set of environmental requirements and tolerances, resulting in asynchronous community dynamics leading to increased community stability (Yachi & Loreau 1999; Loreau & de Mazancourt 2013). This association has been observed in many real-world systems (Elmqvist *et al.* 2003; Catano *et al.* 2020), including wild bee populations wherein increased response diversity – measured by changes in species' abundance after perturbations – contributes to the stability of pollinator abundance (Winfree & Kremen 2009). On the other hand, communities with high diversity of effect traits are expected to have higher mean levels of ecosystem function delivery, thereby enhancing ecosystem service provision; for example, providing greater levels of pollen transfer in a given year, reducing the likelihood of pollination deficit and reduced crop yield. Such communities may deliver ecosystem services more efficiently because higher niche partitioning and reduced competitive exclusion allows species to coexist and have larger populations (Macarthur & Levins 1967; Cardinale 2011). In practice, the mean and stability of ecosystem functions provided over time are related (Oliver *et al.* 2015b; Redhead *et al.* 2020). For example, Garibaldi *et al.* (2011) found pollinator communities with low abundance provided less stable and lower rates of pollination services, which could be driven by low response diversity. However, it has not yet been investigated whether functional diversity metrics calculated using different combinations of response and effect traits provide different insights into the functioning of ecological communities, despite the growing use of functional diversity metrics in guiding ecosystem restoration (Cadotte *et al.* 2011; Manning *et al.* 2019).

Here, we compiled data on the ecological and morphological traits of functionally important bird species to examine how long-term community dynamics are related to the diversity of response and effect traits. We focus on 105 British bird species that provide two key ecosystem functions: seed dispersal and insect predation. In the absence of direct measures of these functions, and their variation over time, we analyse the total abundance of the relevant community. We do not presume that total abundance equates to ecosystem functioning, simply that the two are related (Kleijn *et al.* 2015; Winfree *et al.* 2015). Total community abundance refers to the total number of individuals contributing a particular function within a community, often related to biomass, and is a good predictor of ecosystem functioning in a variety of ecosystems (Grime 1998; Smith & Knapp 2003; Dangles & Malmqvist 2004). The link between total community abundance and any particular ecosystem function can arise due to the ‘mass ratio hypothesis’ whereby the level of function delivered is driven by the most common species in a community (Grime 1998). This is supported by empirical evidence in pollination systems where dominant species provide greater ecosystem services than rarer species (Kleijn *et al.* 2015; Winfree *et al.* 2015). Therefore, total community abundance is assessed here as an important metric that is relevant to ecosystem functioning. However, we recognise that levels of functional redundancy versus complementarity between species, as well as the existence of saturating relationships between abundance and ecosystem function, can potentially make relationships non-linear.

We test whether functional diversity is associated with either the mean or stability of total community abundance over time, and how this relationship varies according to whether metrics are calculated using response traits, effect traits, or a mix of both. To measure total community abundance for each functional group (seed dispersers and insectivores), we use Breeding Bird Survey (hereafter BBS) data over 15 breeding seasons (2004–2018) at 200 sites. We then relate these community dynamics to functional diversity measured using functional dispersion (F_{DIS}) (Laliberté & Legendre 2010) using three different combinations of traits: i) effect only, ii) response only, and iii) effect only, response only and both (i.e. traits classed as both effect and response) traits pooled together (hereafter 'all traits'). Based on the ecological theory outlined above, we test *a priori* hypotheses where we hypothesize that higher functional diversity measured using response traits will provide a more stable community abundance, whereas higher functional diversity measured using effect traits will have a higher mean community abundance measured as the total community abundance, averaged over time. Our goal is to establish how trait choice in functional diversity metrics is related to our ability to observe patterns in community structure and dynamics, and thus to enable more appropriate use of such metrics in ecosystem management.

4.3 Methods

4.3.1 Bird abundance data

We obtained abundance data from the Breeding Bird Survey (BBS), which has been running since 1994 with over 4,000 sites currently monitored. The BBS uses a stratified random sampling design with skilled volunteers surveying two parallel 1-km transects twice a year (April to early May to capture the early breeding season and late May to June for the late breeding season) between 6am and 7am, avoiding poor weather conditions. Birds seen and heard are recorded along the two 1-km line transects in four distance categories (0–25 m from the line, 25–100 m, >100 m and flying over). Each transect is split into 200-m sections, in each of which habitat is recorded using a hierarchical coding system with nine broad categories (woodland, scrubland, semi-natural grassland / marsh, farmland, waterbodies, human sites, coastal, inland rock, and miscellaneous; Crick 1992). The total number of adult birds of each species detected in each 1-km square, i.e. summed over all distance categories, and transect sections, are calculated for each year. We obtained complete time series of annual abundances for a 15-year period (2004–2018) for 108 species, which represents the time period where the greatest number of BBS sites were surveyed. Abundance data were adjusted for detectability, using calculations outlined below by supplementing our data with additional BBS transect data.

4.3.2 Site selection

Sites were only included if they were surveyed during each of the 15 years (2004-2018) of the study. Population dynamics can be mediated by both landscape heterogeneity and position in geographic range (Oliver *et al.* 2010; Mills *et al.* 2017). These factors also influence species richness (Jonsen & Fahrig 1997; Weibull *et al.* 2000) and functional diversity. Sites with higher species richness have been shown to have higher community-level stability by promoting diversity in their response to environmental fluctuations (Ives *et al.* 2000). Our sampling controlled for these issues by being restricted to one bioclimatic zone – i.e. the Atlantic Central (Metzger *et al.* 2013) – with survey sites distributed evenly along a gradient of species richness. Finally, sites were split into 10 categories of increasing species richness and 20 random sites from each category of species richness were chosen, resulting in 200 selected sites (Figure C1).

4.3.3 Accounting for detectability

As heterogeneity in detectability may result in biased abundance estimates, we calculated detectability estimates for each species-site-visit combination using a distance-sampling approach using data for all BBS squares south of 54°N within England and Wales (Buckland *et al.* 2001; Massimino *et al.* 2015). To estimate site-, visit- and species-specific detection probabilities, analysis was conducted at the 200m transect level (assuming that birds on the transect line were detected), using the number of individual birds of each species detected in each distance band. We then estimated the half-normal detection function for each species, with ‘habitat type’ and ‘visit’ as co-variates. Detectability estimates were produced for each species, BBS square and visit (early or late). The detectability estimated from this model was used to adjust the abundance value at each site (adjusted abundance = observed abundance/detectability probability). Finally, the maximum adjusted abundance value of the two visits (early and late) were used as the annual measure of abundance at each site (Harris *et al.* 2019). Detectability data were missing for 70 sites and 12 species (*Anas querquedula, Anthus petrosus, Bucephala clangula, Caprimulgus europaeus, Coccothraustes coccothraustes, Coturnix coturnix, Grus grus, Melanitta nigra, Pernis apivorus, Pyrrhocorax*

pyrrhocorax, Scolopax rusticola, and Turdus iliacus) either due to lack of BBS data to fit a detection function, or sites were missing habitat data for at least one year. To deal with this we took two approaches. First, we removed the missing data, resulting in the removal of 12 species and 70 sites from our analysis, resulting in a complete detectability dataset (n = 96 species and 130 sites). Second, we filled in data gaps in detectability using available data from Johnston *et al.* (2014) for 9 out of the 12 species (removing *Grus grus*, *Melanitta nigra*, and *Pernis apivorus* from the analysis). To fill in gaps for the site-species combinations with no detectability data (i.e., the 70 sites with missing habitat data), we took the average of non-missing values for the site-species combinations, resulting in an interpolated dataset (n = 105 species and 200 sites, with 7.2% of the total dataset interpolated). We ran the analysis separately on the complete dataset and the one with interpolated detectability. The two datasets produced very similar results, so we present those from the interpolated detectability dataset here with the alternative results presented in the tables C10 and C11.

4.3.4 Functional groups

We used dietary data for the world's birds (Tobias & Pigot 2019) to identify species performing functions as seed dispersers and insectivores, which include a combination of both breeding and non-breeding diets depending on where data were available. Seed dispersers included both frugivores and granivores; insectivores included terrestrial invertivores (i.e. non-aquatic invertivores) which use a variety of foraging techniques (e.g. invertivore glean, invertivore aerial, invertivore ground; Pigot *et al.* 2020). Specifically, we classified species as important seed dispersers if their diets comprised at least 30% of seeds and fruit combined, and as insectivores if their diet comprised at least 30% of terrestrial invertebrates (see Table C1 for species list and functional group classification). To focus on species most closely associated with control of insect populations, we excluded aquatic invertivores consuming non-insect prey – including molluscs, crustaceans, annelids worms – following more recent published dietary classifications (Pigot *et al.* 2020).

4.3.5 Functional traits

We grouped traits into two types – those that reflect species' response to environmental conditions (i.e. 'response traits'; Lavorel & Garnier 2002) and those that determine the effect species has on ecosystem functioning (i.e. 'effect traits'; Lavorel & Garnier 2002), with some traits occurring in both categories (i.e. 'both traits'; rationale outlined in Table 1; Luck *et al.*

2012). Our trait selection resulted in four effect traits, seven response traits and five both traits (Table 4.1). Where species had missing trait data, we selected congeneric species to fill in these gaps, because deleting taxa with missing data can reduce statistical power and lead to biased results (Nakagawa & Freckleton 2008). The only gaps in data that needed filling in this way were lifespan for *Sylvia undata* (surrogate species: *Sylvia melanocephala*) and *Regulus ignicapillus* (surrogate species: *Regulus regulus*), and gape width for *Actitis hypoleucos* (surrogate species: *Actitis macularius*). The resulting dataset had 48 seed dispersing bird species and 87 insect eating bird species, with some species performing both functions, making a combined total of 105 species (Table C1).

Table 4.1. Functional traits chosen for the analysis, description of each trait, the category chosen (effect, response or both), the rationale for including the trait as either effect, response or both and source of trait data.

Trait	Description	Category	Rationale	Source
Beak length	Length from the anterior edge of the nostril to the tip of the beak	Effect	Bill shape and size predicts the size and type of food (i.e. seeds and insects) to be handled and consumed (Wheelwright 1985; Luck *et al.* 2012).	Pigot *et al.* 2020
Beak width	Width of the beak measured from the anterior edge of the nostril			
Beak depth	Vertical height measured from the anterior edge of the nostril			
Gape width	The external distance between commissural points			
Species specialization index	Coefficient of variation (SD/mean) of the species density in six habitat categories – high values indicate more specialized species and low values indicate more generalized species	Response	More specialized species have traits associated with slow reproduction (Mckinney & Lockwood 1999) and are less able to respond to environmental variation and novel environments (Sol *et al.* 2002).	Johnston *et al.* 2014
Species temperature index	Long-term average temperature experienced by individuals over its breeding range		Species temperature index indicates a species climate envelope, with warm species better able to adapt to increasing temperatures (Devictor *et al.* 2012).	Devictor *et al.* 2012
Thermal maximum	Mean temperature of the 5% hottest cells of the breeding range		Species with a lower thermal maximum are less tolerant to changing climatic conditions and show negative population trends (Jiguet *et al.* 2007)	Jiguet *et al.* 2007
Mean latitude	The mean latitude of an individual species calculated from its geographic range		Changes in temperature are strongest at northern latitudes, hence these species are likely to respond more strongly to these changes (Parmesan 2007)	http://datazone.birdlife.org/

Trait	**Description**	**Category**	**Rationale**	**Source**
Lifespan	Maximum recorded longevity for a species	Response	Long lifespan can be correlated with small clutch size and infrequent breeding (Zammuto 1986), therefore species are less able to recover from environmental perturbations (Luck *et al.* 2012)	Myhrvold *et al.* 2015
Clutch size	Number of eggs per clutch		These traits measure the reproductive potential of species, and species with high clutch size/multiple broods will recover more quickly after an environmental disturbance (Newbold *et al.* 2013)	Myhrvold *et al.* 2015
Number of broods	Number of clutches produced per year			Myhrvold *et al.* 2015 Johnston *et al.* 2014
Body mass	Geometric mean of average values provided for both sexes	Both	Body size is strongly related to resource use and foraging behaviour, hence indicates species' capacity to consume seeds and invertebrates (Luck *et al.* 2012). Body mass is also strongly related to reproductive output, longevity and dispersal abilities (Luck *et al.* 2012), and hence species' response to environmental conditions	Pigot *et al.* 2020 Sheard *et al.* 2020
Hand-wing index	Aspect ratio of the wing		Wing and leg morphological traits align with movement or dispersal ability, which in turn influences resource use and frugivore (Miles *et al.* 1987; Luck *et al.* 2012; Sheard *et al.* 2020). These traits also indicate locomotory behaviour (Miles *et al.* 1987) and provide species with the ability to withstand environmental changes e.g. disrupted landscape connectivity (Luck *et al.* 2012)	
Kipp's distance	The distance between the tip of the longest primary and the first secondary feather measured on the folded wing			
Wing length	The distance between the bend of the wing and the tip of the longest primary feather			
Tarsus length	Length from the middle of the rear ankle joint to the end of the last scale of acrotarsium			

4.3.6 Total community abundance of functional groups

To estimate key aspects of community dynamics, we calculated the mean total community abundance and stability of total community abundance over time for both our focal functional groups. To calculate mean abundance at each site, we used the total community abundance of species in either functional group averaged across all 15 years. To measure stability over time, we took the reciprocal of the coefficient of variation in annual abundance, 1/CV (e.g. Hautier *et al.* 2015), also known as invariability (Schlapfer & Schmid 1999). This resulted in an estimate of mean total abundance and stability of each functional group for each site.

4.3.7 Functional diversity metrics

To visualize trait variation among species, we projected species-level data into a multivariate trait space (termed 'morpho-space'), commonly used to assess the volume of variation in functional traits, i.e. functional diversity. To quantify functional diversity at each survey site, we used functional dispersion (F_{DIS}) (Laliberté & Legendre 2010) which measures the mean distance of all species, weighted by abundance, relative to the community mean trait value. While a number of different functional diversity metrics exist, each with different advantages and drawbacks, F_{DIS} is less sensitive to species richness *per se* and more sensitive to the overall spread of traits in morpho-space than most alternative metrics (Laliberté & Legendre 2010) and is widely used in studies of functional diversity in ecological communities (Bregman *et al.* 2016; Cadotte 2017). All functional traits were standardized with a mean of 0 and standard deviation of 1. As functional traits in birds are often strongly correlated, we used a principal component analysis (PCA) to obtain independent trait axes and reduce dimensionality (Villéger *et al.* 2008). PCAs were undertaken separately on three groups of traits: effect, response and all traits together (see Tables C2-C7 for trait loadings). Previous studies have shown that description of species niche space requires at least a 3-dimensional trait morphospace (Maire *et al.* 2015; Pigot *et al.* 2020). Hence, we selected a minimum of 3 PCA axes while also maintaining a minimum of 85% explained variation which resulted in three axes for effect traits, four axes for response traits, and five axes for all traits. See figures 4.1 and 4.2 for the variation in effect and response traits for each ecological function. F_{DIS} was calculated for each site using a species x species distance matrix and a matrix containing the average abundance of species at each site using the *dbFD* function (*FD* package, Laliberté *et al.* 2014). This analysis was undertaken for each functional group separately.

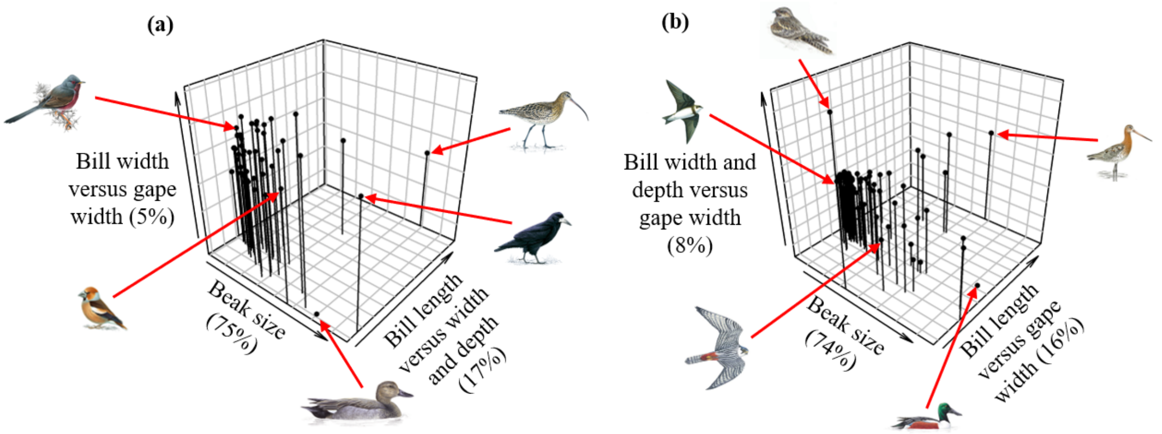

Figure 4.1. Variation in effect traits (beak length, width, depth, and gape width) for (a) seed dispersers and (b) insectivores. Each point represents a single bird species and each axis is derived from a principal component analysis showing percentage of variance in functional traits explained. See Tables C2 & C5 for trait loadings. Images reproduced with permission from Mike Langman (www.rspb-images.com).

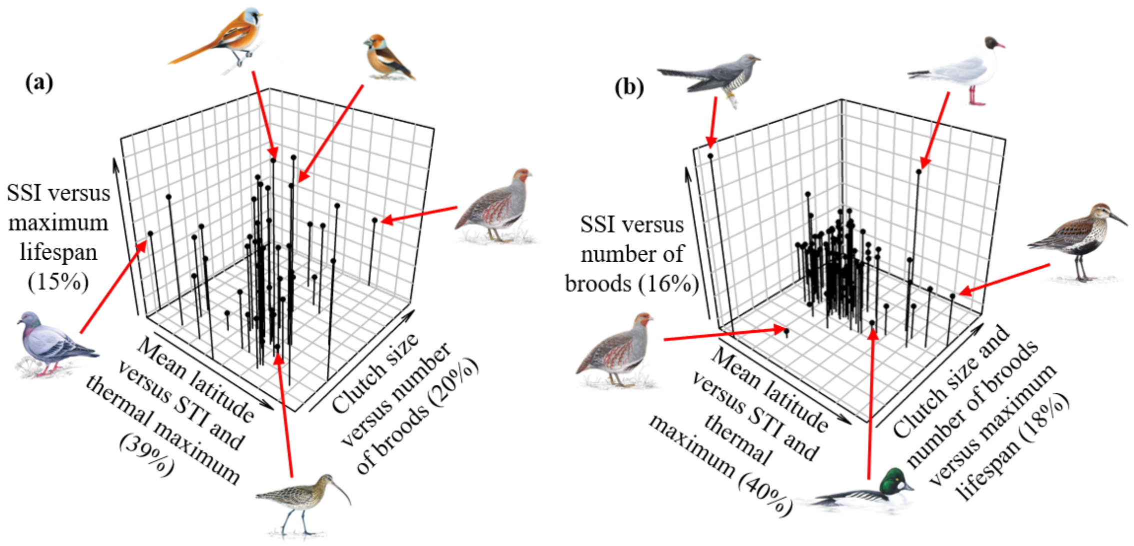

Figure 4.2. Variation in response traits for (a) seed dispersers and (b) insectivores. Each point represents a single bird species and each axis is derived from a principal component analysis showing percentage of variance in functional traits explained. Abbreviations as follows: SSI— species specialisation index; STI — species temperature index; mean latitude— average latitude calculated from all grid cells in the global geographical range; thermal max— mean temperature of the 5% hottest cells of the breeding range. See Tables C3 & C6 for trait loadings. Images reproduced with permission from Mike Langman (www.rspb-images.com)

4.3.8 Statistical analysis

All statistical analysis was undertaken using R version 3.5.3 (R Core Team 2019).

We fitted linear regression models with either the mean total abundance of species or stability of total community abundance over time as the response variable and functional dispersion using different combinations of traits as the explanatory variable. Mean and stability measures were log-transformed to meet assumptions of normal distribution. As sites that are closer together could have more similar abundances, we tested for spatial autocorrelation in the residuals from each model. We used the *correlog* function (*ncf* package, Bjornstad 2020) to estimate the spatial dependence and plot Mantel correlograms, which showed no evidence of spatial autocorrelation. Furthermore, we examined the Pearson's correlation between F_{DIS} effect and F_{DIS} response values for both functional groups. The resulting correlation between effect and response trait diversity could be due to the co-occurrence of traits within individuals, i.e. effect and response traits are positively or negatively correlated within individuals – indicated by our simulated communities showing this correlation, or due to differences in the composition of the specific communities we observed – indicated by this correlation being present in real communities but absent in simulated communities. To test for this, we compared the correlations between F_{DIS} effect diversity and F_{DIS} response diversity for the observed communities with correlations of simulated communities. We used the same species richness at each site over time to select 100 random communities (by randomly drawing species) and calculated F_{DIS} using effect traits and response traits separately for each simulated community. The Pearson's correlation coefficients between F_{DIS} effect diversity and F_{DIS} response diversity for simulated communities was then compared with that of the true observed communities.

4.4 Results

4.4.1 Summary statistics

Species richness at each site ranged from 12 to 35 species for seed dispersing communities, and 18 to 56 species for insectivore communities. Total community abundance averaged over time for each site ranged from 70.9 to 1432.5 for seed dispersing communities and 107.0 to 1005.4 for insectivore communities. Stability of total community abundance for each site, as measured by 1/CV, ranged from 1.89 to 11.94 for seed dispersing communities and 1.42 to 18.72 for insectivore communities.

4.4.2 Seed dispersers

We found a positive relationship between response trait diversity and mean total community abundance for seed dispersers (Figure 4.3c, Table C8). A similar result was found for ‘all trait’ diversity (i.e. both response and effect trait diversity; Figure 4.3b). However, we found a negative relationship for effect trait diversity (Figure 4.3a), although this result was non-significant in the complete case data, i.e. where we removed species and sites where detectability could not be estimated (Table C10). For community stability, we found a positive relationship with response trait diversity (Figure 4.3f, Table C8), as predicted, and a similar result for all trait diversity (Figure 4.3e). However, we found no significant relationship with effect trait diversity (Figure 4.3d). These results were the same when we used the complete case data (Table C10). Our significant positive results here could have been driven by outlying points with high functional diversity driving positive trends (Figure 4.3b, 4.3c, 4.3e and 4.3f). Therefore, we removed outlying points as identified using Cook’s distance with a threshold of $D < 4/n$. Our results remained the same after these points were removed (Figure C2).

Functional dispersion of effect and response traits were negatively correlated (Pearson’s $r = -0.29$, $p<0.001$; Fig. 4.5a). To understand whether this relationship was due to the relationship between the traits themselves or due to differences in the composition of the specific communities we observed, we compared this to 100 randomly selected communities of the same species richness which showed similar negative relationships (Fig. 4.5a). The average correlation coefficient of the 100 iterations was -0.19. We found a weak positive relationship between mean and stability of total community abundance of observed communities (Pearson’s $r=0.39$, $p<0.001$).

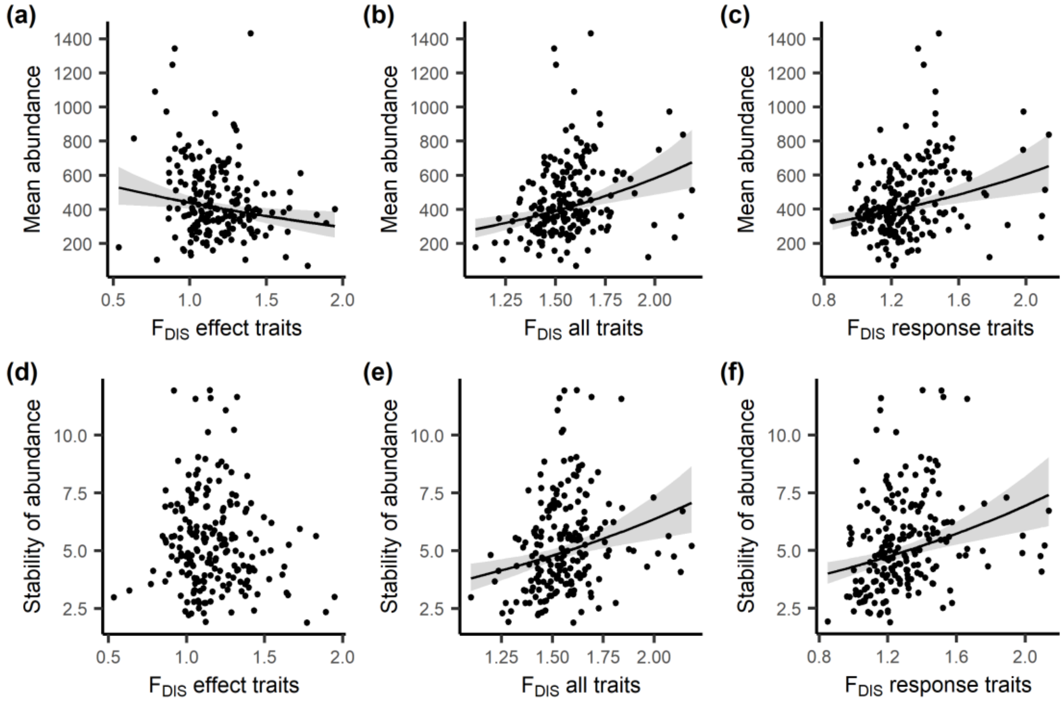

Figure 4.3. Relationships between the mean total community abundance of seed dispersers and functional dispersion (F_{DIS}) of effect traits (a), all traits (b), and F_{DIS} response traits (c). Lower panel shows relationships between the temporal stability of total seed disperser abundance and functional dispersion of effect traits (d), all traits (e) and response traits (f). In both cases results are for 48 birds at 200 sites. Shaded areas around the line show 95% confidence intervals around significant slope coefficients (see Table C8).

4.4.3 Insectivores

For insectivores, we found no significant relationships between functional diversity and mean total community abundance (Figure 4.4a-c, Table C9). For community stability, we found a negative relationship with effect trait diversity (Figure 4.4d, Table C9) and all trait diversity (Figure 4.4e). However, we found no significant relationship with response trait diversity (Figure 4.4f). These results were consistent when the complete case data were used (Table C11).

Functional dispersion of effect and response traits were not significantly correlated (Pearson's r = -0.12, p=0.08). When compared to 100 randomly selected communities of the same species richness, we found relationships in the same negative direction between functional dispersion of effect and response traits compared to the observed communities (Fig. 4.5b). The average correlation coefficient of the 100 iterations was -0.08. We found a weak positive relationship between mean and stability of total community abundance of observed communities (Pearson's r=0.26, p<0.001).

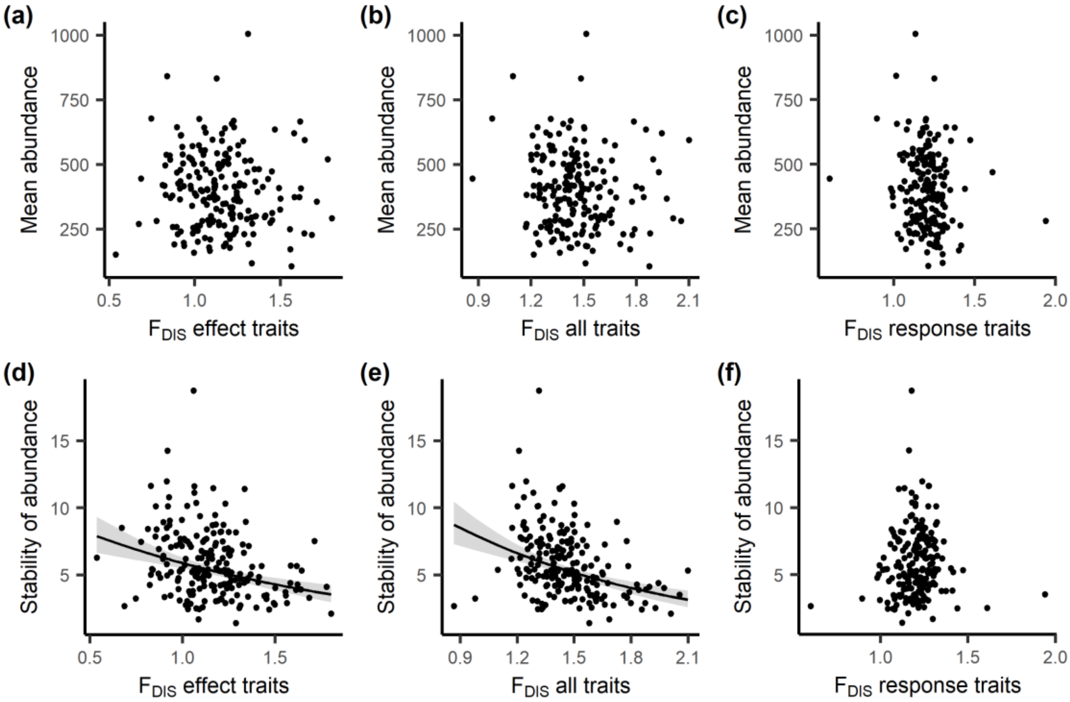

Figure 4.4. Relationships between the mean total abundance of insectivores and functional dispersion (F_{DIS}) of effect traits (a), all traits (b), and F_{DIS} response traits (c). Lower panel shows relationships between the temporal stability of total insectivore abundance and functional dispersion of effect traits (d), all traits (e) and response traits (f) for 87 birds at 200 sites. Shaded areas around the line show 95% confidence intervals around significant slope coefficients (see Table C9).

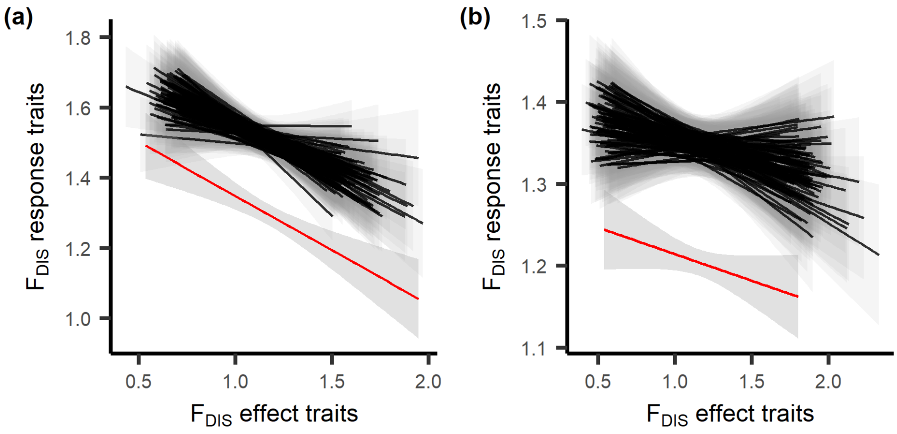

Figure 4.5. Correlation between F_{DIS} response traits and F_{DIS} effect traits for (a) seed dispersers and (b) insectivores. Red line shows results from observed communities; black lines show results from 100 randomly selected communities of the same species richness. Grey areas around the lines represent 95% confidence intervals.

4.5 Discussion

Our results show that communities of seed dispersers with high response trait diversity have more stable total community abundance over time, in line with predictions of the insurance hypothesis (Yachi & Loreau 1999). Most existing support for this hypothesis has been found in synthetic plant communities, often at small spatial scales (Allan *et al.* 2011; Pillar *et al.* 2013; Craven *et al.* 2016; van Klink *et al.* 2019, but see Wilcox *et al.* 2017). Our finding that response trait diversity in assemblages of wild birds can predict stability in a property linked closely to ecosystem function suggests that the insurance hypothesis applies more generally and at larger spatial scales, with implications for how functional diversity metrics are used in ecosystem management (Manning *et al.* 2019). In particular, the relationship we establish between response (but not effect) trait diversity and the stability of total community abundance over time suggests that the type of traits used to calculate functional diversity metrics influences which aspect of ecosystem function these metrics are likely to reflect.

Focusing on a different type of trait, we tested the hypothesis that communities with high effect trait diversity should have higher mean total community abundance. In other words, an assemblage composed of species with divergent niche requirements should have more available resources due to reduced interspecific competition, and therefore populations of each species may be larger, generating higher total community abundance (Macarthur & Levins 1967; Abrams 1983). However, our results run counter to these predictions in that communities of seed dispersers with high effect trait diversity had lower mean total community abundance (Figure 4.3a), while effect traits had no significant relationship with total abundance of insectivores (Figure 4.4a). Our findings therefore add to a growing number of empirical studies finding little support for a positive association between effect trait diversity and total community abundance (e.g. see Thompson *et al.* 2010). This is perhaps unsurprising since the core regions of trait morphospace can be densely packed in bird assemblages (Pigot *et al.* 2016b) with trait overdispersion in co-occurring species being relatively slight (Ulrich *et al.* 2017), and mostly at smaller spatial scales (Trisos *et al.* 2014). In addition, vertebrate species at the periphery of morphospace tend to be rarer than those at the core (Ripple *et al.* 2017), suggesting that assemblages with a higher proportion of morphologically unusual species may have fewer individuals, perhaps explaining the negative relationship we detected between effect diversity and community abundance in avian seed dispersers.

A surprising result from our study was that insectivore bird communities with higher effect trait diversity tended to have less stable total abundance over time (Figure 4.4d). A possible explanation is the negative correlation we found between effect and response diversity for both functional groups. To assess whether this relationship was a result of species composition in real communities (i.e. a product of environmental filtering and/or competitive interactions), we also tested for correlations in simulated communities. There was no relationship between effect and response diversity of randomly selected insectivore communities, whereas real communities showed a weak negative relationship, although this was non-significant (Figure 4.5b). Randomly selected seed dispersing communities showed much weaker negative relationships between effect and response diversity because response diversity was consistently high compared to real communities (Figure 5.5a). Therefore, as these simulated communities did not show the same relationship as our real communities, the negative correlation between effect and response diversity is likely due to environmental filtering and/or competitive interactions.

In real communities, environmental filtering, which selects for species that are well suited to the average environmental conditions (Kraft *et al.* 2015), can lead to a subset of species with more similar response traits (i.e. lower response diversity) than the full range possible. Competitive exclusion is also common among species with more similar traits, which leads to overdispersion in traits of coexisting species. However, competitive exclusion can result in trait clustering (Cadotte & Tucker 2017) if particular traits are associated with higher average fitness (Kraft *et al.* 2015). Disentangling environmental filtering and competitive exclusion is difficult because the two processes can leave similar signatures in the phylogenetic or trait structures of assemblages and may operate simultaneously (Mayfield & Levine 2010; Kraft *et al.* 2015). However, our results suggest that the latter process is important here because we found that seed dispersing communities are less likely to be formed of species with low diversity of both effect and response traits (Figure 4.5). In contrast, when response diversity is high then species with low effect trait diversity can coexist. A possible explanation is that temporal variation in the environment promotes coexistence in species which would otherwise compete (Hutchinson 1961; Kirk 2002), i.e. responding differently to weather conditions leads to reduced competition between species with similar effect traits allowing them to coexist in the same communities (Hutchinson 1961; Roth & Schreiber 2014; Li & Chesson 2016).

Having shown the influence of response trait diversity on community abundance differs from that of effect trait diversity, we tested whether the standard approach of mixing both types of trait together result in a best-of-both-worlds scenario for functional diversity metrics. This was true for seed disperser communities, where we found that combined functional trait diversity was positively related to mean community abundance (Figure 4.3b) and to the stability of total abundance (Figure 4.3e), equivalent to the results found for response diversity. However, for insectivore communities, we found a negative relationship of all trait diversity with stability of total abundance (Figure 4.4e), comparable to the relationship found with effect diversity. These inconsistent results highlight an important trade-off between evidence for mean and stability of abundance in UK bird communities. Studies using indices of functional diversity often use traits regarded as effect traits (e.g. foraging type) and both traits (e.g. body size; (Prescott *et al.* 2016). Our results highlight that communities with high diversity of such traits can potentially indicate low stability. Ecologists have suggested maximising functional diversity when restoring communities (Cadotte *et al.* 2011), but depending on how this is calculated it could lead to communities with unstable abundance, risking years of low ecosystem functioning (as well as high).

Our results also emphasise that different functional groups of birds respond differently to the same group of traits used in our measure of functional diversity. Response trait diversity acts similarly to all trait diversity for seed dispersers, whereas effect trait diversity acts similarly to all trait diversity in insectivores. Therefore, it may be advisable to maximise functional diversity within functional groups, as opposed to the entire bird community; with the specific traits used in metrics of functional diversity guided by research such as that shown here. It is unclear to what extent our results hold for bird guilds in different bioregions (e.g. desert, tropics), emphasising the need for further work on this topic.

Our approach has some limitations worth outlining. The proportion of variance in community dynamics explained by functional diversity was low; varying from 3.1-15.0% (Table C8-C11). Our predictive ability was not improved by removing outlying points in our seed disperser dataset (Figure C1) where some sites had extreme functional diversity values. The low proportion of variance could partly be due observer bias including identification mistakes or sampling error related to habitat type (Johnston *et al.* 2014), however, we accounted for heterogeneity in detectability, by adjusting the raw abundance data by a detectability probability coefficient (Johnston *et al.* 2014; Massimino *et al.* 2015). Furthermore, our measurements of functional diversity could also be imprecise due to missing data in functional trait datasets leading to low r-squared values. ‘Hard’ functional traits with more proximate effects on ecosystem functioning are often more difficult or expensive to measure (Hodgson *et al.* 1999; Violle *et al.* 2007b). Due to this, some ‘soft’ traits were used in this analysis (e.g. reproductive traits such as clutch size), although these often correlate with hard traits (Violle *et al.* 2007b). A further source of error in functional diversity estimates could be due to the use of mean trait values per species. Including intraspecific variation in traits has been shown to improve the ability to detect niche differentiation processes (Jung *et al.* 2010). Disregarding this variation underestimates the degree of niche and trait overlap between species (Violle *et al.* 2012), however, Pigot *et al.* (2020) found most variation in global bird trait values existed across rather than within species. Finally, there was higher variance in total mean abundance between sites versus variance in functional diversity, which might also reduce the degree of fit in their relationship.

Although we find many significant relationships between functional diversity and mean and stability of abundance, our low predictive ability highlights the difficulty in linking functional traits to community abundance, and the additional step of linking to ecosystem functioning. However, we demonstrate that effect and response traits provide different information on community abundance which can be used to inform management actions to maintain ecosystem functioning.

Our findings extend previous research emphasising the importance of trait choice methodology in producing accurate functional diversity measures and deriving accurate ecological conclusions (Maire *et al.* 2015; Zhu *et al.* 2017) while demonstrating a novel link between trait choice and community dynamics. This can help infer whether increased functional diversity will lead to higher mean or stability of community dynamics, and therefore ecosystem functioning. In particular, to measure stability of total community abundance it appears crucial to include in functional diversity metrics traits reflecting the response of species to environmental conditions. Selecting functional traits appropriately will enable conservation practitioners to use functional diversity metrics in informative ways to ensure the long-term stability of ecosystem functioning.

Chapter 5. Resolution of data used in functional diversity metrics affects ability to predict community dynamics of avian functional guilds

5.1 Abstract

Functional diversity, measured using species traits, can be used to understand changes in community dynamics of functionally important species. More resolved trait data provides higher quality information on the niche requirements of species, but the impact of the resolution of trait and abundance data on functional diversity metrics and their ability to explain community dynamics is largely unknown. Here, we compile nine functional traits for 105 British birds supplying two key ecological services – seed dispersal and insect predation – to understand how the number, type and weighting of traits used in analysis (continuous versus categorical; abundance versus presence-absence) could influence the ability to predict community abundance. Overall, the explanatory power of functional traits was low, with a maximum of 9.5% of variance in community abundance explained. We found inconsistent results when we investigated whether continuous or non-continuous traits increased explanatory power, depending on whether our metric was weighted with abundance and the functional group being investigated. In most instances, a lower number of traits increased the mean R^2 and increased the variation around our R^2 values. Our predictive ability was influenced by the identity of the traits which are included in our functional diversity metric, which differed between our functional groups. These findings highlight the practical difficulty in making meaningful predictions of community dynamics with implications for a predictive ecology of ecosystem functioning.

5.2 Introduction

Biodiversity is being lost at an increasing rate across the globe due to human activity, potentially threatening crucial ecosystem functions and the ecosystem functions that humans derive from them (Cardinale *et al.* 2012; IPBES 2019). Initial attempts to capture biodiversity to understand the impact on ecosystem functioning used basic measures such as species richness (Díaz & Cabido 2001). However, research has shown species richness alone to be a poor determinant of ecosystem functioning (Gagic *et al.* 2015). Increasingly, studies now use functional diversity, the breadth of functions performed by a species in a community, to provide further insight into ecological processes (Hooper *et al.* 2005; Violle *et al.* 2007a;

Cadotte *et al.* 2011). Functional diversity has been shown to be a better predictor of ecosystem processes in a wide variety of taxa compared to species richness (Gagic *et al.* 2015).

Initial techniques to calculate functional diversity (FD) were based on functional dendrograms where a matrix of functional traits is used to calculate the sum of branch lengths of the dendrogram, producing a multivariate measure of functional diversity (Petchey & Gaston 2002). More recent methods are based on a multidimensional functional space where species are plotted along trait axes, which allow the computation and visualisation of functional diversity (Villéger *et al.* 2008; Laliberté & Legendre 2010; Mammola & Cardoso 2020). Research has demonstrated a definitive link between trait morphospace (i.e. species traits visualised in a multivariate space) and trophic niches of avian species, providing compelling evidence for using these methods to understand ecosystem functioning (Pigot *et al.* 2020).

Selecting the most informative traits for the ecological function of interest will increase the success of using trait-based methods (Hortal *et al.* 2015). However, there exists a trade-off between collecting a large amount of low quality information, and a small amount of high quality information (Petchey & Gaston 2006). The number of functional traits selected can influence multivariate functional diversity metrics (Legras *et al.* 2019) highlighting how sensitive these metrics are to the type of data used to calculate them. Trait spaces with low dimensionality (i.e. low number of traits) reduced the quality of functional trait space, i.e. the ability to represent initial functional distance between species (Maire *et al.* 2015). Furthermore, increasing the dimensionality of trait space has been shown to more accurately predict trophic niches (Pigot *et al.* 2020) and adequately capture phenotypic differences between species (Carscadden *et al.* 2017). However, using more traits increases the likelihood of the inclusion of correlated traits which do not provide any additional phenotypic information and can increase the probability of detecting functional redundancy (Petchey *et al.* 2007; Calba *et al.* 2014). For example, when correlated traits are used, the ability to accurately identify plant species within trait space is reduced, compared to using uncorrelated traits (Laughlin 2014). Traits chosen are often those easily measurable and captured as basic categorical variables, which leads to lower quality estimates of functional diversity, and thus require more dimensions to capture unique functional strategies (Maire *et al.* 2015). Whereas continuous traits can provide more in-depth information on species resource use, they tend to be more difficult to collect (Kohli & Jarzyna 2021).

Some functional diversity metrics have the ability to be weighted by the average abundance of species, giving more weight to common species based on their greater contribution to ecosystem functioning (Grime 1998; Villéger *et al.* 2008; Winfree *et al.* 2015). Functional diversity measures that integrate abundance in this way have been shown to better predict key ecosystem functions compared to those which do not weight by abundance (Gagic *et al.* 2015). In practice, however, abundance data are not always readily available, and presence-absence data may be the only option, resulting in each species being given equal weighting regarding its contribution to the ecosystem function. Despite these studies exploring how data resolution influences different aspects of the functional diversity calculation, it has not yet been investigated what are the consequences for predicting total community abundance of functional guilds. Aspects of community dynamics, such as total community abundance over time are highly relevant to ecosystem functioning (Grime 1998; Kleijn *et al.* 2015; Winfree *et al.* 2015).

Here, we compile data on the ecological and morphological traits of functionally important bird species to examine how altering the resolution of functional trait and abundance data used in functional diversity metrics influences the ability to predict community abundance. We focus on 105 British bird species that provide two key ecosystem functions: seed dispersal and insect predation. In the absence of direct measures of these functions we use the total abundance of the relevant community. We do not presume that total abundance equates to ecosystem functioning, simply that the two are related (Kleijn *et al.* 2015; Winfree *et al.* 2015); thus if the functional composition of communities relates to total abundance then there are likely to be cascade effects on ecosystem functioning too. Total community abundance refers to the total number of individuals contributing a particular function within a community, often related to biomass, and is a good predictor of ecosystem functioning in a variety of ecosystems (Grime 1998; Smith & Knapp 2003; Dangles & Malmqvist 2004). The link between total community abundance and any particular ecosystem function can arise due to the ‘mass ratio hypothesis’ whereby the level of function delivered is driven by the most common species in a community (Grime 1998). This is supported by empirical evidence in pollination systems where dominant species provide greater ecosystem services than rarer species (Kleijn *et al.* 2015; Winfree *et al.* 2015).

We use abundance data from the Breeding Bird Survey (hereafter BBS) dataset for over 15 breeding seasons (2004–2018) at 200 sites to measure total community abundance for each functional group (seed dispersers and insect predators). We then relate this to functional dispersion (F_{DIS}) (Laliberté & Legendre 2010) calculated using species effect traits, which determine a species' effect on ecosystem functioning. We expect effect trait diversity and community abundance to be related because communities with high effect trait diversity may deliver ecosystem services more efficiently due to higher niche partitioning and reduced competitive exclusion which allows species to coexist and have larger populations (Macarthur & Levins 1967; Cardinale 2011). We investigated the ability for F_{DIS} to explain variation in community abundance while: (1) varying the number of traits (from 2-9); (2) altering the variable type (continuous or categorical); and (3) shifting between abundance and presence-absence data. We hypothesise that more resolved data (i.e. a higher number of continuous functional traits and abundance data) used in our measure of F_{DIS} will explain more variation in community abundance.

5.3 Methods

Bird abundance data

We obtained abundance data from the Breeding Bird Survey (BBS), which has been running since 1994 with over 4,000 sites currently monitored. The BBS uses a stratified random sampling design with skilled volunteers surveying two parallel 1-km transects twice a year (April to early May to capture the early breeding season and late May to June for the late breeding season). Birds seen and heard are recorded in four distance categories (0–25 m from the line, 25–100 m, >100 m and flying over). The total number of adult birds of each species detected in each 1-km square, i.e. summed over all distance categories, and transect sections, are calculated for each year. We obtained complete time series of annual abundances for a 15-year period (2004–2018) for 108 species, which represents the time period where the greatest number of BBS sites were surveyed. Abundance data were adjusted for detectability, using calculations outlined below by supplementing our data with additional BBS transect data.

Site selection

Sites were only included if they were surveyed during each of the 15 years (2004-2018) of the study. Population dynamics can be mediated by both landscape heterogeneity and position in geographic range (Oliver *et al.* 2010; Mills *et al.* 2017). These factors also influence species richness (Jonsen & Fahrig 1997; Weibull *et al.* 2000) and functional diversity. Sites with higher species richness have been shown to have higher community-level stability through a diversity in species' responses to environmental fluctuations (Ives *et al.* 2000). Our sampling controlled for these issues by being restricted to one bioclimatic zone – i.e. the Atlantic Central (Metzger *et al.* 2013) – with survey sites distributed evenly along a gradient of species richness. Sites were split into 10 categories of increasing species richness and 20 random sites from each category of species richness were chosen, resulting in 200 selected sites.

Accounting for detectability

As heterogeneity in detectability may result in biased abundance estimates, we calculated detectability estimates for each species-site-visit combination using a distance-sampling approach using data for all BBS squares south of 54°N within England and Wales (Buckland *et al.* 2001; Massimino *et al.* 2015). To estimate site-, visit- and species-specific detection probabilities, analysis was conducted at the 200m transect level (assuming that birds on the transect line were detected), using the number of individual birds of each species detected in each distance band. We then estimated the half-normal detection function for each species, with 'habitat type' and 'visit' as co-variates. Detectability estimates were produced for each species, BBS square and visit (early or late). The detectability estimated from this model was used to adjust the abundance value at each site (adjusted abundance = observed abundance/detectability probability). Finally, the maximum adjusted abundance value of the two visits (early and late) were used as the annual measure of abundance at each site (Harris *et al.* 2019). Detectability data were missing for 70 sites and 12 species (*Anas querquedula, Anthus petrosus, Bucephala clangula, Caprimulgus europaeus, Coccothraustes coccothraustes, Coturnix coturnix, Grus grus, Melanitta nigra, Pernis apivorus, Pyrrhocorax pyrrhocorax, Scolopax rusticola,* and *Turdus iliacus*) either due to lack of BBS data to fit a detection function, or sites were missing habitat data for at least one year. To deal with this we took two approaches. First, we removed the missing data, resulting in the removal of 12 species and 70 sites from our analysis, resulting in a complete detectability dataset (n = 96 species and 130 sites). Second, we filled in data gaps in detectability using available data from Johnston *et al.* (2014) for 9 out of the 12 species (removing *Grus grus*, *Melanitta nigra*, and *Pernis apivorus* from the analysis). To fill in gaps for the site-species combinations with no detectability data (i.e., the 70 sites with missing habitat data), we took the average of non-missing values for the site-species combinations, resulting in an interpolated dataset (n = 105 species and 200 sites, with 7.2% of the total dataset interpolated). We ran the analysis separately on the complete dataset and the one with interpolated detectability. The two datasets produced very similar results, so we present those from the interpolated detectability dataset here with the alternative results presented in figures D1 and D2.

Feeding guilds

We used dietary data for the world's birds (Tobias & Pigot 2019) to identify species performing functions as seed dispersers and insectivores, which include a combination of both breeding and non-breeding diets depending on where data were available. Seed dispersers included both frugivores and granivores; insectivores included terrestrial invertivores (i.e. non-aquatic invertivores) which use a variety of foraging techniques (e.g. invertivore glean, invertivore aerial, invertivore ground; Pigot *et al.* 2020). Specifically, we classified species as important seed dispersers if their diets comprised at least 30% of seeds and fruit combined, and as insectivores if their diet comprised at least 30% of terrestrial invertebrates (see Table D1 for species list and functional group classification). To focus on species most closely associated with control of insect populations, we excluded aquatic invertivores consuming non-insect prey – including molluscs, crustaceans, annelids worms – following more recent published dietary classifications (Pigot *et al.* 2020).

Functional traits

To investigate how the relationship between functional diversity and mean total community abundance is affected by the resolution of data, we selected functional traits which determine species' effects on ecosystem functioning (i.e. functional 'effects traits'; Díaz *et al.* 2013). We selected 9 traits in total: beak length, width and depth, gape width, body mass, wing length, hand-wing index, Kipp's distance and tarsus length. We had missing trait data for one species: gape width for *Actitis hypoleucos*. As deleting taxa with missing data can reduce statistical power and lead to biased results (Nakagawa & Freckleton 2008), we selected gape width data from a morphologically similar congeneric species (*Actitis macularius*). The resulting dataset had 48 seed dispersing bird species and 87 insect eating bird species, with some species performing both functions, making a combined total of 105 species.

Total community abundance of feeding guilds

We calculated the mean total community abundance over time for both our focal feeding guilds at each site. To calculate this, we used the total community abundance of species in either functional group averaged across all 15 years. This resulted in an estimate of mean abundance of each functional group for each site. Species richness at each site ranged from 12 - 35 species for seed dispersing communities, and 18 - 56 species for insect predating communities. Total average community abundance averaged over time for each site ranged from 70.9 – 1432.5 for seed dispersing communities and 107 – 1005.4 for insect predating communities.

Functional diversity metrics

Functional diversity metrics require both functional traits and either abundance or presence-absence data to calculate multivariate indices (Laliberté & Legendre 2010). Here, to modify the resolution of input data into FD metrics, we investigated the impact of both changing the number of traits and the proportion of continuous traits used to calculate FD metrics. We analysed the effect of trait number (from 2-9 traits), removing a different trait each time and repeating, so all combinations were used. To assess the effect of proportion of continuous traits ($P_{continuous}$) used in functional diversity metrics, for each number of traits selected, we initially calculated functional diversity when $P_{continuous} = 1$, i.e. when all traits are continuous. Subsequently, at the other extreme, we investigate the lowest possible level of trait resolution by converting any given trait into a categorical variable with two factor levels (low and high) until all proportions and combinations are used. For example, when 4 traits are selected, functional diversity is calculated when all traits are continuous ($P_{continuous} = 1$), when all traits are categorical ($P_{continuous} = 0$), and for $P_{continuous} = 0.25$, 0.5 or 0.75 using different combinations of traits each time (in this example, sample sizes are 126, 126, 504, 756 and 504 respectively).

To measure functional diversity at each bird monitoring site, we used functional dispersion (F_{DIS}) (Laliberté & Legendre 2010). First, we use Gower's distance (Gower 1971) to calculate a dissimilarity matrix between all pairs of species as it can be used for all types of trait data (Podani & Schmera 2006). F_{DIS} was calculated for each site using the species x species distance matrix constructed from raw trait data and a matrix firstly weighted using the average detectability-adjusted abundance of each species at each site (hereafter abundance-weighted FDis), and secondly using presence-absence data (hereafter unweighted FDis) using the *dbFD* function (*FD* package, Laliberte *et al.* 2014). When $P_{continuous} = 1$, the traits were standardized with a mean of 0 and standard deviation of 1. This analysis was undertaken for each ecosystem function separately.

Statistical analysis

All statistical analysis was undertaken using R version 4.0.4 (R Core Team 2021).

We fitted linear models with the mean total community abundance at each site as the response variable and corresponding F_{DIS} values at each site as our explanatory variable (i.e. separate models using F_{DIS} calculated with different numbers of traits and different proportions continuous). Mean total community abundance was log-transformed to meet the assumptions of normality. We extracted the R^2 from each model to show how much variation in mean total community abundance was explained by each F_{DIS} value as well as the direction of relationship. Then we calculated the mean R^2 with associated standard deviation across all combinations for each trait number and proportion of continuous traits.

To further explore how trait number and the proportion of continuous traits was impacting the R^2 values, we also tested whether continuous traits or categorical/mixed traits have significantly different mean R^2 using a Mann-Whitney Wilcoxon test as the data were not normally distributed. As we found a significant difference in R^2 values between the variable trait types, we used linear models with the mean R^2 from categorical/mixed traits only as the response variable and as explanatory variables: trait number, proportion of continuous traits and the interaction term between these two.

As there were non-linear relationships between mean R^2 and number of continuous traits, we further investigated whether this could be due to redundant traits being present in the F_{DIS} measure. We calculated the absolute average correlation coefficient for each of the 9 traits relative to each other trait. F_{DIS} was then calculated by removing each of the 9 traits in turn and re-fitting the linear models with mean total community abundance and extracting each R^2 value. This was compared with the R^2 value from the model with F_{DIS} calculated using all 9 traits, i.e. the difference in R^2 as each trait is removed showing its individual explanatory power. Finally, linear models were used to analyse the relationship between R^2 difference and absolute average correlation coefficient for each of the 9 traits.

5.4 Results

Seed dispersers

The maximum R^2 values from the relationship between total community abundance and F_{DIS} was 9.4% for abundance weighted F_{DIS} (Figure 5.1a) and 4.9% for unweighted F_{DIS} (Figure 5.1d). The highest mean R^2 values for abundance weighted F_{DIS} occur when both a larger number of traits were used (i.e. $n = 9$) and the trait type was continuous (Figure 5.1b), and there was corresponding low variation around these R^2 values (Figure 5.1c). These results were qualitatively similar when using the complete case data, i.e. where species without detectability estimates were removed (Figure D1). Across all numbers of traits used, we found that continuous traits have a significantly higher mean R^2 compared to categorical traits or a mix of the two types for abundance weighted F_{DIS} (Mann-Whitney Wilcoxon W = 352, $p<0.001$; Figure D3a). When we looked at mean R^2 from continuous traits separately, we found that more continuous traits both increase the mean R^2 and decrease the variation for abundance weighted F_{DIS} (Figure D4a). Considering the mean R^2 from categorical/mix traits for abundance weighted F_{DIS}, we found that as both trait number and $P_{continuous}$ increased the mean R^2 increased in an additive fashion (Figure 5.2a; Table D2).

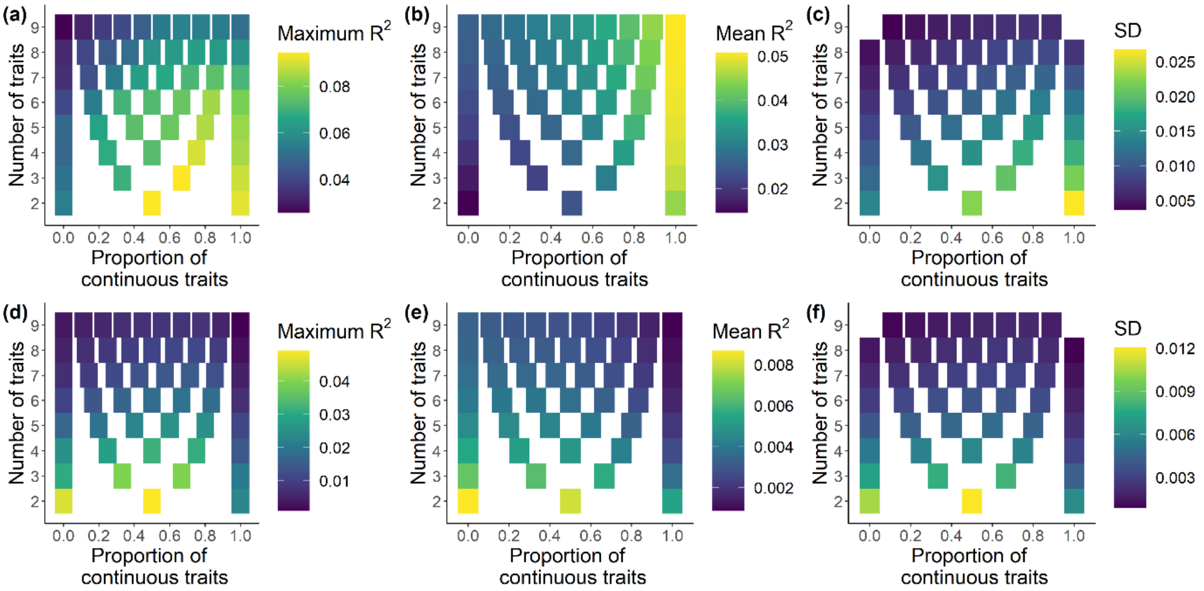

Figure 5.1. Maximum R^2 values (a) and mean R^2 values (b) with associated standard deviation (c) produced from abundance weighted F$_{\mathrm{DIS}}$, and maximum R^2 values (d) and mean R^2 values (e) with associated standard deviation (f) produced from unweighted F$_{\mathrm{DIS}}$ for seed dispersing birds.

In contrast, for unweighted F$_{\mathrm{DIS}}$ we found that using the *fewest* traits (i.e. $n = 2$) and the trait type as a categorical variable provided the highest mean R^2 values (Figure 5.1e), although this had high variation, suggesting results differ depending on which specific traits are included (Figure 5.1f). Across all numbers of traits used, categorical or a mix of variable types had a significantly higher mean R^2 compared to continuous trait types (Mann-Whitney Wilcoxon $W = 75$, $p = 0.009$; Figure D3b). When considering mean R^2 from continuous traits separately, a low number of continuous traits led to higher mean R^2, but with large variation (Figure D4b). Considering the mean R^2 from categorical/mix traits for unweighted F$_{\mathrm{DIS}}$, there was a negative relationship between the number of continuous traits and mean R^2, and a significant interaction between trait number and P$_{\mathrm{continuous}}$ (Table D2), showing that as trait number increases, the negative relationship between P$_{\mathrm{continuous}}$ and mean R^2 becomes slightly weaker (Figure 5.2b).

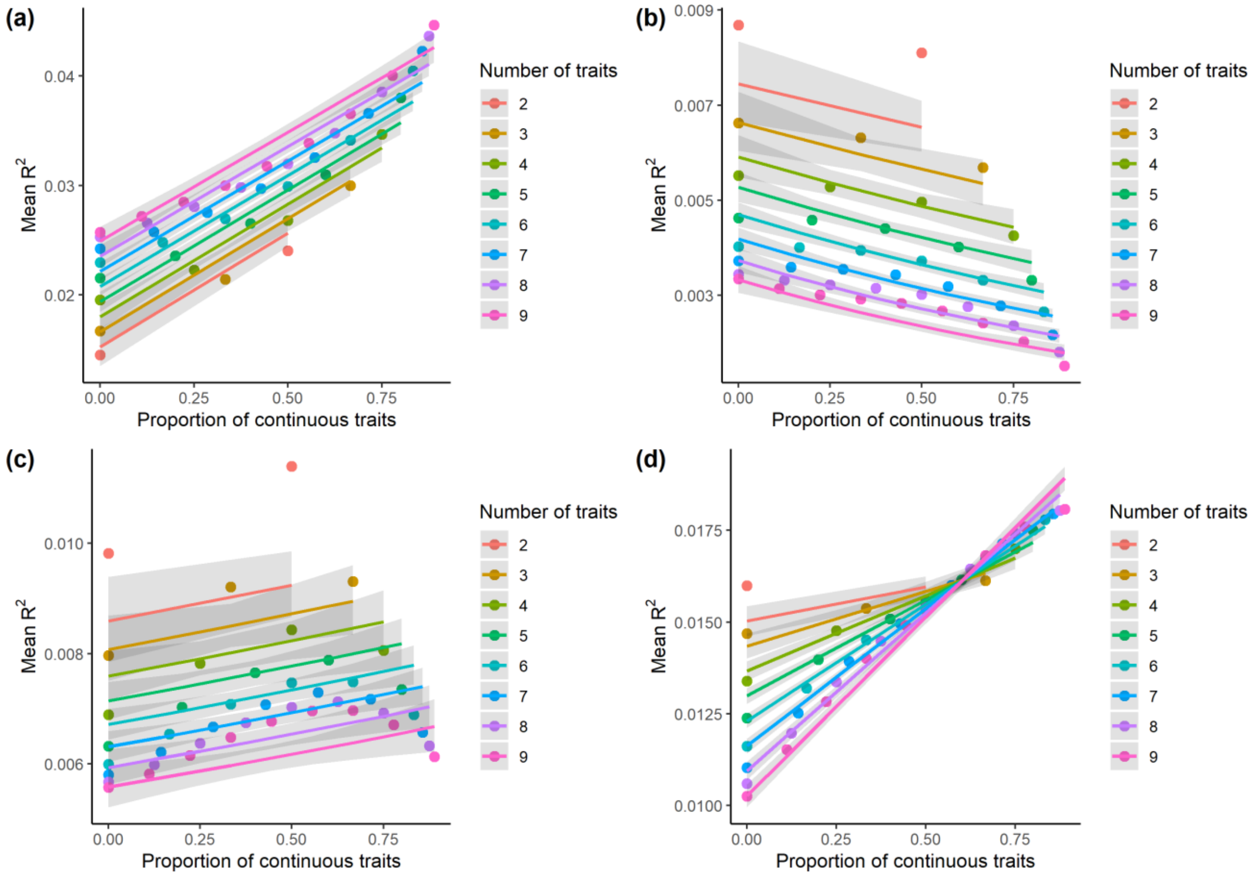

Figure 5.2. The relationship between mean R^2 and trait number and the proportion of continuous traits for non-continuous traits for seed dispersers with abundance weighted F_{DIS} (a), and insect predators with unweighted F_{DIS} (b). Lines represents the linear regression with shaded 95% confidence intervals.

To understand why the mean R^2 differed when using a different number of continuous traits, we investigated the difference in R^2 when we removed each of the 9 traits separately and related this to the average correlation coefficient of the removed trait. For seed dispersers, we found a significant positive relationship between the difference in R^2 and average correlation coefficient using abundance weighted F_{DIS} (Figure 5.3; Table D3). This demonstrated that traits which are highly correlated, for example, Kipp's distance, wing length and body mass, caused substantial increase in R^2 values when removed, meaning that their inclusion hampers the ability to predict total community abundance using abundance weighted F_{DIS} (Figure 5.4a). In contrast, removing traits such as bill width, bill depth and gape width caused a substantial decrease in R^2 values, showing that they are important to include to improve prediction of total community abundance using abundance weighted F_{DIS} (Figure 5.4a). This sensitivity to trait identity may explain the very high variation in R^2 values when just a few continuous traits are used in the calculation of abundance weighted F_{DIS} (Figure 5.1c). However, the relationship between difference in R^2 and average correlation coefficient was non-significant when using presence-absence data (Table D3), and the calculation of unweighted F_{DIS} appears relatively insensitive to trait identity (Figure 5.4b). This is probably because using continuous traits for this metric resulted in poor predictive capacity, as outlined above (and shown in Figure 5.1e).

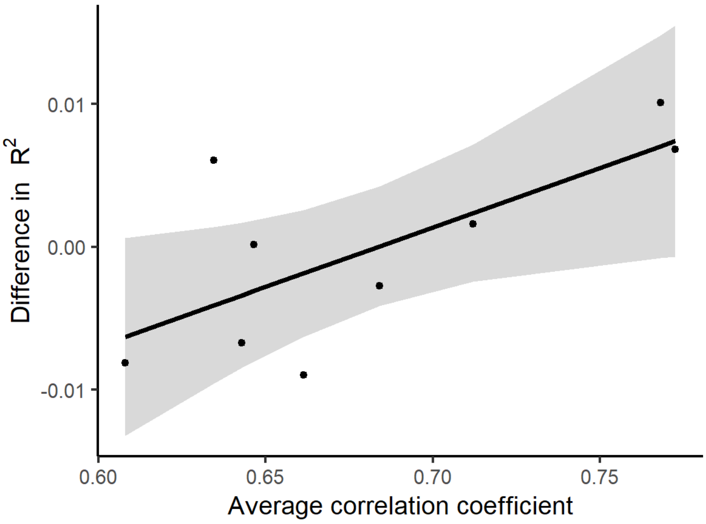

Figure 5.3. Relationship between the difference in R^2 and average correlation coefficient of each continuous trait from abundance weighted F_{DIS} for seed dispersers. Shaded area around the line shows 95% confidence intervals around significant slope coefficients (see Table S2).

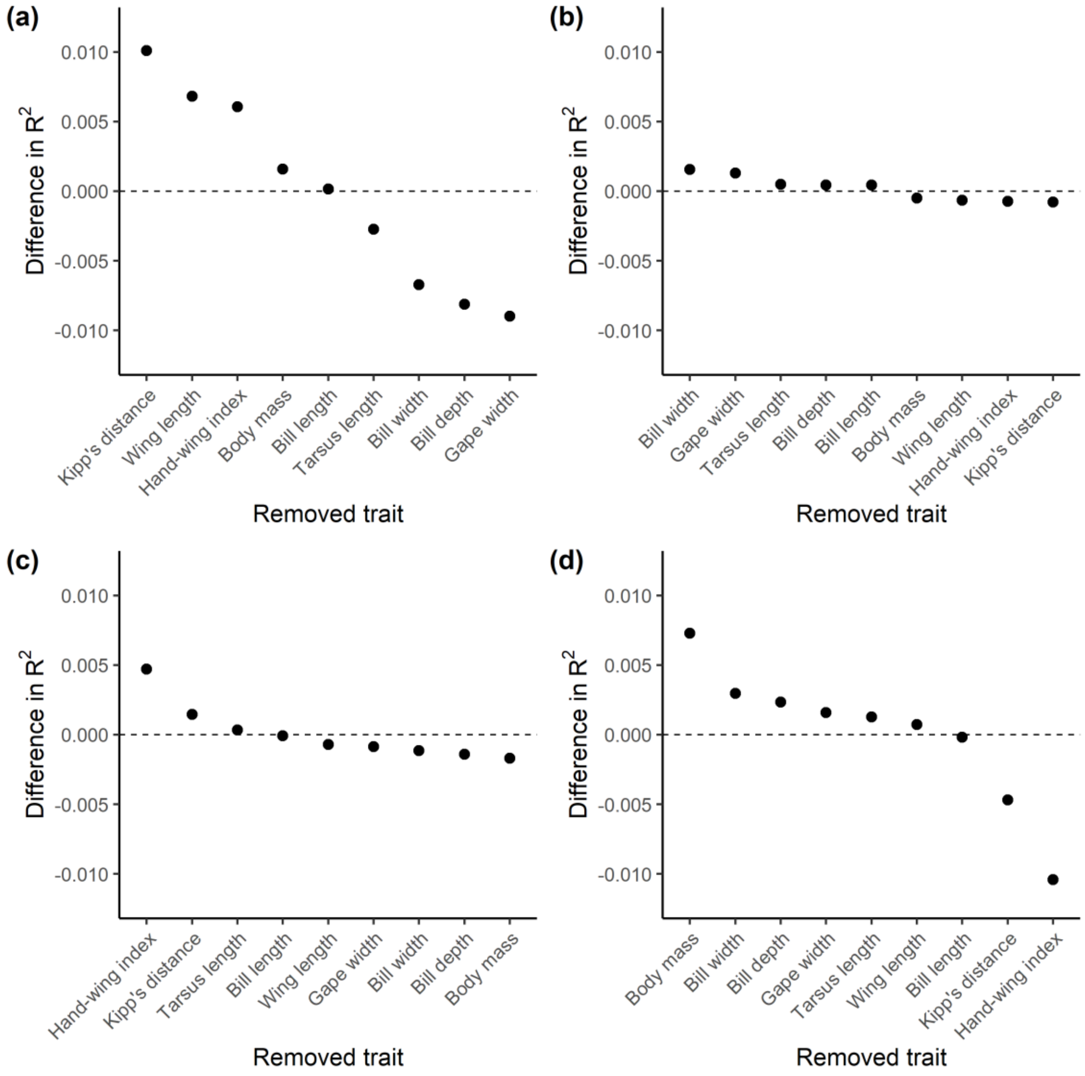

Figure 5.4. The difference in R^2 when each of the 9 continuous traits is removed from the calculation of F_{DIS} for seed dispersers with abundance-weighed F_{DIS} (a) and unweighted F_{DIS} (b), and insect predators with abundance-weighted F_{DIS} (c) and unweighted F_{DIS} (d). Negative values for the difference in R^2 indicate that when a trait is removed, the R^2 is lower, suggesting that including that trait in the F_{DIS} calculation improves the ability to predict total community abundance.

Insectivores

In contrast to seed dispersers, the highest R^2 values from the relationship between total community abundance and F_{DIS} for insectivorous birds was obtained using unweighted F_{DIS} (i.e. presence-absence data). The maximum R^2 value was 4.3% for abundance weighted F_{DIS} (Figure 5.5a) and 7.5% for unweighted F_{DIS} (Figure 5.5d). Using abundance weighted F_{DIS}, the highest R^2 values arise when a low number of traits (i.e., n=2) with mixed variable type are used (i.e., $P_{continuous} = 0.5$) (Figure 5.5b), however this results in high variation (Figure 5.5c). These results were qualitatively similar when using the complete case data, i.e. where species without detectability estimates were removed (Figure D2). Across all numbers of traits used, we found that using categorical traits or a mix of the two types had significantly higher mean R^2 values compared to continuous traits for abundance weighted F_{DIS} (Mann-Whitney Wilcoxon W = 84, p = 0.019; Figure D3c). When we looked at mean R^2 from continuous traits separately, we found that less continuous traits both increase the mean R^2 but also increase the variation (Figure D4c) for abundance weighted F_{DIS}. Considering the mean R^2 from categorical/mix traits for abundance weighted F_{DIS}, we found that as the number of traits increase, the mean R^2 decreases (Figure 5.2c; Table D2).

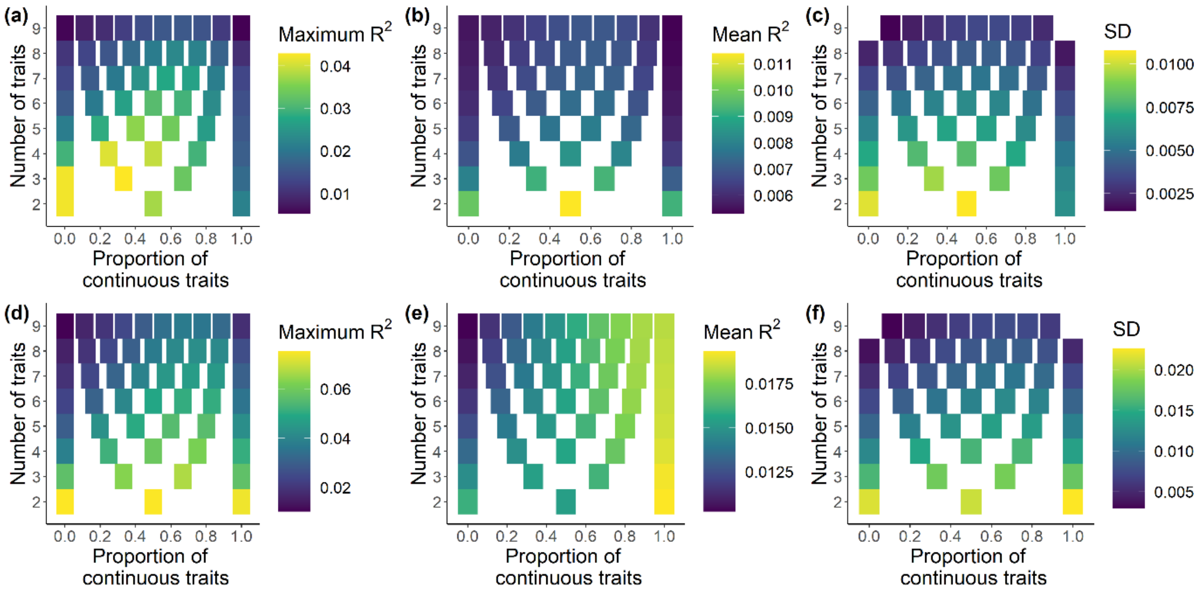

Figure 5.5. Maximum R^2 values (a) and mean R^2 values (b) with associated standard deviation (c) produced from abundance weighted F_{DIS}, and maximum R^2 values (d) and mean R^2 values (e) with associated standard deviation (f) produced from unweighted F_{DIS} for insectivore birds.

In contrast, for unweighted F_{DIS}, the highest mean R^2 values occur when we use a low number of continuous traits (Figure 5.5e), although this had high variation, again suggesting that obtaining the highest R^2 values depend on the specific traits included in the F_{DIS} calculation (Figure 5.5f). Across all numbers of traits used, continuous traits had significantly higher mean R^2 values compared to categorical traits or a mix of variable types (Mann-Whitney Wilcoxon W = 352, p<0.001; Figure S3d). When considering the mean R^2 from categorical/mix traits from unweighted F_{DIS} we found a negative relationship between trait number and mean R^2 (Table D2), however when $P_{continuous}$ is high, a higher number of traits increases the mean R^2 (Figure 5.2d).

For insectivores, we found no significant relationships between the difference in R^2 and the absolute average correlation coefficient for both abundance weighted and unweighted F_{DIS} (Table D3). For abundance weighted F_{DIS}, the identity of individual traits has very little impact on the R^2 (Figure 5.4c), likely because continuous traits resulted in poor predictive capacity (Figure 5.5b). However, when using presence absence data, removing certain traits, for example, body mass, bill width, and bill depth which, caused a substantial increase in R^2 values, meaning that their inclusion reduces the ability to predict total community abundance using presence-absence data (Figure 5.4d). In contrast, traits such as Kipp's distance and hand-wing index, reduce the R^2 values when they are removed, showing that they improve our predictive ability (Figure 5.4d). Again, this could explain the high variation in our R^2 values when few continuous traits are used in the calculation of unweighted F_{DIS} (Figure 5.5f).

5.5 Discussion

Our analyses show that altering the resolution of data used to calculate metrics of functional dispersion affects our ability to predict community abundance of functionally important birds. Recent studies have highlighted the influence of trait type and number on values of functional diversity and the quality of functional trait space represented by these values (Lefcheck *et al.* 2015; Maire *et al.* 2015; Legras *et al.* 2019), but not the impact of using abundance to weight functional diversity metrics (but see Kohli & Jarzyna 2021). Additionally, there been no investigation into how these factors could influence our ability to predict community abundance of functionally important species. We show that, for seed dispersing bird communities, using a higher number of continuous traits improved our ability to predict variation in community abundance, but only when our metric of functional diversity (F_{DIS}) was weighted by species' relative abundance. However, this result was not reflected when each species was given equal weighting (i.e., using presence-absence data), where overall explanatory power was lower.

When our metric of functional diversity was unweighted, we found that using categorical traits, or a mix of continuous and categorical traits, improved our predictive ability compared to using continuous traits alone (Figure D3b). We found a similar result in insectivore communities when F_{DIS} was weighted by species' relative abundance (Figure D3c). This is a surprising result, as studies have shown that categorical traits do not reflect the true functional distance between species (Maire *et al.* 2015) and can alter the ability to detect community assembly processes (Kohli & Jarzyna 2021), ultimately affecting the ability to draw robust ecological conclusions. Continuous traits are thought to provide in-depth information on species resource use, therefore more accurately representing unique functional strategies (Maire *et al.* 2015). Some co-occurring bird assemblages can have densely packed trait morphospace and low levels of trait overdispersion (Pigot *et al.* 2016a; Ulrich *et al.* 2017). These communities may be better represented by categorical traits which can capture under dispersion, i.e. clumped regions of trait morphospace more accurately than continuous traits.

In instances where a mix of continuous and categorical traits resulted in poor predictive capacity, using a higher number of traits only counteracted our low R^2 values for seed dispersers using abundance weighted F_{DIS} (Figure 5.2a). This was consistent with the results from Maire et al., (2015), who found that using more dimensions is required when using categorical traits to capture unique functional strategies. However, across the remaining datasets, using a higher number of categorical traits, or a mix of categorical and continuous, did not improve our predictive ability (Figure 5.2b & 5.2c). Explanatory power was better when a high proportion of those traits are continuous (Figure 5.2d). Similarly, when we looked at continuous traits separately, using more traits only increased our predictive ability for seed dispersers using abundance weighted F_{DIS} (Figure D4a), whereas using *fewer* traits actually increased the mean R^2 across the other datasets (Figure D4b-d). Many studies have shown that using a higher number of traits can better detect unique functional strategies and represent the true functional diversity of communities (Villéger *et al.* 2011; Laughlin 2014; Maire *et al.* 2015; Pigot *et al.* 2020). However, more traits is not always better (Lefcheck *et al.* 2015). Using low dimensional functional diversity metrics has been shown improve the association with species richness compared to using a higher number of traits (Zhu *et al.* 2017) and can better help understand the structure of ecological networks (Eklöf *et al.* 2013), suggesting trait identity is more important than the number of traits used.

A consistent result across all datasets is that using a low number of continuous traits results in greater variation around our mean R^2 value (Figure D4). This is further shown whereby a given trait number did not provide both the highest mean R^2 value and the highest maximum R^2 value. For example, using two continuous traits can provide the highest maximum R^2 value of 0.09, whereas the mean R^2 across all possible combinations of two traits reduces our R^2 to 0.04, with corresponding high variation (±0.02) (Figure 5.1a). This suggests that when certain combinations of traits are included in our metric of functional diversity, we are able to obtain the highest predictive ability. This could be due to the exclusion of traits which are highly correlated, therefore when more traits are added into our functional diversity estimate, the predictive power saturates due to additional traits being correlated with those already included, therefore increasing functional redundancy, and providing no additional contribution to the dimensionality of trait space (Petchey *et al.* 2007). Previous research has shown that using traits that are independent of each other (i.e. uncorrelated) maximises the intrinsic dimensionality of trait space, which increases the ability to predict species distributions and predict phenotypic differences (Laughlin 2014; Carscadden *et al.* 2017). We found further support for this in seed dispersing communities using abundance weighted F_{DIS}, whereby when traits which have a high absolute correlation coefficient are removed from our F_{DIS} calculation, the resulting R^2 increases (Figure 5.3). Including these highly correlated traits, such as Kipp's distance, wing length, and body mass, hamper our ability to explain variation in community abundance when they are included in our metric of functional diversity (Figure 5.4a). In contrast, traits relating to species morphology, such as beak size and tarsus length, are crucial to include to capture differences in species' resource use and markedly improve the ability to predict total abundance (Figure 5.4a). When using presence-absence data in calculating functional diversity for seed dispersers, the identity of traits is less sensitive to changes in R^2 (Figure 5.4b; Table D3) likely because using categorical traits explained more variation in community abundance compared to continuous traits as explained above (Figure 5.1e). In insectivore communities, traits relating to species flight ability, i.e. Kipp's distance and hand-wing index, are detrimental to predicting community abundance when our metric of F_{DIS} is weighted by abundance, with the remaining traits making little impact on the R^2 when removed (Figure 5.4c) again likely to be due to continuous traits being worse at predicting community abundance compared to categorical traits. In contrast, in our unweighted F_{DIS} metric, including mobility traits is crucial to produce higher R^2 values (Figure 5.4d). Our results here reinforce conclusions from previous studies stating that the identity of traits is more important than trait number (Carscadden *et al.* 2017; Zhu *et al.* 2017).

This could explain why our results for seed dispersers and insectivores differ when using abundance weighted vs unweighted F_{DIS} to predict community abundance. Weighting functional dispersion metrics by species' relative abundance gives more weight to common species based on their greater contribution to ecosystem functioning (Grime 1998; Villéger *et al.* 2008; Winfree *et al.* 2015) which have been shown to better predict key ecosystem functions (Gagic *et al.* 2015). However, we find for insectivore communities that using abundance weighted F_{DIS} resulted in lower R^2 and just using presence-absence data (i.e., giving each species equal weighting) improved our predictive ability. This could be due to insectivore communities containing rarer species which contribute greatly to functional diversity as they possess outlying trait values. This has been shown in vertebrate communities where species at the periphery of morphospace tend to be rarer than those at the core (Ripple *et al.* 2017). Therefore, when such species are included in our abundance weighted F_{DIS}, they are penalised for being rare, causing their unique traits to contribute less to functional diversity. Such traits are linked to some insectivore species, for example goldeneye and shoveler, which have low relative abundance and extreme values of body size and bill width (Figure D5), which were found to be important in predicting community abundance (Figure 5.4c). Therefore, we must consider not only the identity of traits, but the composition of the communities of interest to determine whether weighting functional diversity metrics by species' relative abundance will improve our ability to detect changes in community dynamics.

There are many methodological choices to make when calculating functional diversity, and choosing the correct traits to measure functional diversity is a frequent challenge (Petchey & Gaston 2006; Lefcheck *et al.* 2015). Ideally, traits should only be included in a measure of functional diversity if they are important for the ecosystem function of interest (Leps *et al.* 2006; Petchey & Gaston 2006). However, there is often a lack of knowledge on the links between specific traits and ecosystem functions, making it difficult to select specific traits (Lefcheck *et al.* 2015). To overcome this challenge, there are multiple trait selection methods to determine which traits should be used to measure functional diversity (Zhu *et al.* 2017). First, all measured traits can be included in the functional diversity measures, but this can include correlated traits, which as we have shown, can lead to reductions in predictive ability.

Other methods include using ordination techniques to reduce the information of all traits into independent axes (Laliberté & Legendre 2010; Maire *et al.* 2015), or trait selection methods to identify a subset of traits which represent the variation of all traits (Zhu *et al.* 2017). Finally, a complete search method can be used which calculates all possible functional diversity indices using many combinations of traits to determine which combination best measures ecosystem functioning (Petchey *et al.* 2004; Maire *et al.* 2015). The complete search method has been recommended to assess the quality of functional diversity metrics using different trait combinations (Zhu *et al.* 2017). Our results have shown that the identity of traits that explain the greatest variation in community abundance vary across functional groups and depend on whether functional diversity metrics are weighted by abundance. This highlights the importance of using techniques such as the complete search to ensure that functional diversity metrics are providing the greatest predictive capacity of ecosystem functioning.

Our approach has some limitations worth outlining. The proportion of variance in community abundance explained by functional diversity was low, with 9.5% maximum R^2 obtained across all datasets (Figure 5.1a). Communities with a high diversity of effect traits are expected to have higher mean levels of ecosystem function delivery. These communities can deliver ecosystem functions more efficiently because higher niche partitioning and reduced competitive exclusion allows species to coexist, and therefore have higher community abundance (Macarthur & Levins 1967; Cardinale 2011). However, this relationship assumes that resources remain constant over time (Macarthur & Levins 1967), which is unrealistic as we consider a 15-year period at multiple sites, possibly explaining our low explanatory power. The low proportion of variance could also be due to observer bias including identification mistakes or sampling error related to habitat type (Johnston *et al.* 2014), however, we did account for heterogeneity in detectability by adjusting the raw abundance data by a detectability probability coefficient (Johnston *et al.* 2014; Massimino *et al.* 2015).

In conclusion, our findings highlight the role of trait resolution, number, and identity in predicting community abundance of functionally important birds. In particular, we show that using highly refined data (i.e. a high number of continuous functional traits and abundance data) can provide the greatest predictive capacity, although the outcome depends on the functional group being investigated. Our findings contribute to previous work emphasising the practical difficulty in making meaningful predictions of community dynamics with implications for a predictive ecology of ecosystem functioning.

Chapter 6: Discussion

Human-mediated environmental impacts, including climate change and habitat loss and fragmentation, have extensive impacts on biodiversity (Millennium Ecosystem Assessment 2005). This has a detrimental effect on humanity, as biodiversity is essential for the provision of ecosystem services that humans rely on (Cardinale *et al.* 2012). Therefore, we need an understanding of how species and populations are changing across time and space to quantify biodiversity change and the consequences for ecosystem functioning. Furthermore, this information is crucial to develop informative indicators of biodiversity which can feed into policy decision making and track progress towards biodiversity targets (Buchanan *et al.* 2020).

The aim of this thesis was to quantify spatiotemporal changes in populations and communities, understand what factors are driving these changes, and how these changes might influence ecosystem functioning and the management of ecosystems under environmental change. In particular, this thesis develops a new method to measure functional connectivity and links functional diversity to changes in community dynamics and ecosystem functioning. Throughout this thesis, a key theme was the use of long-term monitoring data and species trait data, which provided key insights into how certain types of species are changing in response to anthropogenic drivers, and how this could impact ecosystem stability.

In this final chapter I summarise the findings of the previous chapters and discuss the implications of their results for understanding changes in population and community dynamics, and the impact on ecosystem functioning. Then, I discuss the limitations and implications of the current work and potential future research directions.

6.1 Thesis overview

The value of biodiversity for providing ecosystem functions and services was introduced in **Chapter 1**, emphasising the importance of quantifying biodiversity change to understand the impact environmental change on ecosystem service provisioning. I introduced the value of long-term monitoring schemes in providing an estimation of species abundance over space and time using data collected by volunteers. Using such data has been crucial for understanding how species and the environment interact, resulting in spatiotemporal population fluctuations, such as population synchrony. I then discussed the key drivers of synchronised population dynamics (Moran 1953; Hanski & Woiwod 1993; Paradis *et al.* 1999; Ims & Andreassen 2000; Koenig 2002), and the challenges of disentangling each driver to determine which is the dominant force (Kendall *et al.* 2000). A research gap is highlighted here, whereby if we can account for key climatic drivers of population synchrony, we could obtain a signal of dispersal, enabling us to quantify functional connectivity across the UK (Powney *et al.* 2011, 2012; Oliver *et al.* 2017). I discussed how population fluctuations can impact the stability of communities (Ives *et al.* 1999; Tilman 1999; Gonzalez & Loreau 2009), and the resilience of ecosystem functions and services (Greenwell *et al.* 2019). By using functional diversity, measured using species traits (Mason *et al.* 2003; Petchey & Gaston 2006; Villéger *et al.* 2008; Laliberté & Legendre 2010), we can quantify biodiversity's contribution to ecosystem functioning (Cardinale *et al.* 2012). This can be hampered by the many methodological decisions required to accurately measure functional diversity (Laughlin 2014; Maire *et al.* 2015; Carscadden *et al.* 2017; Zhu *et al.* 2017; Legras *et al.* 2019), such as the choice of number and type of input traits, and therefore predict ecosystem function provision. Finally, I provided an overview of the biodiversity ecosystem function (BEF) relationships which can be used to make evidence-based conservation decisions and ensure the resilience of ecosystem functioning.

Having established the need for indicators of biodiversity change in the UK, in **Chapter 2**, I demonstrated the application of long-term monitoring data to develop a novel method to measure functional connectivity of UK birds and butterflies. Quantifying functional connectivity, the ability of species to move between resource patches, is essential for conservation management as habitat loss and fragmentation reduce the permeability of the landscapes to the movement of individuals (Hanski 1998). Previous measurements of functional connectivity are hampered by data availability (Laliberté & St-Laurent 2020), conducted at small spatial scales (Finch *et al.* 2020), or rely on expert opinion (Watts & Handley 2010). Therefore, this chapter represents a significant milestone in our ability to measure connectivity using widely available abundance data which can be updated annually. The indicator of functional connectivity was calculated using a temporal trend in population synchrony for UK birds and butterflies using long-term monitoring data from three recording schemes: UKBMS, CBC, and BBS. It has been used as an experimental indicator of biodiversity by the Joint Nature Conservation Committee (JNCC) and the Department for Environment, Food and Rural Affairs (Defra) as part of the England Biodiversity Indicators (Defra 2020a).

As outlined in Chapter 1, synchronised population fluctuations are driven by not only the movement of individuals between sites, but also shared environmental conditions, i.e. the Moran effect (Moran 1953). Therefore, I accounted for synchrony in temperature and rainfall between monitoring sites over time, representing a dynamic Moran effect. This resulted in a measure of residual population synchrony over time, highlighting how functional connectivity may be changing for UK birds and butterflies. This methodology could be extended to other taxonomic groups where similar long-term monitoring data exists, and ultimately will be useful to improve the effectiveness of land management strategies to negate the impact of habitat loss and fragmentation.

To develop further evidence for the use of population synchrony as an indicator of functional connectivity, in **Chapter 3**, I sought to determine whether dispersal was driving temporal trends in population synchrony after accounting for shared environmental effects. I used the residual population synchrony trend over time for UK butterflies and birds calculating from Chapter 2, to test whether movement-related species attributes were related changes in synchrony over time. Previous evidence has linked species' dispersal ability to population synchrony (Sutcliffe *et al.* 1996; Paradis *et al.* 1999; Bellamy *et al.* 2003; Tittler *et al.* 2009), however there had been no attempt to disentangle climate and dispersal from temporal trends in population synchrony. The results of this study showed associations between mobility-related species attributes and population synchrony, after accounting for synchrony in temperature and rainfall. This suggests that species dispersal is important in driving changes in population synchrony over time but shared environmental conditions must be accounted for.

In **Chapter 4**, I used long-term monitoring data to quantify community abundance and stability of UK bird species which contribute to two ecosystem functions: seed dispersal and insect predation. Chapter 1 reviewed how the total abundance of a community is important for the provisioning of ecosystem functions under the mass ratio hypothesis (Grime 1998; Smith & Knapp 2003; Dangles & Malmqvist 2004). However, no research has assessed whether functional diversity could detect changes in community dynamics, and if this is dependent on whether a trait was classified as an effect or response trait. I show that trait choice in functional diversity metrics is crucial in predicting community dynamics. In particular, to measure community stability, functional diversity needs to be calculated using response traits to capture the diversity in species' responses to environmental conditions.

I further evaluated the impact of methodological choices when using functional diversity to predict community dynamics in **Chapter 5**. Using data on the community abundance of functionally important birds calculated in Chapter 4, I investigated the impact of data resolution in functional diversity metrics. There exists a trade-off between collecting a large amount of less resolved information on species, and a small amount of highly resolved information (Petchey & Gaston 2006) and this study aimed to determine whether collecting high resolution data (i.e. a high number of continuous traits and abundance data) resulted in an increased ability to predict community abundance. I showed that a lower number of continuous traits used to measure functional diversity increased the predictive capacity, and this was linked to the identity of individual traits. Therefore, this suggests that the specific traits which are used to capture species' resource use in our functional diversity metric, impact the ability to detect changes in communities. Overall, across both Chapter 4 and 5, the predictive capacity was low, highlighting the practical difficulty in using functional diversity to predict community dynamics, and further linking this to ecosystem functioning.

Overall, this thesis has demonstrated how we can use long-term monitoring data and functional trait data to understand the drivers of spatiotemporal population dynamics and predict community dynamics of birds which deliver important ecosystem functions and services.

6.2 Limitations

Across all four chapter of my thesis, I have utilised abundance data from long-term monitoring schemes for birds and butterflies, but such schemes have inherent biases that can influence the reliability of the abundance estimates derived from field surveys. These biases include observer bias, site-selection bias, taxonomic bias, temporal coverage, and detectability bias (Johnston *et al.* 2014; Mihoub *et al.* 2017; Proença *et al.* 2017; Fournier *et al.* 2019; Moussy *et al.* 2021). Some biases are difficult to overcome, and there exists a trade-off in long-term monitoring schemes between maximising geographic coverage and sampling effort per site (Couvet *et al.* 2011; Proença *et al.* 2017). For example, the Breeding Bird Survey have maximised geographic coverage across the UK, but volunteers only record sites twice a year. Such trade-offs, and therefore resulting biases, must be taken into account when considering the implications of results gained from using long-term monitoring schemes. Measuring population synchrony requires extensive abundance data, covering many monitoring sites with the least possible missing data. Therefore, in Chapters 1 and 2, our temporal trend in population synchrony relates chiefly to more common birds and butterflies which are detected at multiple sites across multiple years. As a result, our indicator of connectivity over time does not include rare species who are more at risk of habitat loss and fragmentation (Barbaro & Van Halder 2009), and therefore have reduced connectivity. However, I have taken care to try and minimise error in using abundance data to make inferences about ecosystem functioning. As the total community abundance is an important indicator of the contribution to ecosystem functioning (Grime 1998), it is essential that our estimates of abundance are as accurate as possible. Although there are no ways to overcome some biases (e.g. observer error), we were able to adjust bird species' abundances based on their detectability across difference habitat types in Chapters 4 and 5. In light of this, extending this work to other taxonomic groups may be challenging, as extensive monitoring schemes, such as the BBS and UKBMS, focus on popular and conspicuous species groups. Whereas reptiles, amphibians, plants, and other insect groups are not well covered by structured monitoring schemes (Eaton *et al.* 2015; Proença *et al.* 2017).

6.3 Implications and future research

6.3.1 Estimating functional connectivity

Habitat loss and fragmentation, driven by anthropogenic land use change, remains one of the greatest threats to biodiversity loss in the UK (Fahrig 2003; Butchart *et al.* 2010; Pimm *et al.* 2014). This in turn limits landscape permeability, and reduces the ability of species to move across the landscape, i.e. reducing functional connectivity (Hanski 1998; Tischendorf & Fahrig 2000). Despite substantial attempts to quantify functional connectivity in the UK, a cohesive method to track levels of connectivity across the UK was lacking. Therefore, the method and analysis proposed in Chapter 2 offers a novel approach to this problem, using widely available long-term monitoring data, providing a 'species-eye' view of connectivity.

Where sufficient long-term data are available, the method should be easily applicable to other taxonomic groups, enabling policymakers to track progress towards future biodiversity targets. Our indicator aggregates both the structure and quality of habitats used by species and the local abundance of populations that provide potential colonists, combining elements of functional and *structural* connectivity. However, an additional indicator based solely on structural connectivity, i.e. the amount and spatial distribution of suitable habitat across the landscape, could be used to supplement our indicator, or be validated by it. Remote sensing can provide cost-effective and rapid opportunities to map habitats and identify changes to habitats across the UK (Bell *et al.* 2015; Neumann *et al.* 2015), and if obtained at a fine-scale, could be used to develop a structural connectivity indicator (e.g. Guo *et al.* 2018). This would enable the identification of which landscape elements promote species movement between sites, and therefore inform upon conservation management strategies. Furthermore, structural elements of the landscape must enhance functional connectivity, i.e. enable species dispersal between resource patches, to maintain biodiversity (Kimberley *et al.* 2021). Therefore, supplementing our functional connectivity indicator with one on structural connectivity could lead to a useful tool to robustly inform how to enhance landscape connectivity and increase metapopulation persistence.

6.3.2 Drivers of population synchrony

Understanding the mechanisms driving population dynamics is a critical challenge in ecology and conservation. In Chapter 3, I disentangled the two key drivers of population synchrony; climate and dispersal, demonstrating that once spatiotemporal autocorrelation in climate has been accounted for, population synchrony is related to species' movement ability. This work makes an important contribution to the field of population dynamics, as we take an explicit long-term temporal perspective, demonstrating the significance of dispersal in not only driving average levels of population synchrony, but also for producing trends in synchrony over time.

This provides important evidence to support the use of population synchrony as a method to quantify changes in functional connectivity over time, as shown in Chapter 2. Disentangling the drivers of population synchrony and producing a dispersal-driven trend in population synchrony, can enable conservationists to determine whether changes to landscape connectivity are improving species ability to move across the landscape. We also showed that population synchrony is driven by shared weather conditions, i.e. the Moran effect (Moran 1953). Climate change, alongside habitat loss and fragmentation, are predicted to have severe impacts on biodiversity. Future global warming is likely to cause considerable changes to the spatial autocorrelation and variability of the weather, and the frequency of extreme weather events (Koenig 2002; Parmesan & Yohe 2003; Walther 2010; Palmer *et al.* 2017; Black *et al.* 2018a). Such changes can directly alter population synchrony (Hansen *et al.* 2020), possibly leading to increased levels of synchrony over time in parallel with climate change (Allstadt *et al.* 2015; Tack *et al.* 2015; Sheppard *et al.* 2016; Kahilainen *et al.* 2018). Global warming could also impact population synchrony indirectly, whereby higher temperatures can influence species' dispersal rates or by influencing habitat fragmentation, preventing species' from dispersing (Hansen *et al.* 2020).

Therefore, future research could explore how future climate change might influence population synchrony trends. This would enable investigation into whether climate change is influencing population synchrony indirectly through altering species' dispersal abilities (Kuussaari *et al.* 2016; Evans *et al.* 2019) or changing connectivity of the landscape (Oliver *et al.* 2015c; Holyoak & Heath 2016). This would have important implications for conservation management strategies to ensure that species are able to move across the landscape and remain functionally connected under future global warming.

6.3.3 Predicting ecosystem functioning

There is unequivocal evidence that biodiversity enhances the provision of ecosystem functions and services (Cardinale *et al.* 2012). Much research has measured the extent of functional differences within communities, i.e., functional diversity, to predict ecosystem processes. However, a gap exists in linking functional diversity to the community dynamics of functionally important species, where direct measures of ecosystem functioning are difficult to obtain. The results from Chapters 4 and 5 have shown that we can predict community dynamics of birds linked to ecosystem functioning using functional diversity, which is a novel finding in the field of functional ecology and the findings will hopefully help shape conservation management decisions aiming to enhance community abundance and stability. However even when using highly resolved data (e.g., a high number of continuous traits and abundance data) in our measure of functional diversity, our predictive ability was low. This highlights the difficulty in not only using functional diversity to predict community abundance, but also the additional step of linking community abundance to ecosystem functioning.

An ambitious potential avenue of future research could be to obtain direct measurements of ecosystem functions provided by birds to gain a mechanistic understanding of whether community abundance can be used to quantify avian ecosystem functioning. This would be a vital step forward in BEF research and would enable research into the impacts of environmental change on ecosystem functioning using widely available long-term monitoring data and trait data, in regions of the globe where we lack direct measurements of ecosystem functioning. This has been widely executed in plant communities, where direct measures of ecosystem functioning are easily obtainable using experimental field plots. Such studies have quantified ecosystem functioning in plants by measuring plant productivity (e.g. above-ground plant biomass), nutrient capture, nutrient leaching, and decomposition (Naeem *et al.* 1994; Tilman *et al.* 1996; Hector *et al.* 1999; Loreau 2000), which are crucial for providing ecosystem services such as carbon storage (Balvanera *et al.* 2006; Isbell *et al.* 2011). This has also been done for animals, for example quantifying crop pollination services by measuring flower-visitor richness and visitation rate to flowers in bees (Garibaldi *et al.* 2011) and measuring biocontrol of crop pests and weeds, nutrient cycling, dung removal and seed burial through numerous field studies (Gagic *et al.* 2015). Ecosystem functions provided by birds, including seed dispersal and pest control, have been estimated in real-world ecosystems (García & Martínez 2012; Barbaro *et al.* 2017; Denmead *et al.* 2017; García *et al.* 2018). This involves substantial fieldwork to directly measure avian predation or occurrence of seed dispersal and studies often occur at small spatial scales. However, quantification of ecosystem functions by birds in the UK would allow the development of mechanistic models to determine the best predictor of ecosystem functioning. This could be done at a basic level using community abundance alone, whereby function delivery is proportional to the abundance of functionally important species (Grime 1998; Winfree *et al.* 2015), or at a more refined level by combining information on species traits. The latter would weight species functional traits by the relative community abundance, producing an estimation of the community contribution to the function of interest. It could also, in principle, explore interactions between species based on trait data. Functional traits could include diet, body size, and morphological trait (e.g. beak size) as they have been shown to predict species' trophic niches (Pigot *et al.* 2020), and therefore likely to be important for the provisioning of ecosystem functioning. Including traits can be done iteratively to determine which trait(s) are most important to the direct measure of ecosystem functioning, and potentially provide further empirical evidence of the importance of community abundance for ecosystem function delivery.

6.4 Conclusion

The overall aim of this thesis was to understand drivers of spatiotemporal population and community dynamics and ascertain the impact on ecosystem functioning. This has been achieved by using long-term monitoring data and functional trait data for British birds and butterflies. The data were used to produce temporal trends in population synchrony over time, producing a novel method to track changes in functional connectivity across the UK. Next, the importance of dispersal and climate in driving fluctuations in population dynamics was established. Finally, the ability for functional diversity to measure avian community dynamics and how this might impact the delivery of ecosystem functions. The research as a whole has highlighted how long-term monitoring data can be used to describe dynamics related to ecosystem functioning, however, there remains a large body of potential research needed to more accurately predict ecosystem functioning. Quantifying ecosystem functioning will bring a greater understanding of the impact of anthropogenic driven changes on biodiversity and ultimately drive conservation decision-making and policy towards reducing biodiversity loss.

Appendices

Appendix A: Supplementary material for Chapter 2

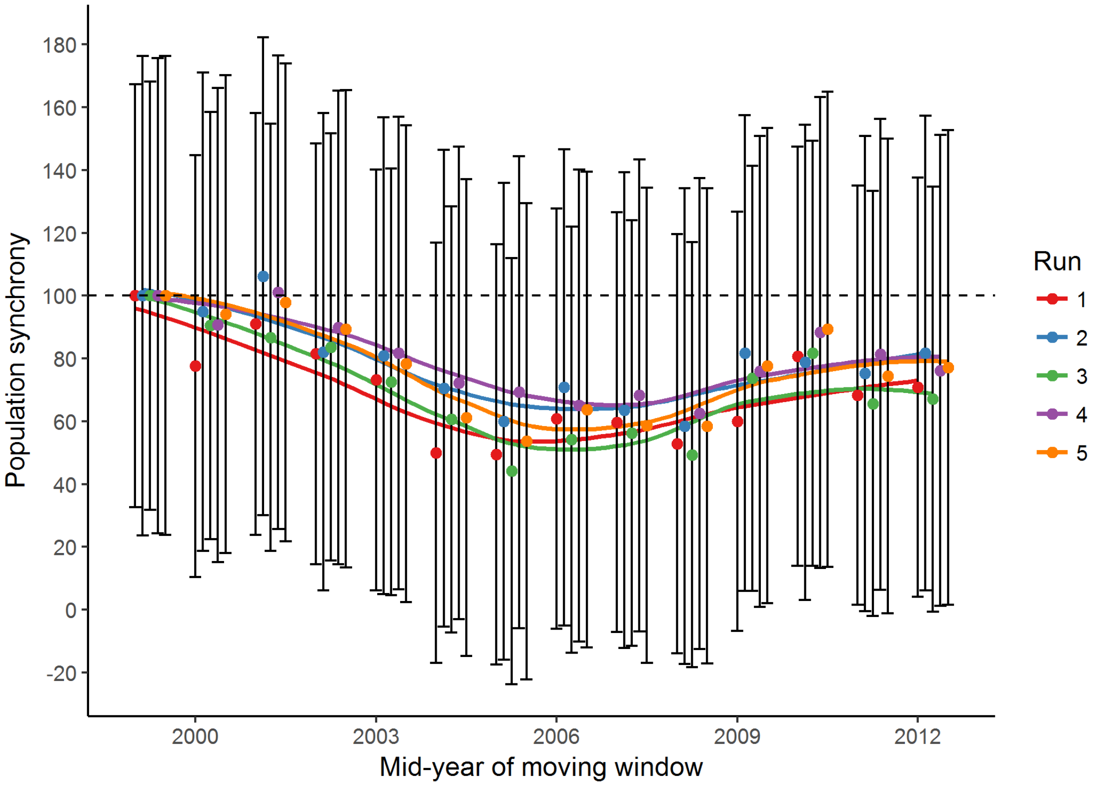

Figure A1. The temporal trend in population synchrony fitted using a LOESS regression function with standard error bars for BBS birds showing the five repeated runs to calculate population synchrony using a different random subset of 10,000 sites when species had large amounts of data.

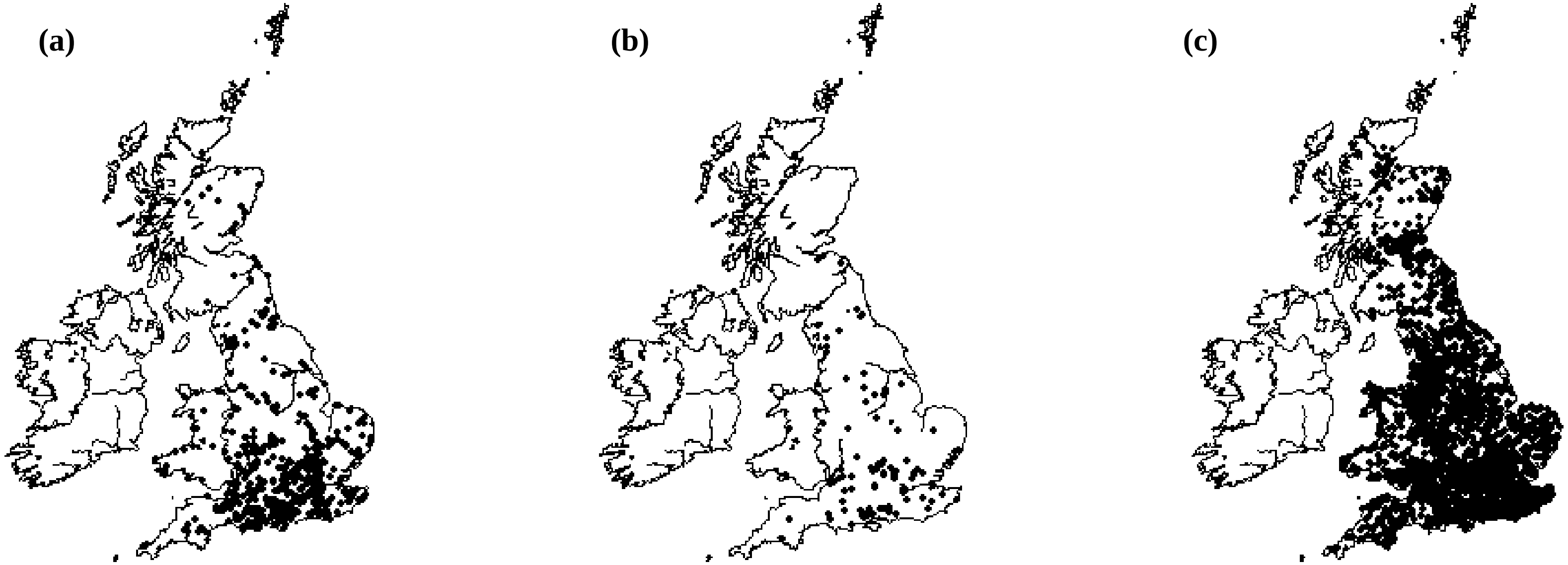

Figure A2. Maps of the UK with points showing locations for all sites included in the analysis for (a) UKBMS, (b) CBC, and (c) BBS schemes with a total of 686, 106 and 2490 sites respectively.

Table A1. Summary data of each butterfly species used in the analysis including common and Latin name, biotype specialism (WC=wider countryside, HS=habitat specialist), relative mobility, average abundance, abundance change, and change in synchrony over time. Dashes represent missing data or species with insufficient data. See main text for source data on species attributes.

Common name	**Latin name**	**Abundance change 85-00**	**Abundance change 00-12**	**Synchrony change 85-00**	**Synchrony change 00-12**
Brimstone	*Gonepteryx rhamni*	Increase	Decrease	Decrease	Increase
Brown argus	*Aricia agestis*	Increase	Decrease	Decrease	Increase
Chalk-hill blue	*Polyommatus coridon*	Increase	Decrease	No change	Increase
Comma	*Polygonia c-album*	Increase	Increase	No change	Increase
Common blue	*Polyommatus icarus*	Increase	Decrease	Decrease	Increase
Dark green fritillary	*Argynnis aglaja*	Increase	Increase	Decrease	No change
Dingy skipper	*Erynnis tages*	Decrease	Increase	No change	Decrease
Essex skipper	*Thymelicus lineola*	Decrease	Decrease	–	No change
Gatekeeper	*Pyronia tithonus*	Increase	Decrease	Decrease	Increase
Grayling	*Hipparchia semele*	Decrease	Decrease	–	Increase
Green hairstreak	*Callophrys rubi*	Decrease	Decrease	–	Increase
Green-veined white	*Pieris napi*	Decrease	Decrease	Increase	Increase
Grizzled skipper	*Pyrgus malvae*	Increase	Decrease	–	No change
Holly blue	*Celastrina argiolus*	Increase	Decrease	–	Decrease
Large skipper	*Ochlodes sylvanus*	Decrease	Decrease	Decrease	Increase
Large white	*Pieris brassicae*	Decrease	Increase	Decrease	Increase
Marbled white	*Melanargia galathea*	Increase	Decrease	Decrease	Increase
Meadow brown	*Maniola jurtina*	Increase	Decrease	Decrease	Increase
Orange tip	*Anthocharis cardamines*	Decrease	Increase	Decrease	Increase
Peacock	*Aglais io*	Increase	Decrease	Decrease	Increase

Common name	**Latin name**	**Abundance change 85-00**	**Abundance change 00-12**	**Synchrony change 85-00**	**Synchrony change 00-12**
Purple hairstreak	*Favonius quercus*	Increase	Decrease	–	No change
Ringlet	*Aphantopus hyperantus*	Increase	Increase	No change	Increase
Silver-washed fritillary	*Argynnis paphia*	Increase	Increase	–	Increase
Small copper	*Lycaena phlaeas*	Decrease	Decrease	Decrease	Increase
Small heath	*Coenonympha pamphilus*	Decrease	Decrease	No change	Decrease
Small pearl-bordered fritillary	*Boloria selene*	Decrease	Decrease	–	–
Small skipper	*Thymelicus sylvestris*	Decrease	Decrease	Decrease	Increase
Small tortoiseshell	*Aglais urticae*	Decrease	Decrease	Decrease	Increase
Small white	*Pieris rapae*	Increase	Decrease	Decrease	Increase
Speckled wood	*Pararge aegeria*	Increase	Increase	Decrease	Increase
Wall brown	*Lasiommata megera*	Decrease	Decrease	Decrease	No change
White admiral	*Limenitis camilla*	Decrease	Decrease	No change	Increase

Table A2. Summary of all CBC bird species used in the analysis including common and Latin names, biotype specialism, relative mobility, average abundance, STI group, abundance change, and change in synchrony over time. Dashes represent missing data or species with insufficient data. See main text for source data on species attributes.

Common name	Latin name	Abundance change	Synchrony change
Blackbird	*Turdus merula*	Decrease	No change
Blackcap	*Sylvia atricapilla*	Increase	No change
Blue tit	*Cyanistes caeruleus*	Increase	No change
Bullfinch	*Pyrrhula pyrrhula*	Decrease	No change
Chaffinch	*Fringilla coelebs*	Increase	No change
Chiffchaff	*Phylloscopus collybita*	Increase	Increase
Coal tit	*Periparus ater*	Increase	No change
Dunnock	*Prunella modularis*	Decrease	No change
Garden warbler	*Sylvia borin*	Increase	No change
Goldcrest	*Regulus regulus*	–	No change
Great spotted woodpecker	*Dendrocopos major*	Increase	No change
Great tit	*Parus major*	Increase	No change
Green woodpecker	*Picus viridis*	–	No change
Jay	*Garrulus glandarius*	Decrease	Increase
Lesser whitethroat	*Sylvia curruca*	Decrease	–
Long-tailed tit	*Aegithalos caudatus*	–	No change
Marsh tit	*Poecile palustris*	Decrease	No change
Nuthatch	*Sitta europaea*	Increase	Increase
Redstart	*Phoenicurus phoenicurus*	Increase	–

Common name	**Latin name**	**Abundance change**	**Synchrony change**
Robin	*Erithacus rubecula*	Increase	Decrease
Song thrush	*Turdus philomelos*	Decrease	No change
Tawny owl	*Strix aluco*	Decrease	Decrease
Treecreeper	*Certhia familiaris*	Decrease	No change
Willow tit	*Poecile montanus*	Decrease	–
Willow warbler	*Phylloscopus trochilus*	–	No change
Wren	*Troglodytes troglodytes*	Increase	Increase

Table A3. Summary of all BBS bird species used in the analysis including common and Latin names, biotype specialism, relative mobility, average abundance, STI group, abundance change, and change in synchrony over time. Dashes represent missing data or species with insufficient data. See main text for source data on species attributes.

Common name	**Latin name**	**Abundance change**	**Synchrony change**
Blackbird	*Turdus merula*	Increase	No change
Blackcap	*Sylvia atricapilla*	Increase	Increase
Blue tit	*Cyanistes caeruleus*	Increase	Decrease
Bullfinch	*Pyrrhula pyrrhula*	Increase	No change
Chaffinch	*Fringilla coelebs*	Increase	No change
Chiffchaff	*Phylloscopus collybita*	Increase	Decrease
Coal tit	*Periparus ater*	Increase	No change
Dunnock	*Prunella modularis*	Increase	No change
Garden warbler	*Sylvia borin*	Decrease	No change
Goldcrest	*Regulus regulus*	–	Increase
Great spotted woodpecker	*Dendrocopos major*	Increase	No change
Great tit	*Parus major*	Increase	No change
Green woodpecker	*Picus viridis*	–	No change
Jay	*Garrulus glandarius*	Increase	No change
Lesser redpoll	*Carduelis cabaret*	–	No change
Long-tailed tit	*Aegithalos caudatus*	–	No change
Nuthatch	*Sitta europaea*	Increase	Decrease
Redstart	*Phoenicurus phoenicurus*	Increase	No change
Robin	*Erithacus rubecula*	Increase	No change

Common name	**Latin name**	**Abundance change**	**Synchrony change**
Song thrush	*Turdus philomelos*	Increase	No change
Tree pipit	*Anthus trivialis*	–	No change
Treecreeper	*Certhia familiaris*	Increase	–
Willow warbler	*Phylloscopus trochilus*	–	No change
Wren	*Troglodytes troglodytes*	Decrease	Decrease

Table A4. Results from linear mixed models for each dataset with population synchrony as the response variable and climate synchrony as explanatory variables. Significant climate variables (p<0.05) were included as covariates in future analyses.

Dataset	**Climate synchrony variable**	**t-value**	**SE**	**p-value**
UKBMS	Spring temperature	4.99	0.02	<0.001***
	Summer temperature	2.71	0.003	0.0068**
	Autumn temperature	-8.12	0.03	<0.001***
	Winter temperature	3.1	0.006	0.0019**
	Spring rainfall	6.86	0.006	<0.001***
	Summer rainfall	7.16	0.003	<0.001***
	Autumn rainfall	10.02	0.009	<0.001***
	Winter rainfall	4.34	0.009	<0.001***
CBC	Spring temperature	1.25	0.27	0.209
	Summer temperature	2.28	0.74	0.023*
	Autumn temperature	0.12	0.39	0.91
	Winter temperature	-1.02	0.7	0.31
	Spring rainfall	-1.87	0.02	0.061
	Summer rainfall	0.97	0.04	0.33
	Autumn rainfall	1.37	0.03	0.17
	Winter rainfall	-0.19	0.02	0.85
BBS	Spring temperature	1.63	0.03	0.103
	Summer temperature	-0.07	0.03	0.94
	Autumn temperature	0.56	0.02	0.57
	Winter temperature	-0.21	0.08	0.83
	Spring rainfall	4.42	0.002	<0.001***
	Summer rainfall	-0.77	0.005	0.44
	Autumn rainfall	2.65	0.005	0.0079**
	Winter rainfall	2.33	0.004	0.019*

Significance is as follows: ***p < .001, **p < .01, *p < .05.

Table A5. Results from F-tests comparing the variation in seasonal mean temperature and total precipitation between 1985-2000 and 2000-2012.

Climate variable	**Season**	**F value**	**95% CI**	**p-value**
Mean temperature	Spring	2.10	[0.66-6.23]	0.20
	Summer	1.21	[0.38-3.60]	0.75
	Autumn	0.80	[0.24-2.25]	0.61
	Winter	1.29	[0.41-3.81]	0.67
Total rainfall	Spring	1.35	[0.42-3.99]	0.61
	Summer	0.74	[0.23-2.18]	0.57
	Autumn	0.93	[0.29-2.76]	0.88
	Winter	1.05	[0.33-3.12]	0.94

Table A6. Results from randomisation tests with 1,000 permutations to determine the significance of individual predictor variables where mixed effect models produced significant results (<0.05).

Dataset	**Explanatory variable**	**Response variable**	**F value**	**p-value**
UKBMS	Northing	Average synchrony	214.27	0***
	Distance	Average synchrony	64.96	0***
	Habitat similarity	Average synchrony	287.35	0***
BBS	Habitat similarity	Average synchrony	47.43	0***

Significance is as follows: ***p < .001, **p < .01, *p < .05.

A1. Mixed effects models

All species model

The ‘all species model’ (discussed section 2.3.6 ‘Accounting for climatic synchrony’) has population synchrony as the response variable, and year, mean northing, habitat similarity, distance and the selected climate synchrony variable(s) as fixed effects, and site pair ID and species as random effects. This was fitted for each dataset separately.

Eq. A1 $Y_{ij} = \beta_0 + \beta_1 X_{1ij} + \beta_2 X_{2ij} + \beta_3 X_{3ij} + \beta_4 X_{4ij} + \beta_5 X_{5ij} + \mu_i + v_j + \varepsilon_{ij}$

where i refers to the site pair ID and j to species and Y is the outcome variable, population synchrony. The model contains a parameter for intercept, β_0, parameters for the slope of the fixed effects, β_1 (year), β_2 (mean northing), β_3 (habitat similarity), β_4 (distance) and β_5 (climate synchrony variable(s)), random intercepts for both site pair ID and species, μ_i and v_j, and residual error term, ε_{ij}.

Single-species model

The ‘single-species model’ (discussed in the ‘Temporal trends in population synchrony’ section) assesses how individual species were changing in population synchrony over time, we refitted the mixed effects model for each species within each dataset separately

Eq. A4 $Y_i = \beta_0 + \beta_1 X_{1i} + \beta_2 X_{2i} + \beta_3 X_{3i} + \beta_4 X_{4i} + \beta_5 X_{5i} + \mu_i + \varepsilon_i$

where i refers to the site pair ID and Y is the outcome variable, population synchrony. The model contains a parameter for intercept, β_0, parameters for the slope of the fixed effects, β_1 (year), β_2 (mean northing), β_3 (habitat similarity), β_4 (distance) and β_5 (climate synchrony variable(s)), random intercepts for site pair ID, μ_i, and residual error term, ε_i.

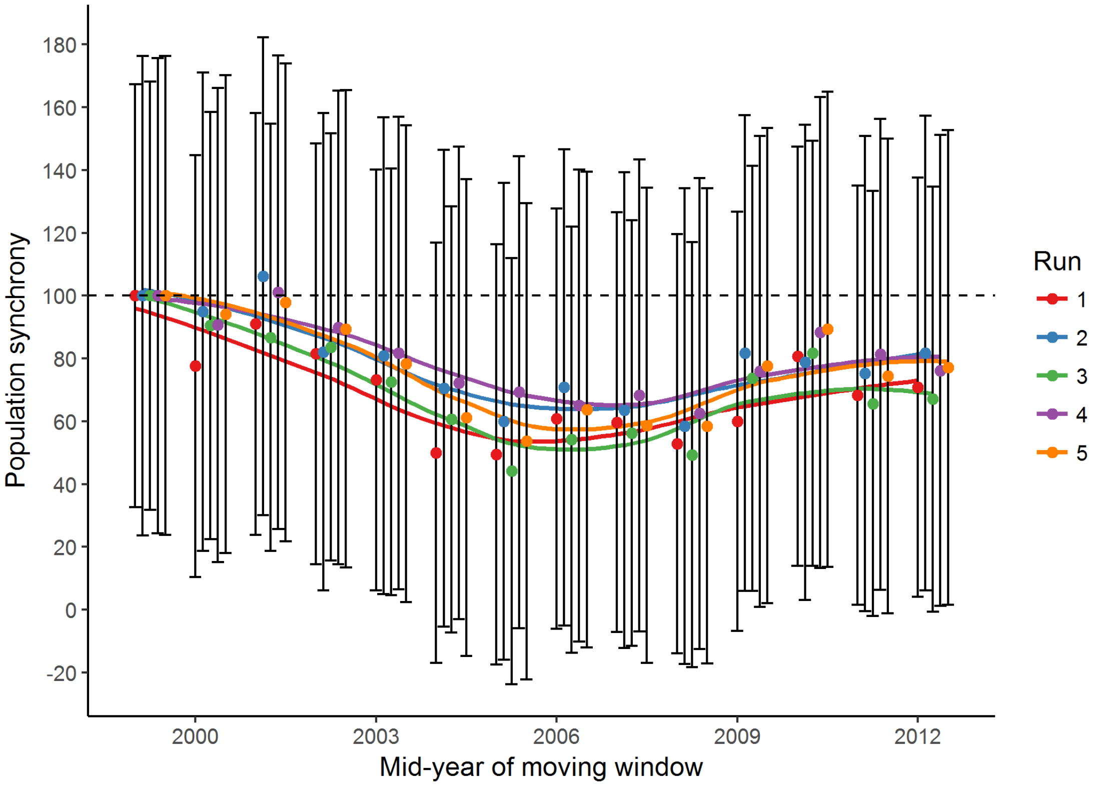

Figure B1. The temporal trend in population synchrony fitted using a LOESS regression function with standard error bars for BBS birds showing the five repeated runs to calculate population synchrony using a different random subset of 10,000 sites when species had large amounts of data.

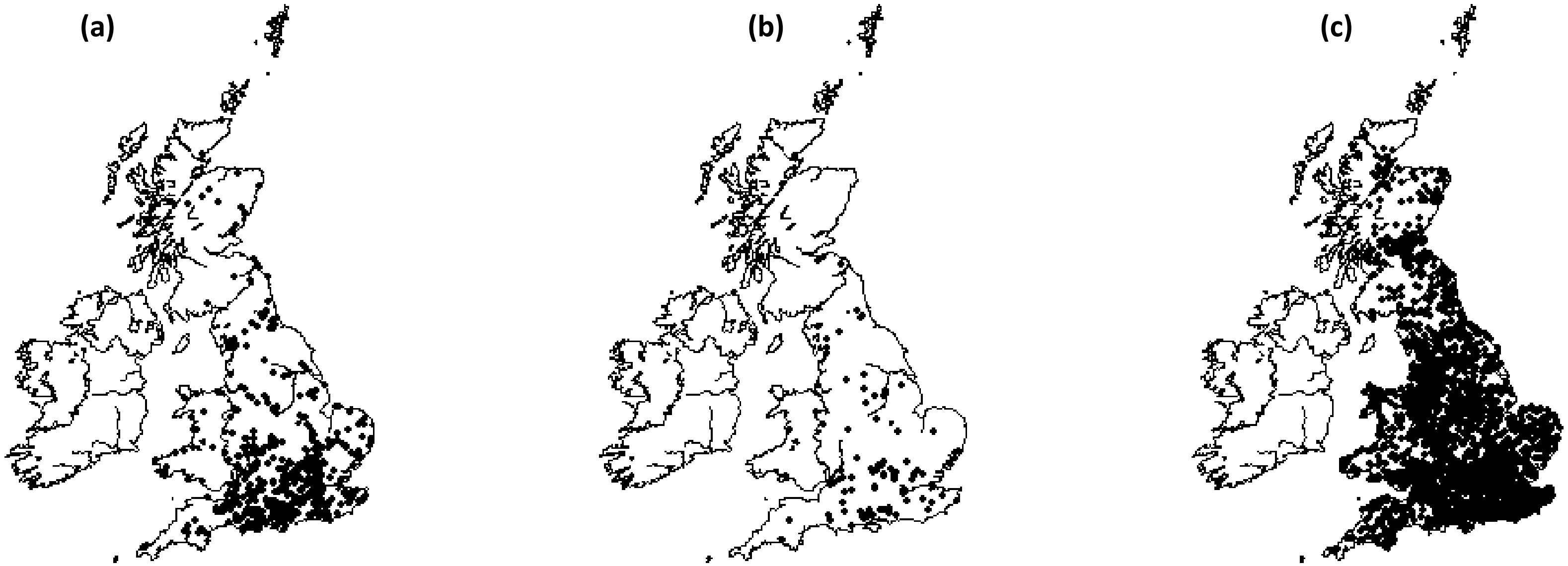

Figure B2. Maps of the UK with points showing locations for all sites included in the analysis for (a) UKBMS, (b) CBC, and (c) BBS schemes with a total of 686, 106 and 2490 sites respectively.

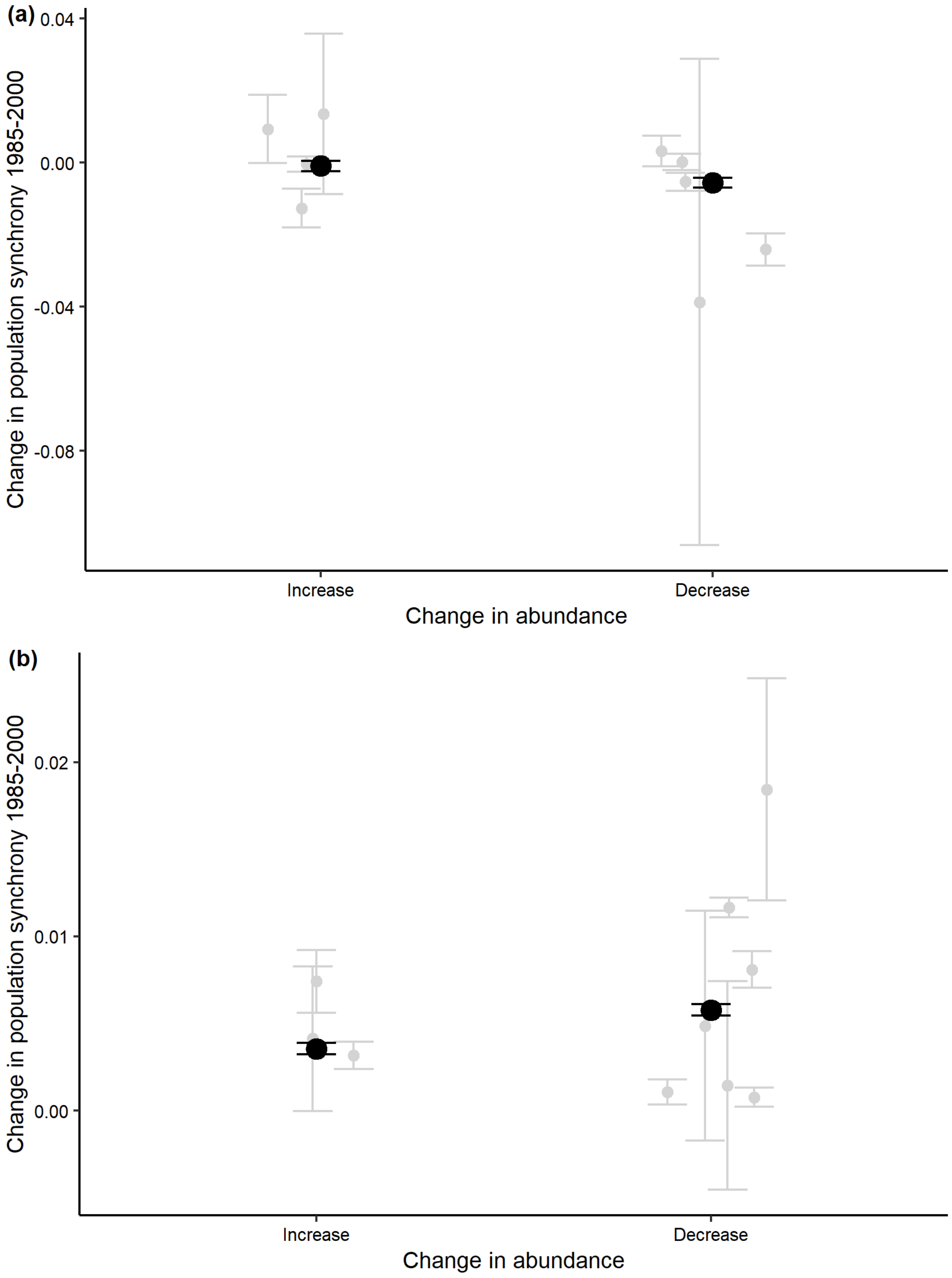

Figure B3. The change in population synchrony over time for butterflies between 1985 and 2000 (a) and 2000 and 2012 (b) in relation to significant changes in abundance over time. Grey points represent each species raw data with standard error bars, and black points represent the slope (i.e. change in synchrony over time) from the mixed effects models with their associated standard errors. Grey points were scattered randomly with a small deviation to increase clarity.

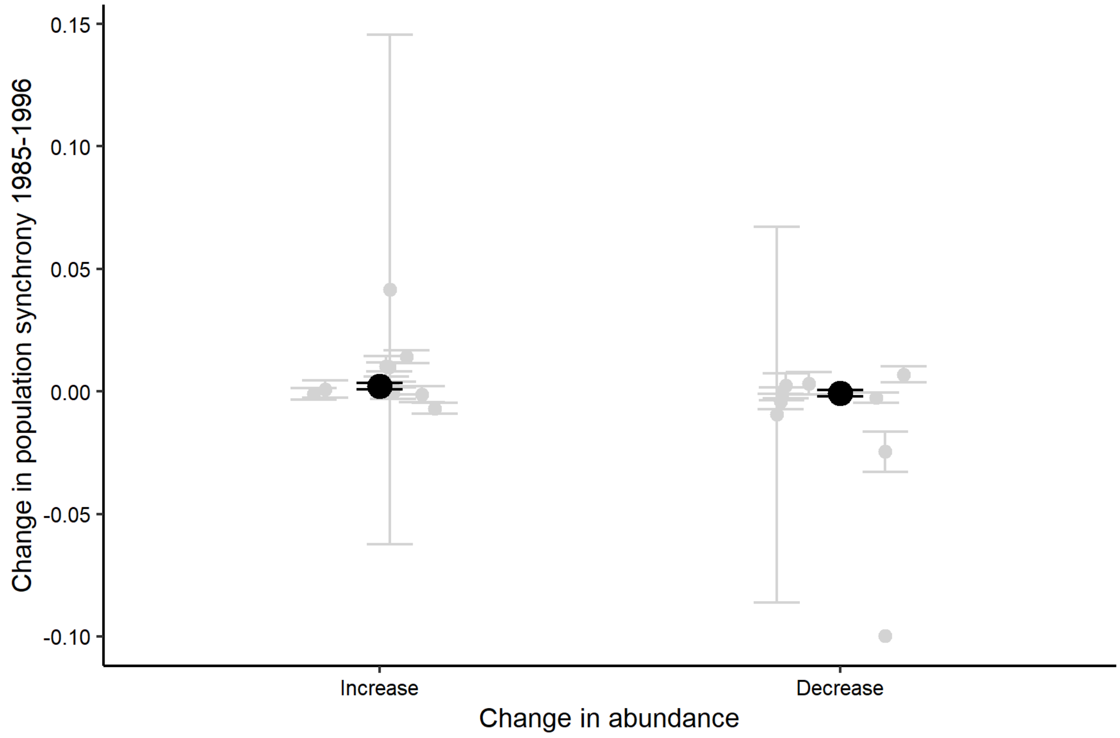

Figure B4. The change in population synchrony over time for CBC birds between 1985 and 1996 in relation to significant changes in abundance over time. Grey points represent each species raw data with standard error bars, and black points represent the slope (i.e. change in synchrony over time) from the mixed effects models with their associated standard errors. Grey points were scattered randomly with a small deviation to increase clarity.

Table B1. Summary data of each butterfly species used in the analysis including common and Latin name, biotype specialism (WC=wider countryside, HS=habitat specialist), relative mobility, average abundance, abundance change, and change in synchrony over time. Dashes represent missing data or species with insufficient data. See main text for source data on species attributes.

Common name	**Latin name**	**Biotype Specialism**	**Mobility rank**	**Average abundance between 2009-2016**	**Abundance change 85-00**	**Abundance change 00-12**	**Synchrony change 85-00**	**Synchrony change 00-12**
Brimstone	*Gonepteryx rhamni*	Generalist	46	279.22	Increase	Decrease	Decrease	Increase
Brown argus	*Aricia agestis*	Generalist	14	139.89	Increase	Decrease	Decrease	Increase
Chalk-hill blue	*Polyommatus coridon*	Specialist	13	65.11	Increase	Decrease	No change	Increase
Comma	*Polygonia c-album*	Generalist	42	680.22	Increase	Increase	No change	Increase
Common blue	*Polyommatus icarus*	Generalist	28	1234.56	Increase	Decrease	Decrease	Increase
Dark green fritillary	*Argynnis aglaja*	Specialist	37	57.56	Increase	Increase	Decrease	No change
Dingy skipper	*Erynnis tages*	Specialist	10	6.44	Decrease	Increase	No change	Decrease
Essex skipper	*Thymelicus lineola*	Generalist	23	286.11	Decrease	Decrease	–	No change
Gatekeeper	*Pyronia tithonus*	Generalist	28	7168.22	Increase	Decrease	Decrease	Increase
Grayling	*Hipparchia semele*	Specialist	29	163.78	Decrease	Decrease	–	Increase
Green hairstreak	*Callophrys rubi*	Specialist	17	4.00	Decrease	Decrease	–	Increase
Green-veined white	*Pieris napi*	Generalist	45	5153.00	Decrease	Decrease	Increase	Increase
Grizzled skipper	*Pyrgus malvae*	Specialist	8	–	Increase	Decrease	–	No change
Holly blue	*Celastrina argiolus*	Generalist	44	244.67	Increase	Decrease	–	Decrease
Large skipper	*Ochlodes sylvanus*	Generalist	27	611.78	Decrease	Decrease	Decrease	Increase

Common name	**Latin name**	**Biotype Specialism**	**Mobility rank**	**Average abundance between 2009-2016**	**Abundance change 85-00**	**Abundance change 00-12**	**Synchrony change 85-00**	**Synchrony change 00-12**
Large white	*Pieris brassicae*	Generalist	57	6853.78	Decrease	Increase	Decrease	Increase
Marbled white	*Melanargia galathea*	Generalist	31	738.67	Increase	Decrease	Decrease	Increase
Meadow brown	*Maniola jurtina*	Generalist	32	15339.44	Increase	Decrease	Decrease	Increase
Orange tip	*Anthocharis cardamines*	Generalist	41	17.44	Decrease	Increase	Decrease	Increase
Peacock	*Aglais io*	Generalist	54	1941.89	Increase	Decrease	Decrease	Increase
Purple hairstreak	*Favonius quercus*	Specialist	18	57.22	Increase	Decrease	–	No change
Ringlet	*Aphantopus hyperantus*	Generalist	22	6600.44	Increase	Increase	No change	Increase
Silver-washed fritillary	*Argynnis paphia*	Specialist	39	202.78	Increase	Increase	–	Increase
Small copper	*Lycaena phlaeas*	Generalist	33	337.56	Decrease	Decrease	Decrease	Increase
Small heath	*Coenonympha pamphilus*	Generalist	23	672.78	Decrease	Decrease	No change	Decrease
Small pearl-bordered fritillary	*Boloria selene*	Specialist	25	37.33	Decrease	Decrease	–	–
Small skipper	*Thymelicus sylvestris*	Generalist	25	1116.11	Decrease	Decrease	Decrease	Increase
Small tortoiseshell	*Aglais urticae*	Generalist	51	3269.56	Decrease	Decrease	Decrease	Increase
Small white	*Pieris rapae*	Generalist	–	9695.56	Increase	Decrease	Decrease	Increase
Speckled wood	*Pararge aegeria*	Generalist	30	2526.00	Increase	Increase	Decrease	Increase
Wall brown	*Lasiommata megera*	Generalist	38	207.33	Decrease	Decrease	Decrease	No change
White admiral	*Limenitis camilla*	Specialist	34	43.44	Decrease	Decrease	No change	Increase

Table B2. Summary of all CBC bird species used in the analysis including common and Latin names, biotype specialism, relative mobility, average abundance, STI group, abundance change, and change in synchrony over time. Dashes represent missing data or species with insufficient data. See main text for source data on species attributes.

Common name	Latin name	Biotype Specialism	Dispersal distance (km)	Average abundance (number of pairs/territories)	Abundance change	Synchrony change
Blackbird	*Turdus merula*	Generalist	3.2	4900000	Decrease	No change
Blackcap	*Sylvia atricapilla*	Specialist	27.5	1100000	Increase	No change
Blue tit	*Cyanistes caeruleus*	Generalist	2.3	3400000	Increase	No change
Bullfinch	*Pyrrhula pyrrhula*	Generalist	2.5	190000	Decrease	No change
Chaffinch	*Fringilla coelebs*	Generalist	2.8	5800000	Increase	No change
Chiffchaff	*Phylloscopus collybita*	Specialist	–	1100000	Increase	Increase
Coal tit	*Periparus ater*	Specialist	1.2	680000	Increase	No change
Dunnock	*Prunella modularis*	Generalist	1.4	2300000	Decrease	No change
Garden warbler	*Sylvia borin*	Specialist	–	170000	Increase	No change
Goldcrest	*Regulus regulus*	Specialist	–	520000	–	No change
Great spotted woodpecker	*Dendrocopos major*	Specialist	3.7	140000	Increase	No change
Great tit	*Parus major*	Generalist	2.5	2500000	Increase	No change
Green woodpecker	*Picus viridis*	Specialist	1.7	52000	–	No change
Jay	*Garrulus glandarius*	Specialist	2.8	4300	Decrease	Increase
Lesser whitethroat	*Sylvia curruca*	Generalist	16.4	74000	Decrease	–
Long-tailed tit	*Aegithalos caudatus*	Generalist	3.7	330000	–	No change
Marsh tit	*Poecile palustris*	Specialist	–	41000	Decrease	No change
Nuthatch	*Sitta europaea*	Specialist	0.8	220000	Increase	Increase

Common name	**Latin name**	**Biotype Specialism**	**Dispersal distance (km)**	**Average abundance (number of pairs/territories)**	**Abundance change**	**Synchrony change**
Redstart	*Phoenicurus phoenicurus*	Specialist	–	100000	Increase	–
Robin	*Erithacus rubecula*	Generalist	8	6000000	Increase	Decrease
Song thrush	*Turdus philomelos*	Generalist	4	1100000	Decrease	No change
Tawny owl	*Strix aluco*	Generalist	3.1	50000	Decrease	Decrease
Treecreeper	*Certhia familiaris*	Specialist	–	180000	Decrease	No change
Willow tit	*Poecile montanus*	Specialist	1.7	3400	Decrease	–
Willow warbler	*Phylloscopus trochilus*	Specialist	16.9	2200000	–	No change
Wren	*Troglodytes troglodytes*	Generalist	6.5	7700000	Increase	Increase

Table B3. Summary of all BBS bird species used in the analysis including common and Latin names, biotype specialism, relative mobility, average abundance, STI group, abundance change, and change in synchrony over time. Dashes represent missing data or species with insufficient data. See main text for source data on species attributes.

Common name	**Latin name**	**Biotype Specialism**	**Dispersal distance (km)**	**Average abundance (number of pairs/territories)**	**Abundance change**	**Synchrony change**
Blackbird	*Turdus merula*	Generalist	3.2	4900000	Increase	No change
Blackcap	*Sylvia atricapilla*	Specialist	27.5	1100000	Increase	Increase
Blue tit	*Cyanistes caeruleus*	Generalist	2.3	3400000	Increase	Decrease
Bullfinch	*Pyrrhula pyrrhula*	Generalist	2.5	190000	Increase	No change
Chaffinch	*Fringilla coelebs*	Generalist	2.8	5800000	Increase	No change
Chiffchaff	*Phylloscopus collybita*	Specialist	2.8	1100000	Increase	Decrease
Coal tit	*Periparus ater*	Specialist	–	680000	Increase	No change
Dunnock	*Prunella modularis*	Generalist	1.2	2300000	Increase	No change
Garden warbler	*Sylvia borin*	Specialist	1.4	170000	Decrease	No change
Goldcrest	*Regulus regulus*	Specialist	–	520000	–	Increase
Great spotted woodpecker	*Dendrocopos major*	Specialist	–	140000	Increase	No change
Great tit	*Parus major*	Generalist	2.5	2500000	Increase	No change
Green woodpecker	*Picus viridis*	Specialist	1.7	52000	–	No change
Jay	*Garrulus glandarius*	Specialist	2.8	4300	Increase	No change
Lesser redpoll	*Carduelis cabaret*	Specialist	–	190000	–	No change
Long-tailed tit	*Aegithalos caudatus*	Generalist	3.7	330000	–	No change
Nuthatch	*Sitta europaea*	Specialist	0.8	220000	Increase	Decrease
Redstart	*Phoenicurus phoenicurus*	Specialist	–	100000	Increase	No change

Common name	**Latin name**	**Biotype Specialism**	**Dispersal distance (km)**	**Average abundance (number of pairs/territories)**	**Abundance change**	**Synchrony change**
Robin	*Erithacus rubecula*	Generalist	8	6000000	Increase	No change
Song thrush	*Turdus philomelos*	Generalist	4	1100000	Increase	No change
Tree pipit	*Anthus trivialis*	Specialist	–	88000	–	No change
Treecreeper	*Certhia familiaris*	Specialist	–	180000	Increase	–
Willow warbler	*Phylloscopus trochilus*	Specialist	16.9	2200000	–	No change
Wren	*Troglodytes troglodytes*	Generalist	6.5	7700000	Decrease	Decrease

Table B4. Results from linear mixed models for each dataset with population synchrony as the response variable and climate synchrony as explanatory variables. Significant climate variables (p<0.05) were included as covariates in future analyses.

Dataset	Climate synchrony variable	t-value	SE	p-value
UKBMS	Spring temperature	4.99	0.02	<0.001***
	Summer temperature	2.71	0.003	0.0068**
	Autumn temperature	-8.12	0.03	<0.001***
	Winter temperature	3.1	0.006	0.0019**
	Spring rainfall	6.86	0.006	<0.001***
	Summer rainfall	7.16	0.003	<0.001***
	Autumn rainfall	10.02	0.009	<0.001***
	Winter rainfall	4.34	0.009	<0.001***
CBC	Spring temperature	1.25	0.27	0.209
	Summer temperature	2.28	0.74	0.023*
	Autumn temperature	0.12	0.39	0.91
	Winter temperature	-1.02	0.7	0.31
	Spring rainfall	-1.87	0.02	0.061
	Summer rainfall	0.97	0.04	0.33
	Autumn rainfall	1.37	0.03	0.17
	Winter rainfall	-0.19	0.02	0.85
BBS	Spring temperature	1.63	0.03	0.103
	Summer temperature	-0.07	0.03	0.94
	Autumn temperature	0.56	0.02	0.57
	Winter temperature	-0.21	0.08	0.83
	Spring rainfall	4.42	0.002	<0.001***
	Summer rainfall	-0.77	0.005	0.44
	Autumn rainfall	2.65	0.005	0.0079**
	Winter rainfall	2.33	0.004	0.019*

Significance is as follows: ***p < .001, **p < .01, *p < .05.

Table B5. Results from F-tests comparing the variation in seasonal mean temperature and total precipitation between 1985-2000 and 2000-2012.

Climate variable	**Season**	**F value**	**95% CI**	**p-value**
Mean temperature	Spring	2.10	[0.66-6.23]	0.20
	Summer	1.21	[0.38-3.60]	0.75
	Autumn	0.80	[0.24-2.25]	0.61
	Winter	1.29	[0.41-3.81]	0.67
Total rainfall	Spring	1.35	[0.42-3.99]	0.61
	Summer	0.74	[0.23-2.18]	0.57
	Autumn	0.93	[0.29-2.76]	0.88
	Winter	1.05	[0.33-3.12]	0.94

Table B6. Results from linear mixed effects models for butterflies using species attributes and control variables as explanatory variables with either average synchrony, or change in synchrony over two time periods, as the response variable.

Explanatory variable	**Response variable**	**No. of species**	**Estimate**	**t value**	**SE**	**p-value**	**Direction of change**
Biotype specialism	Average synchrony	32	0.046	1.07	0.04	0.29	Non-significant
	Change in synchrony 1985-2000		-0.12	-3.88	0.03	<0.001**	Generalists decline in synchrony more steeply compared to specialists
	Change in synchrony 2000-2012		0.064	6.27	0.01	<0.001**	Generalists increase in synchrony more steeply compared to specialists
Mobility	Average synchrony	31	0.004	2.99	0.001	0.0056**	More mobile species have higher average levels of synchrony
	Change in synchrony 1985-2000		0.0002	-0.45	0.0005	0.65	Non-significant
	Change in synchrony 2000-2012		0.003	21.61	0.0002	<0.001***	Species with high mobility show a greater increase in synchrony over time compared to species with low mobility
Average abundance	Average synchrony	31	0.038	1.51	0.025	0.14	Non-significant
Non-significant changes in abundance	Change in synchrony 1985-2000	32	-0.014	-1.22	0.012	0.22	Non-significant
	Change in synchrony 2000-2012		0.033	9.10	0.004	<0.001***	Species increasing in abundance increase in synchrony more rapidly
Significant changes in abundance	Change in synchrony 1985-2000	9	0.0047	2.18	0.002	0.029*	Species increasing in abundance increase in synchrony more rapidly
	Change in synchrony 2000-2012	10	-0.002	-3.65	0.0006	<0.001***	Species increasing in abundance decline in synchrony more rapidly

Significance is as follows: ***p < .001, **p < .01, *p < .05.

Table B7. Results from linear mixed effects models for CBC birds using species attributes and control variables as explanatory variables with either average synchrony, or change in synchrony over two time periods, as the response variable.

Explanatory variable	**Response variable**	**No. of species**	**Estimate**	**t value**	**SE**	**p-value**	**Direction of change**
Biotype specialism	Average synchrony	26	-0.067	-1.79	0.038	0.09	Non-significant
	Change in synchrony		0.05	3.45	0.014	<0.001***	Specialists show a more positive change in synchrony over time
Mobility	Average synchrony	20	0.014	0.62	0.022	0.545	Non-significant
	Change in synchrony		0.0096	1.30	0.007	0.192	Non-significant
Average abundance	Average synchrony	26	0.057	2.72	0.021	0.013*	Species which are more abundant have higher average levels of synchrony
Non-significant changes in abundance	Change in synchrony	22	0.029	1.88	0.016	0.06	Non-significant
Significant changes in abundance	Change in synchrony	19	0.032	1.97	0.016	0.0492*	Species increasing in abundance increase in synchrony more rapidly

Significance is as follows: ***p < .001, **p < .01, *p < .05.

Table B8. Results from linear mixed effects models for BBS birds using species attributes and control variables as explanatory variables with either average synchrony or change in synchrony over two time periods as the response variable.

Explanatory variable	**Response variable**	**No. of species**	**Estimate**	**t value**	**SE**	**p-value**	**Direction of change**
Biotype specialism	Average synchrony	24	0.0033	0.22	0.015	0.828	Non-significant
	Change in synchrony		0.0084	2.00	0.004	0.045*	Generalists show a more negative change in synchrony over time
Mobility	Average synchrony	17	0.0062	1.09	0.006	0.29	Non-significant
	Change in synchrony		0.0065	3.61	0.002	<0.001***	More mobile species have a greater change in synchrony over time
Average abundance	Average synchrony	24	0.01	1.34	0.007	0.195	Non-significant
Non-significant changes in abundance	Change in synchrony	18	-0.081	-1.12	0.072	0.261	Non-significant
Significant changes in abundance	Change in synchrony	17	-0.074	-1.03	0.072	0.31	Non-significant

Significance is as follows: ***p < .001, **p < .01, *p < .05.

Table B9. Results from randomisation tests with 1,000 permutations to determine the significance of individual predictor variables where mixed effect models produced significant results (<0.05).

Dataset	Explanatory variable	Response variable	F value	p-value
UKBMS	Biotype specialism	Change in synchrony 1985-2000	15.12	0***
		Change in synchrony 2000-2012	39.34	0***
	Mobility	Average synchrony	8.95	0.004**
		Change in synchrony 2000-2012	466.94	0***
	Non-significant abundance	Change in synchrony 2000-2012	82.84	0***
	Significant abundance	Change in synchrony 1985-2000	4.77	0.017*
		Change in synchrony 2000-2012	12.68	0***
BBS	Biotype specialism	Change in synchrony	4.02	0.068
	Mobility	Change in synchrony	13.01	0***
CBC	Biotype specialism	Change in synchrony	11.88	0***
	Abundance	Average synchrony	7.71	0.008**
	Significant abundance	Change in synchrony	3.68	0.045*

Significance is as follows: ***p < .001, **p < .01, *p < .05.

B1. Mixed effects models

The ‘all species model’ (discussed in section 3.3.6 ‘Accounting for climatic synchrony’) has population synchrony as the response variable, and year, mean northing, habitat similarity, distance and the selected climate synchrony variable(s) as fixed effects, and site pair ID and species as random effects. This was fitted for each dataset separately.

Eq. A1 $Y_{ij} = \beta_0 + \beta_1 X_{1ij} + \beta_2 X_{2ij} + \beta_3 X_{3ij} + \beta_4 X_{4ij} + \beta_5 X_{5ij} + \mu_i + v_j + \varepsilon_{ij}$

where i refers to the site pair ID and j to species and Y is the outcome variable, population synchrony. The model contains a parameter for intercept, β_0, parameters for the slope of the fixed effects, β_1 (year), β_2 (mean northing), β_3 (habitat similarity), β_4 (distance) and β_5 (climate synchrony variable(s)), random intercepts for both site pair ID and species, μ_i and v_j, and residual error term, ε_{ij}.

To understand whether mobility-attributes could explain differences in population synchrony, we fitted a variant of the ‘all species model’ for each dataset (discussed in the ‘Population synchrony and species attributes’ section). Firstly, we included each mobility attribute as a fixed effect.

Eq. A2 $Y_{ij} = \beta_0 + \beta_1 X_{1ij} + \beta_2 X_{2ij} + \beta_3 X_{3ij} + \beta_4 X_{4ij} + \beta_5 X_{5ij} + \beta_6 X_{6ij} + \mu_i + v_j + \varepsilon_{ij}$

where β_6 is the mobility attribute of interest (specialism, mobility or mean abundance).

Secondly, we included an interaction between each mobility attribute and year to determine whether certain types of species increase or decrease in population synchrony over time.

Eq. A3 $Y_{ij} = \beta_0 + \beta_1 X_{1ij} + \beta_2 X_{2ij} + \beta_3 X_{3ij} + \beta_4 X_{4ij} + \beta_5 X_{5ij} + \beta_6 X_{6ij} + \beta_7 X_{1ij} X_{6ij} + \mu_i + v_j + \varepsilon_{ij}$

where β_7 is the interaction between the mobility attribute of interest and year.

Figure C1. A map of all 200 sites included in the analysis.

Table C1. List of species and their corresponding function (seed disperser, insectivore, or both) n=105.

English name	Scientific name	Functional group
Bearded Tit	*Panurus biarmicus*	Both
Black Redstart	*Phoenicurus ochruros*	Both
Blackbird	*Turdus merula*	Both
Blackcap	*Sylvia atricapilla*	Both
Black-headed Gull	*Chroicocephalus ridibundus*	Insectivore
Black-tailed Godwit	*Limosa limosa*	Insectivore
Blue Tit	*Cyanistes caeruleus*	Both
Bullfinch	*Pyrrhula pyrrhula*	Seed disperser
Carrion Crow	*Corvus corone*	Insectivore
Cetti Warbler	*Cettia cetti*	Insectivore
Chaffinch	*Fringilla coelebs*	Both
Chiffchaff	*Phylloscopus collybita*	Insectivore
Chough	*Pyrrhocorax pyrrhocorax*	Insectivore
Coal Tit	*Periparus ater*	Insectivore
Collared Dove	*Streptopelia decaocto*	Seed disperser
Common Sandpiper	*Actitis hypoleucos*	Insectivore
Coot	*Fulica atra*	Seed disperser
Corn Bunting	*Emberiza calandra*	Both
Crossbill	*Loxia curvirostra*	Seed disperser
Cuckoo	*Cuculus canorus*	Insectivore
Curlew	*Numenius arquata*	Seed disperser
Dartford Warbler	*Sylvia undata*	Both
Dipper	*Cinclus cinclus*	Insectivore
Dunlin	*Calidris alpina*	Insectivore
Dunnock	*Prunella modularis*	Both
Firecrest	*Regulus ignicapillus*	Insectivore
Gadwall	*Mareca strepera*	Seed disperser
Garden Warbler	*Sylvia borin*	Both

English name	**Scientific name**	**Functional group**
Garganey	*Anas querquedula*	Insectivore
Goldcrest	*Regulus regulus*	Insectivore
Golden Plover	*Pluvialis apricaria*	Insectivore
Goldeneye	*Bucephala clangula*	Insectivore
Goldfinch	*Carduelis carduelis*	Seed disperser
Grasshopper Warbler	*Locustella naevia*	Insectivore
Great Spotted Woodpecker	*Dendrocopos major*	Insectivore
Great Tit	*Parus major*	Both
Green Woodpecker	*Picus viridis*	Insectivore
Greenfinch	*Chloris chloris*	Seed disperser
Greenshank	*Tringa nebularia*	Insectivore
Grey Partridge	*Perdix perdix*	Both
Grey Wagtail	*Motacilla cinerea*	Insectivore
Hawfinch	*Coccothraustes coccothraustes*	Seed disperser
Hobby	*Falco subbuteo*	Insectivore
House Martin	*Delichon urbicum*	Insectivore
House Sparrow	*Passer domesticus*	Seed disperser
Jackdaw	*Coloeus monedula*	Both
Jay	*Garrulus glandarius*	Both
Lapwing	*Vanellus vanellus*	Insectivore
Lesser Spotted Woodpecker	*Dendrocopos minor*	Insectivore
Lesser Whitethroat	*Sylvia curruca*	Both
Linnet	*Linaria cannabina*	Seed disperser
Little Ringed Plover	*Charadrius dubius*	Insectivore
Long-tailed Tit	*Aegithalos caudatus*	Insectivore
Marsh Tit	*Poecile palustris*	Both
Meadow Pipit	*Anthus pratensis*	Insectivore
Mediterranean Gull	*Larus melanocephalus*	Insectivore
Mistle Thrush	*Turdus viscivorus*	Both
Moorhen	*Gallinula chloropus*	Seed disperser

English name	**Scientific name**	**Functional group**
Nightingale	*Luscinia megarhynchos*	Insectivore
Nightjar	*Caprimulgus europaeus*	Insectivore
Nuthatch	*Sitta europaea*	Insectivore
Pied Flycatcher	*Ficedula hypoleuca*	Insectivore
Pied Wagtail	*Motacilla alba*	Insectivore
Quail	*Coturnix coturnix*	Seed disperser
Redstart	*Phoenicurus phoenicurus*	Insectivore
Redwing	*Turdus iliacus*	Both
Reed Bunting	*Emberiza schoeniclus*	Both
Reed Warbler	*Acrocephalus scirpaceus*	Insectivore
Ring Ouzel	*Turdus torquatus*	Both
Ringed Plover	*Charadrius hiaticula*	Insectivore
Robin	*Erithacus rubecula*	Insectivore
Rock Dove	*Columba livia*	Seed disperser
Rock Pipit	*Anthus petrosus*	Insectivore
Rook	*Corvus frugilegus*	Both
Sand Martin	*Riparia riparia*	Insectivore
Sedge Warbler	*Acrocephalus schoenobaenus*	Insectivore
Shoveler	*Anas clypeata*	Insectivore
Siskin	*Spinus spinus*	Seed disperser
Skylark	*Alauda arvensis*	Both
Snipe	*Gallinago gallinago*	Insectivore
Song Thrush	*Turdus philomelos*	Both
Spotted Flycatcher	*Muscicapa striata*	Insectivore
Starling	*Sturnus vulgaris*	Both
Stock Dove	*Columba oenas*	Seed disperser
Stonechat	*Saxicola rubicola*	Insectivore
Swallow	*Hirundo rustica*	Insectivore
Swift	*Apus apus*	Insectivore
Teal	*Anas crecca*	Insectivore

English name	**Scientific name**	**Functional group**
Tree Pipit	*Anthus trivialis*	Insectivore
Tree Sparrow	*Passer montanus*	Both
Treecreeper	*Certhia familiaris*	Insectivore
Turtle Dove	*Streptopelia turtur*	Seed disperser
Wheatear	*Oenanthe oenanthe*	Insectivore
Whimbrel	*Numenius phaeopus*	Both
Whinchat	*Saxicola rubetra*	Insectivore
Whitethroat	*Sylvia communis*	Both
Willow Tit	*Poecile montanus*	Both
Willow Warbler	*Phylloscopus trochilus*	Insectivore
Wood Warbler	*Phylloscopus sibilatrix*	Insectivore
Woodcock	*Scolopax rusticola*	Insectivore
Woodlark	*Lullula arborea*	Both
Woodpigeon	*Columba palumbus*	Seed disperser
Wren	*Troglodytes troglodytes*	Insectivore
Yellow Wagtail	*Motacilla flava*	Insectivore
Yellowhammer	*Emberiza citrinella*	Both

Table C2. Loadings for each seed disperser effect trait resulting from the principal components analysis. Large loadings indicate that a trait has a strong relationship to a particular principal component, and the sign indicates whether they are positively or negatively correlated.

Trait	**PC1**	**PC2**	**PC3**	**PC4**
Bill length	0.38	0.91	-0.17	0.09
Bill width	0.53	-0.29	-0.65	-0.46
Bill depth	0.54	-0.30	0.01	0.79
Gape width	0.54	-0.05	0.74	-0.40
Variance %	75.7	17.2	4.9	2.2
Cumulative variance	75.7	92.9	97.8	100

Table C3. Loadings for each seed disperser response trait resulting from the principal components analysis. Large loadings indicate that a trait has a strong relationship to a particular principal component, and the sign indicates whether they are positively or negatively correlated.

Trait	**PC1**	**PC2**	**PC3**	**PC4**	**PC5**	**PC6**	**PC7**
Mean latitude	0.51	-0.28	0.08	-0.06	-0.07	-0.80	-0.02
SSI	-0.07	0.26	0.64	0.70	-0.05	-0.13	0.10
Clutch size	0.13	0.72	-0.22	-0.05	0.59	-0.24	-0.07
Maximum longevity	-0.12	-0.22	-0.68	0.64	0.07	-0.13	0.18
STI	-0.50	0.27	-0.06	-0.27	-0.36	-0.38	0.57
Thermal maximum	-0.56	-0.02	-0.03	0.02	-0.10	-0.32	-0.75
Brood size	-0.38	-0.45	0.26	-0.11	0.71	-0.11	0.24
Variance %	39.5	20	15.4	12.9	6.3	3.6	2.3
Cumulative variance	39.5	59.5	74.9	87.8	94.1	97.7	100

Table C4. Loadings for each seed disperser effect, response, and both traits resulting from the principal components analysis. Large loadings indicate that a trait has a strong relationship to a particular principal component, and the sign indicates whether they are positively or negatively correlated.

Trait	**PC1**	**PC2**	**PC3**	**PC4**	**PC5**	**PC6**	**PC7**	**PC8**	**PC9**	**PC10**	**PC11**	**PC12**	**PC13**	**PC14**	**PC15**	**PC16**
Bill length	0.31	-0.08	0.16	-0.23	-0.13	0.32	0.20	-0.10	0.41	-0.14	-0.37	-0.38	0.21	0.11	-0.33	0.11
Bill width	0.30	0.00	-0.27	0.29	0.21	-0.26	-0.13	0.08	0.27	0.08	-0.03	-0.35	0.36	-0.33	0.41	0.09
Bill depth	0.29	0.01	-0.26	0.37	0.27	0.13	-0.16	0.07	0.04	0.15	-0.35	0.02	-0.49	0.46	-0.03	-0.03
Gape width	0.31	-0.01	-0.08	0.33	0.26	0.29	0.06	0.11	-0.14	-0.38	0.19	0.29	0.15	-0.34	-0.42	-0.15
Mean latitude	0.03	-0.49	0.26	0.12	0.07	-0.36	0.02	-0.12	0.39	-0.43	0.27	0.03	-0.33	0.09	0.04	0.05
SSI	0.04	0.08	-0.01	-0.59	0.66	0.13	-0.35	-0.08	0.12	-0.03	0.17	0.06	0.02	0.05	0.04	0.04
Clutch size	0.00	-0.13	-0.62	-0.32	-0.29	-0.21	-0.16	0.38	-0.01	-0.39	-0.06	0.05	0.08	0.17	-0.10	-0.02
Maximum longevity	0.22	0.17	0.14	0.12	-0.45	0.17	-0.71	-0.24	0.14	-0.05	0.16	0.17	0.09	0.07	0.05	0.03
STI	-0.05	0.48	-0.29	0.03	-0.02	-0.10	0.36	-0.29	0.51	0.00	0.08	0.42	0.02	0.07	0.00	0.04
Thermal maximum	-0.03	0.56	0.01	0.03	0.02	-0.07	0.00	-0.18	-0.22	-0.52	0.03	-0.49	-0.29	-0.04	0.05	-0.02
Brood size	-0.12	0.36	0.43	0.07	0.05	-0.08	-0.09	0.74	0.30	-0.06	-0.10	0.09	0.00	0.02	-0.02	-0.02
Kipps' distance	0.36	0.07	0.15	-0.10	-0.01	-0.25	0.13	-0.03	-0.08	0.06	0.13	-0.03	0.22	0.34	0.07	-0.75
Wing length	0.35	0.10	0.11	0.02	0.01	-0.10	0.20	0.12	-0.28	0.01	0.34	0.03	0.20	0.42	0.03	0.60
Tarsus length	0.33	-0.05	0.04	-0.23	-0.17	0.38	0.24	0.14	-0.04	-0.16	-0.06	0.22	-0.26	-0.19	0.64	-0.03
Body size	0.34	0.09	-0.10	-0.21	-0.18	-0.13	0.03	0.15	0.11	0.41	0.36	-0.18	-0.45	-0.33	-0.32	0.00
Hand-wing index	0.30	0.07	0.19	-0.17	0.03	-0.51	-0.09	-0.17	-0.22	-0.04	-0.53	0.33	-0.05	-0.25	-0.11	0.15
Variance %	43.2	17.7	9.9	8.1	6	4	3.6	2.4	1.4	1.2	1.1	0.7	0.3	0.2	0.1	0.1
Cumulative variance	43.2	60.9	70.8	78.9	84.9	88.9	92.5	94.9	96.3	97.5	98.6	99.3	99.6	99.8	99.9	100

Table C5. Loadings for each insectivore effect trait resulting from the principal components analysis. Large loadings indicate that a trait has a strong relationship to a particular principal component, and the sign indicates whether they are positively or negatively correlated.

Trait	**PC1**	**PC2**	**PC3**	**PC4**
Bill length	0.42	0.83	0.34	0.17
Bill width	0.54	-0.18	-0.53	0.63
Bill depth	0.56	0.01	-0.34	-0.76
Gape width	0.47	-0.53	0.70	0.03
Variance %	74	16.4	7.9	1.7
Cumulative variance	74	90.4	98.3	100

Table C6. Loadings for each insectivore response trait resulting from the principal components analysis. Large loadings indicate that a trait has a strong relationship to a particular principal component, and the sign indicates whether they are positively or negatively correlated.

Trait	**PC1**	**PC2**	**PC3**	**PC4**	**PC5**	**PC6**	**PC7**
Mean latitude	0.55	-0.08	0.11	-0.04	0.09	0.81	-0.09
SSI	0.18	0.16	-0.70	0.46	-0.49	0.07	0.02
Clutch size	-0.01	-0.65	-0.28	-0.60	-0.37	0.00	0.08
Maximum longevity	0.17	0.54	0.36	-0.37	-0.63	-0.07	0.01
STI	-0.55	0.13	-0.13	-0.12	-0.08	0.32	-0.73
Thermal maximum	-0.56	0.15	-0.01	-0.01	-0.07	0.47	0.66
Brood size	-0.14	-0.46	0.53	0.52	-0.45	0.05	-0.08
Variance %	39.9	17.9	15.8	11.5	10.2	2.9	1.8
Cumulative variance	39.9	57.8	73.6	85.1	95.3	98.2	100

Table C7. Loadings for each insectivore effect, response, and both traits resulting from the principal components analysis. Large loadings indicate that a trait has a strong relationship to a particular principal component, and the sign indicates whether they are positively or negatively correlated.

Trait	**PC1**	**PC2**	**PC3**	**PC4**	**PC5**	**PC6**	**PC7**	**PC8**	**PC9**	**PC10**	**PC11**	**PC12**	**PC13**	**PC14**	**PC15**	**PC16**
Bill length	0.31	-0.07	-0.03	0.17	-0.15	-0.39	-0.30	0.28	-0.40	-0.27	-0.37	-0.09	-0.31	0.23	0.06	-0.01
Bill width	0.31	0.17	0.33	-0.04	0.00	0.16	0.18	-0.14	-0.43	-0.01	0.01	0.01	0.08	-0.39	0.58	0.03
Bill depth	0.33	0.17	0.20	0.00	-0.16	0.00	0.06	-0.17	-0.35	0.11	0.13	0.45	0.18	0.13	-0.60	0.07
Gape width	0.26	0.27	0.01	-0.21	-0.03	-0.11	0.51	-0.19	0.36	-0.11	-0.52	-0.12	-0.21	-0.06	-0.15	0.10
Mean latitude	0.10	-0.50	0.08	-0.18	-0.07	0.08	0.12	0.21	-0.06	0.72	-0.33	0.03	-0.01	0.05	0.03	0.01
SSI	0.09	-0.17	-0.04	0.55	0.63	-0.16	0.02	-0.43	-0.02	0.13	-0.16	0.05	0.01	0.00	-0.01	0.01
Clutch size	-0.02	0.03	0.72	-0.01	0.20	0.18	-0.39	0.15	0.34	-0.13	-0.24	0.18	0.02	0.04	-0.02	-0.01
Maximum longevity	0.24	-0.07	-0.29	-0.13	-0.22	0.39	-0.55	-0.52	0.08	0.03	-0.19	-0.09	-0.05	-0.10	-0.01	0.01
STI	-0.06	0.52	-0.07	0.22	0.01	0.02	-0.18	0.18	0.05	0.45	0.06	0.12	-0.53	-0.30	-0.06	-0.07
Thermal maximum	-0.09	0.51	-0.18	0.08	0.11	0.16	-0.09	0.17	-0.13	0.19	-0.34	-0.20	0.55	0.32	0.07	0.07
Brood size	-0.05	0.12	0.01	-0.67	0.40	-0.48	-0.27	-0.15	-0.13	0.14	0.07	-0.06	0.01	-0.05	-0.02	0.00
Kipps’ distance	0.35	0.01	-0.19	-0.08	0.22	0.14	-0.02	0.18	0.18	0.00	0.25	0.21	-0.14	0.27	0.22	0.67
Wing length	0.37	0.09	-0.12	-0.07	0.04	-0.03	0.05	0.00	0.24	0.06	0.15	0.26	0.02	0.36	0.29	-0.68
Tarsus length	0.31	-0.03	-0.06	0.19	-0.24	-0.47	-0.17	0.14	0.37	0.10	0.06	0.01	0.46	-0.41	0.03	0.10
Body size	0.34	0.03	0.28	0.08	0.04	0.06	-0.01	-0.01	0.05	0.15	0.36	-0.75	-0.07	0.17	-0.19	-0.04
Hand-wing index	0.28	-0.11	-0.26	-0.12	0.42	0.32	0.02	0.43	-0.10	-0.23	-0.05	-0.04	0.08	-0.40	-0.31	-0.21
Variance %	41.9	18.4	9.4	7.5	6.1	4.9	3.9	2.2	1.7	1	1	0.8	0.7	0.3	0.3	0.2
Cumulative variance	41.6	60	69.4	76.9	83	87.9	91.8	94	95.7	96.7	97.7	98.5	99.2	99.5	99.8	100

Table C8. Results from linear regression models for seed disperser species using interpolated data i.e. where we filled in missing detectability data gaps. Mean or stability of total community abundance was the response variable and functional dispersion calculated using three trait combinations (effect, response, and all traits) as the explanatory variable.

Response variable	**Trait combination**	**t-value**	**SE**	**p-value**	**R^2**
Mean	Effect	-2.51	0.16	0.013*	0.031
	Response	3.75	0.15	<0.001***	0.066
	All	4.06	0.2	<0.001***	0.077
Stability	Effect	-1.56	0.13	0.12	0.012
	Response	4.09	0.12	<0.001***	0.078
	All	3.6	0.16	<0.001***	0.061

Table C9. Results from linear regression models for insectivorous species using interpolated data i.e. where we filled in missing detectability data gaps. Mean or stability of total community abundance was the response variable and functional dispersion calculated using three trait combinations (effect, response, and all traits) as the explanatory variable.

Response variable	**Trait combination**	**t-value**	**SE**	**p-value**	**R^2**
Mean	Effect	-1.06	0.13	0.29	0.0056
	Response	-1.81	0.23	0.072	0.016
	All	-1.53	0.14	0.13	0.012
Stability	Effect	-4.77	0.13	<0.001***	0.1
	Response	0.93	0.26	0.36	0.0043
	All	-5.64	0.15	<0.001***	0.14

Table C10. Results from linear regression models for seed disperser species with complete case data, i.e. where species and sites without detectability estimates were removed. Mean or stability of total community abundance was the response variable and functional dispersion calculated using three trait combinations (effect, response, and all traits) as the explanatory variable.

Response variable	**Trait combination**	**t-value**	**SE**	**p-value**	**R^2**
Mean	Effect	-1.11	0.18	0.27	0.0094
	Response	3.05	0.2	0.0028**	0.068
	All	3.6	0.25	<0.001***	0.092
Stability	Effect	-0.92	0.14	0.36	0.007
	Response	3.23	0.16	0.0016**	0.075
	All	2.4	0.2	0.018**	0.043

Table C11. Results from linear regression models for insectivorous species with complete case data, i.e. where species and sites without detectability estimates were removed. Mean or stability of total community abundance was the response variable and functional dispersion calculated using three trait combinations (effect, response, and all traits) as the explanatory variable.

Response variable	**Trait combination**	**t-value**	**SE**	**p-value**	**R^2**
Mean	Effect	0.03	0.15	0.97	0.000008
	Response	-0.24	0.28	0.81	0.0004
	All	-0.61	0.17	0.54	0.0029
Stability	Effect	-3.7	0.15	<0.001***	0.1
	Response	0.49	0.3	0.62	0.0019
	All	-4.81	0.16	<0.001***	0.15

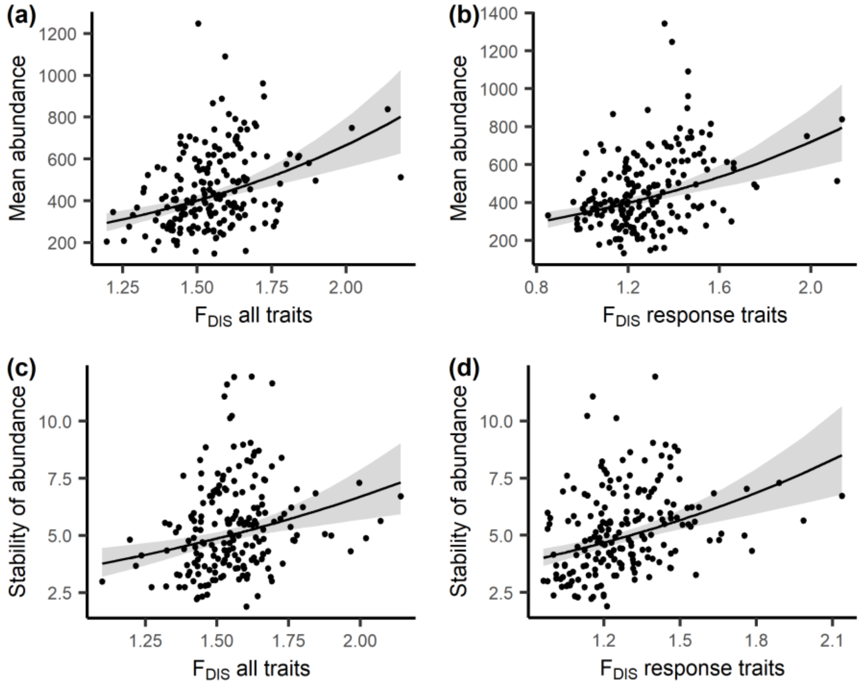

Figure C2. Relationships between the mean total community abundance of seed dispersers and functional dispersion (F_{DIS}) of all traits (a), and F_{DIS} response traits (b) after removing outlying points identified using Cook's distance. Lower panel shows relationships between the temporal stability of total seed disperser abundance and functional dispersion of all traits (c) and response traits (d) after removing outlying points identified using Cook's distance.

Appendix D: Supplementary material for Chapter 5

Table D1. List of species and their corresponding function (seed disperser, insectivore, or both) n=105.

English name	Scientific name	Functional group
Bearded Tit	*Panurus biarmicus*	Both
Black Redstart	*Phoenicurus ochruros*	Both
Blackbird	*Turdus merula*	Both
Blackcap	*Sylvia atricapilla*	Both
Black-headed Gull	*Chroicocephalus ridibundus*	Insectivore
Black-tailed Godwit	*Limosa limosa*	Insectivore
Blue Tit	*Cyanistes caeruleus*	Both
Bullfinch	*Pyrrhula pyrrhula*	Seed disperser
Carrion Crow	*Corvus corone*	Insectivore
Cetti Warbler	*Cettia cetti*	Insectivore
Chaffinch	*Fringilla coelebs*	Both
Chiffchaff	*Phylloscopus collybita*	Insectivore
Chough	*Pyrrhocorax pyrrhocorax*	Insectivore
Coal Tit	*Periparus ater*	Insectivore
Collared Dove	*Streptopelia decaocto*	Seed disperser
Common Sandpiper	*Actitis hypoleucos*	Insectivore
Coot	*Fulica atra*	Seed disperser
Corn Bunting	*Emberiza calandra*	Both
Crossbill	*Loxia curvirostra*	Seed disperser
Cuckoo	*Cuculus canorus*	Insectivore
Curlew	*Numenius arquata*	Seed disperser
Dartford Warbler	*Sylvia undata*	Both
Dipper	*Cinclus cinclus*	Insectivore
Dunlin	*Calidris alpina*	Insectivore
Dunnock	*Prunella modularis*	Both
Firecrest	*Regulus ignicapillus*	Insectivore
Gadwall	*Mareca strepera*	Seed disperser

English name	**Scientific name**	**Functional group**
Garden Warbler	*Sylvia borin*	Both
Garganey	*Anas querquedula*	Insectivore
Goldcrest	*Regulus regulus*	Insectivore
Golden Plover	*Pluvialis apricaria*	Insectivore
Goldeneye	*Bucephala clangula*	Insectivore
Goldfinch	*Carduelis carduelis*	Seed disperser
Grasshopper Warbler	*Locustella naevia*	Insectivore
Great Spotted Woodpecker	*Dendrocopos major*	Insectivore
Great Tit	*Parus major*	Both
Green Woodpecker	*Picus viridis*	Insectivore
Greenfinch	*Chloris chloris*	Seed disperser
Greenshank	*Tringa nebularia*	Insectivore
Grey Partridge	*Perdix perdix*	Both
Grey Wagtail	*Motacilla cinerea*	Insectivore
Hawfinch	*Coccothraustes coccothraustes*	Seed disperser
Hobby	*Falco subbuteo*	Insectivore
House Martin	*Delichon urbicum*	Insectivore
House Sparrow	*Passer domesticus*	Seed disperser
Jackdaw	*Coloeus monedula*	Both
Jay	*Garrulus glandarius*	Both
Lapwing	*Vanellus vanellus*	Insectivore
Lesser Spotted Woodpecker	*Dendrocopos minor*	Insectivore
Lesser Whitethroat	*Sylvia curruca*	Both
Linnet	*Linaria cannabina*	Seed disperser
Little Ringed Plover	*Charadrius dubius*	Insectivore
Long-tailed Tit	*Aegithalos caudatus*	Insectivore
Marsh Tit	*Poecile palustris*	Both
Meadow Pipit	*Anthus pratensis*	Insectivore
Mediterranean Gull	*Larus melanocephalus*	Insectivore
Mistle Thrush	*Turdus viscivorus*	Both

English name	**Scientific name**	**Functional group**
Moorhen	*Gallinula chloropus*	Seed disperser
Nightingale	*Luscinia megarhynchos*	Insectivore
Nightjar	*Caprimulgus europaeus*	Insectivore
Nuthatch	*Sitta europaea*	Insectivore
Pied Flycatcher	*Ficedula hypoleuca*	Insectivore
Pied Wagtail	*Motacilla alba*	Insectivore
Quail	*Coturnix coturnix*	Seed disperser
Redstart	*Phoenicurus phoenicurus*	Insectivore
Redwing	*Turdus iliacus*	Both
Reed Bunting	*Emberiza schoeniclus*	Both
Reed Warbler	*Acrocephalus scirpaceus*	Insectivore
Ring Ouzel	*Turdus torquatus*	Both
Ringed Plover	*Charadrius hiaticula*	Insectivore
Robin	*Erithacus rubecula*	Insectivore
Rock Dove	*Columba livia*	Seed disperser
Rock Pipit	*Anthus petrosus*	Insectivore
Rook	*Corvus frugilegus*	Both
Sand Martin	*Riparia riparia*	Insectivore
Sedge Warbler	*Acrocephalus schoenobaenus*	Insectivore
Shoveler	*Anas clypeata*	Insectivore
Siskin	*Spinus spinus*	Seed disperser
Skylark	*Alauda arvensis*	Both
Snipe	*Gallinago gallinago*	Insectivore
Song Thrush	*Turdus philomelos*	Both
Spotted Flycatcher	*Muscicapa striata*	Insectivore
Starling	*Sturnus vulgaris*	Both
Stock Dove	*Columba oenas*	Seed disperser
Stonechat	*Saxicola rubicola*	Insectivore
Swallow	*Hirundo rustica*	Insectivore
Swift	*Apus apus*	Insectivore

English name	**Scientific name**	**Functional group**
Teal	*Anas crecca*	Insectivore
Tree Pipit	*Anthus trivialis*	Insectivore
Tree Sparrow	*Passer montanus*	Both
Treecreeper	*Certhia familiaris*	Insectivore
Turtle Dove	*Streptopelia turtur*	Seed disperser
Wheatear	*Oenanthe oenanthe*	Insectivore
Whimbrel	*Numenius phaeopus*	Both
Whinchat	*Saxicola rubetra*	Insectivore
Whitethroat	*Sylvia communis*	Both
Willow Tit	*Poecile montanus*	Both
Willow Warbler	*Phylloscopus trochilus*	Insectivore
Wood Warbler	*Phylloscopus sibilatrix*	Insectivore
Woodcock	*Scolopax rusticola*	Insectivore
Woodlark	*Lullula arborea*	Both
Woodpigeon	*Columba palumbus*	Seed disperser
Wren	*Troglodytes troglodytes*	Insectivore
Yellow Wagtail	*Motacilla flava*	Insectivore
Yellowhammer	*Emberiza citrinella*	Both

Table D2. Impact of trait number, proportion of continuous traits and the interaction on the R^2 values from linear models between mean total community abundance and F_{DIS} using a mix of continuous and categorical traits.

Feeding guild	**F_{DIS} metric**	**Explanatory**	**Estimate**	**SE**	**t-value**	**p-value**
Seed dispersers	Abundance-weighted	Trait number	0.0014	0.00018	7.67	<0.001***
		Prop. continuous	0.021	0.0026	7.99	<0.001***
		Trait number * prop. continuous	-0.00013	0.00039	-0.34	0.74
	Unweighted	Trait number	-0.12	0.012	-9.68	<0.001***
		Prop. continuous	-0.14	0.17	-0.78	0.44
		Trait number * prop. continuous	-0.062	0.025	-2.44	0.019*
Insectivores	Abundance-weighted	Trait number	-0.061	0.0093	-6.59	<0.001***
		Prop. continuous	0.13	0.14	0.96	0.34
		Trait number * prop. continuous	0.008	0.02	0.39	0.7
	Unweighted	Trait number	-0.00068	0.00004	-15.99	<0.001***
		Prop. continuous	0.00041	0.00062	-0.65	0.518
		Trait number * prop. continuous	0.0011	0.000091	12.37	<0.001***

Table D3. Results from linear regression models with the difference in R2 when a trait is removed as the response variable, and the absolute correlation coefficient of a trait as the explanatory variable using abundance weighted and unweighted FDIS for seed dispersers and insectivores.

Feeding guild	**FDIS metric**	**Estimate**	**SE**	**t-value**	**p-value**
Seed dispersers	Abundance-weighted	0.083	0.022	2.6	0.035*
	Unweighted	-0.0088	0.0046	-1.89	0.102
Insectivores	Abundance-weighted	-0.014	0.0077	-1.78	0.12
	Unweighted	0.023	0.021	1.35	0.22

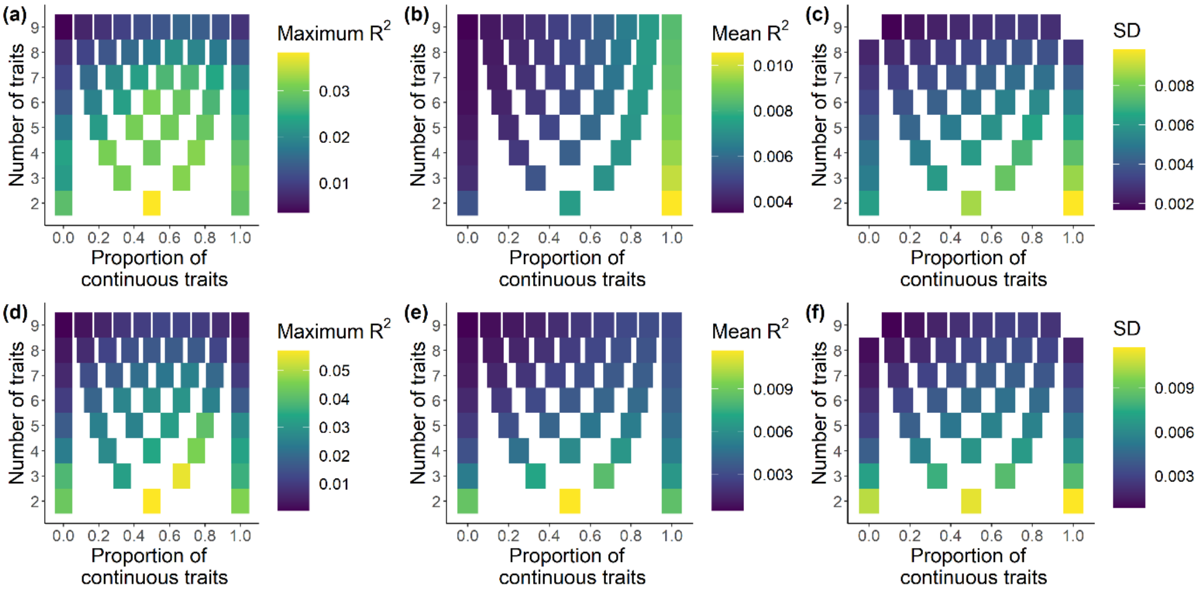

Figure D1. Maximum R^2 values (a) and mean R^2 values (b) with associated standard deviation (c) produced from abundance weighted F_{DIS}, and maximum R^2 values (d) and mean R^2 values (e) with associated standard deviation (f) produced from unweighted F_{DIS} for seed dispersing birds using the complete case data, i.e. where species and sites without detectability estimates were removed.

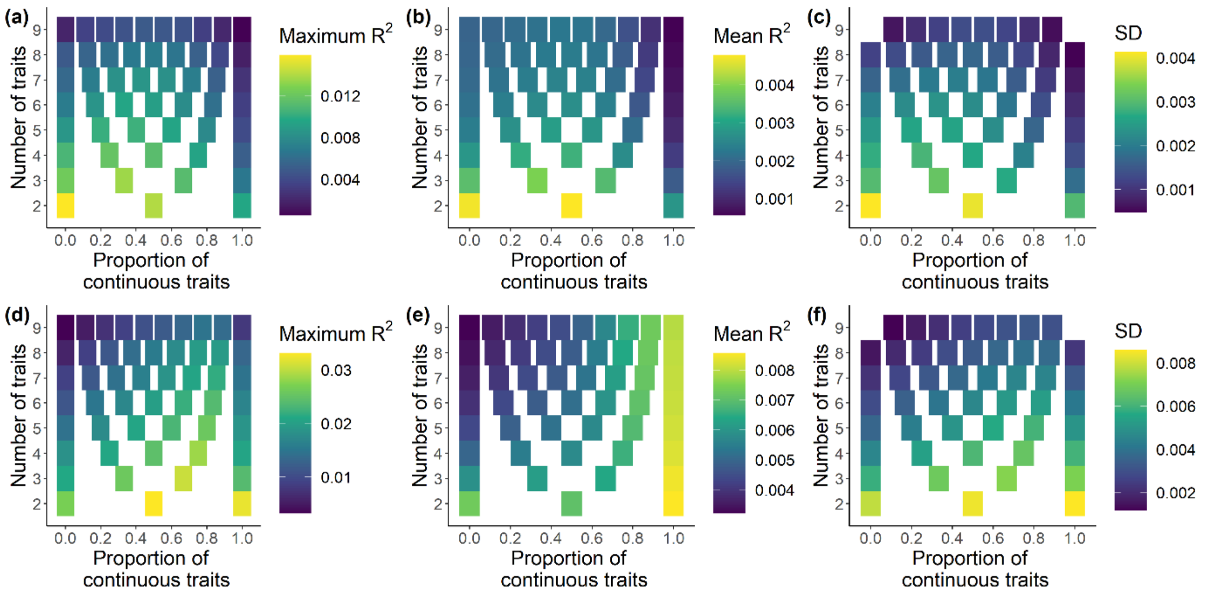

Figure D2: Maximum R^2 values (a) and mean R^2 values (b) with associated standard deviation (c) produced from abundance weighted F$_{DIS}$, and maximum R^2 values (d) and mean R^2 values (e) with associated standard deviation (f) produced from unweighted F$_{DIS}$ for insectivore birds. using the complete case data, i.e. where species and sites without detectability estimates were removed.

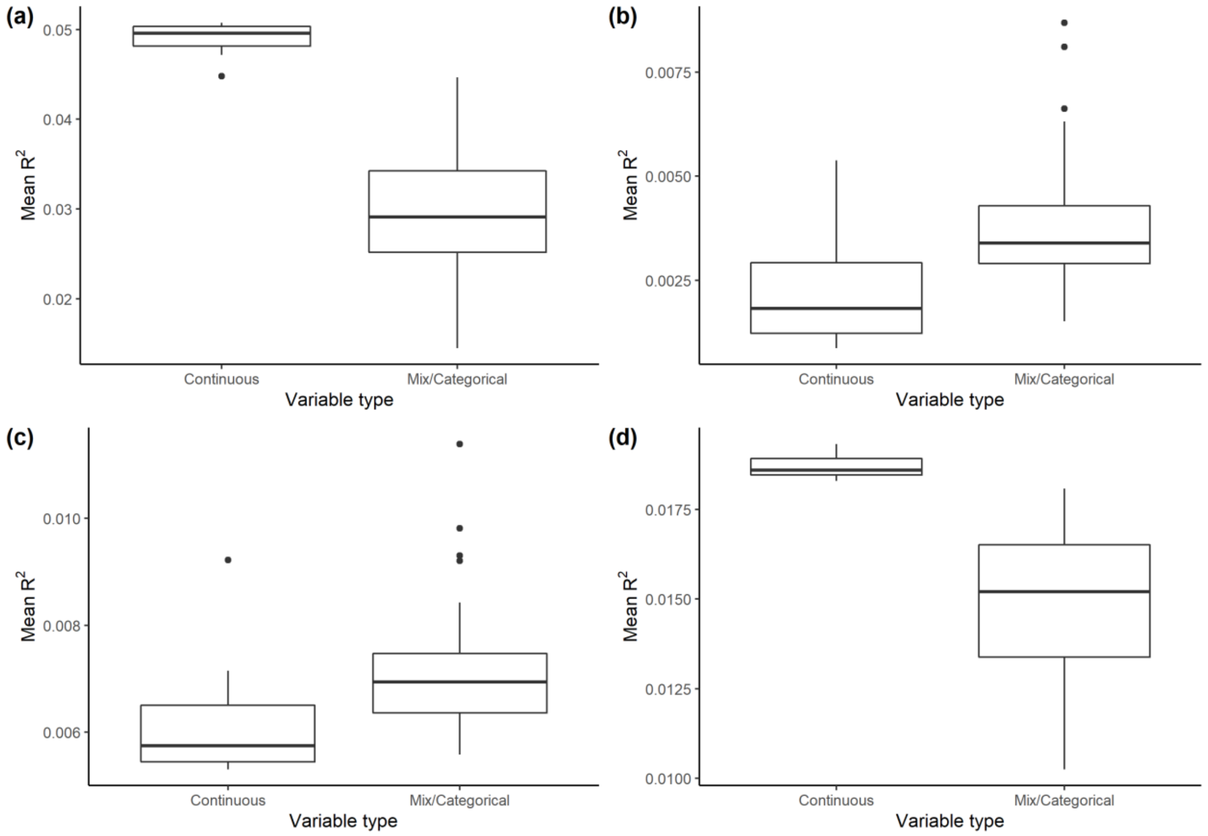

Figure D3. The relationship between mean R^2 and the variable type used to calculate F_{DIS} for seed dispersers with abundance-weighed F_{DIS} (a) and unweighted F_{DIS} (b), and insectivores with abundance-weighted F_{DIS} (c) and unweighted F_{DIS} (d).

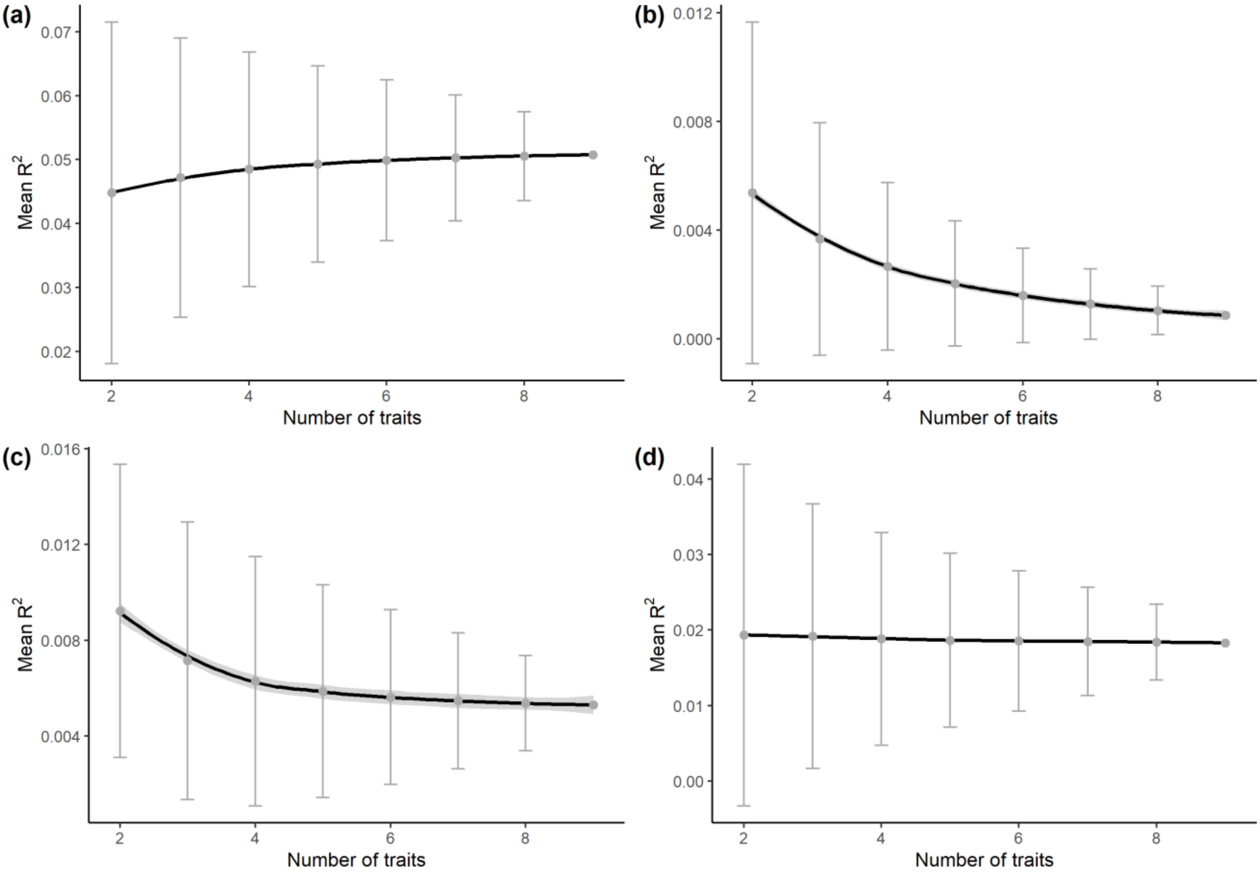

Figure D4. The relationship between mean R^2 and number of continuous traits used to calculate F_{DIS} for seed dispersers with abundance-weighed F_{DIS} (a) and unweighted F_{DIS} (b), and insectivores with abundance-weighted F_{DIS} (c) and unweighted F_{DIS} (d). Black line represents the LOESS regression with shaded 95% confidence intervals.

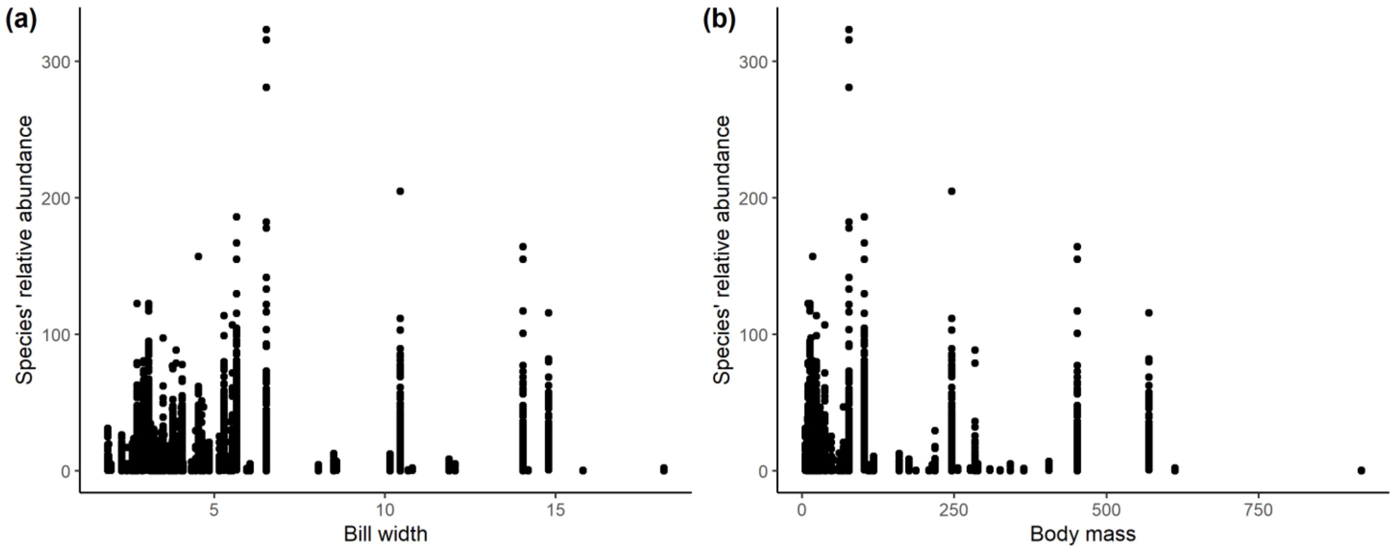

Figure D5. The relationship between insectivore species' relative abundance and two traits (a) bill width and (b) body size.

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