Extrapolating insect biodiversity across spatial scales

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The candidate confirms that the work submitted is his / her own, except where work which has formed part of jointly-authored publications has been included. The contribution of the candidate and the other authors to this work has been explicitly indicated below. The candidate confirms that appropriate credit has been given within the thesis where reference has been made to the work of others.

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Abstract

Extrapolating biodiversity patterns across spatial scales can address shortfalls in our knowledge of species distributions, inform conservation and further our understanding of spatial patterns in biodiversity. I compared fine grain predictions of occupancy for British Odonata species among ten downscaling models. I observed a sigmoidal occupancy-area relationship for the best performing model and found that predictive success for Odonata species varied systematically with species traits. Species with high dispersal abilities had greater predictive error. Poorer predictions for species with a climatic range limit in Britain suggest that environmental information is required to fully capture spatial patterns in biodiversity. I modelled the distribution of the Brindled Green moth at two spatial grains using a hierarchical Bayesian model to quantify associations with climate, landcover and elevation, whilst accounting for residual spatial autocorrelation and spatial patterns in recording effort. Model predictions improved at the finer spatial grain and identified unsurveyed grid cells with high suitability for future recording. The overlap between individual species distributions underpins spatial patterns in multi-species assemblages. I used simulated species assemblages to evaluate 29 abundance-based metrics of β-diversity against a set of desirable and 'personality' properties. Metrics accounting for unseen shared and unshared species were lacking. I identified a trade-off between robustness in the face of undersampling and sensitivity to turnover in rare species. The findings were borne out when a selection of metrics were applied to assemblages of British macro-moths: variation in β-diversity was best explained by climate, landcover and distance when using standardised data and abundance-based metrics, as opposed to opportunistic data and presence-absence metrics. This thesis has demonstrated the value of using biological records to explore biodiversity patterns at multiple spatial scales and has highlighted some of the methodological challenges that remain.

Table of Contents

List of Tables

List of Figures

Chapter 1
General introduction

1.1 Scope

Understanding the distribution, abundance and biodiversity of living organisms in time and space is a fundamental goal of ecology. The intention of this research is to explore spatial patterns in insect biodiversity at multiple spatial scales. The patterns of interest and the methods applied include elements of multiple ecological sub-disciplines. Macroecology is concerned with the statistical description of large-scale patterns in biodiversity, and the problem of inferring causality when manipulative experiments are impossible (Keith *et al.* 2012). The regional-scale patterns at the heart of this thesis share the observational nature of macroecological data. Other parts of the thesis fall under the remit of spatial ecology, which emphasises spatial structure in the distribution and abundance of species (Legendre & Fortin 1989). Biogeography focuses on this spatial structure at regional scales (Townsend Peterson *et al.* 2011). Describing and explaining spatial patterns, in individual species and communities, is a key aim of this thesis. Finally, community ecology is the study of the structure of species communities and the local and regional processes responsible for their assembly and dynamics. The distribution and abundance of species is determined by the interplay between climate, habitat (abiotic niche), intra- and interspecific interactions (biotic niche), spatial processes (dispersal limitation) and stochastic events (Stoll & Prati 2001; Potts *et al.* 2004; Palmer 2007; Soberón 2007). The relative importance of these processes is not well understood, partly because these processes differ in the spatial scale at which they operate. Moreover, establishing causality and identifying confounding effects is particularly difficult over large spatial extents where experimental manipulations are unfeasible. In the chapters to follow, I investigate the signature of these processes in individual species distributions and multi-species assemblages. I take a predominantly macroecological approach focussing on statistical descriptions of spatial patterns, and statistical links with environmental variables over large spatial extents. This is a top-down approach which will facilitate the characterisation of general patterns in biodiversity. These methods often require very little information beyond the known distributions of the focal taxa, but this is at the expense of a truly mechanistic approach to the questions I ask. In Chapter 6, I discuss the limitations of this approach, and suggest an alternative way of describing and explaining spatial patterns in biodiversity.

I investigate spatial patterns in insect biodiversity using observed data on the distribution and abundance of British moths and dragonflies and also simulated communities of species. The observed data vary in structure from opportunistic biological records of species occurrences to a standardised protocol for recording abundances. In each of the following chapters, I acknowledge the sources of the data used and describe each data set as it is introduced. Underpinning all chapters is a motivation to bridge the gap between methodological advances in quantifying biodiversity patterns and the application of these methods to the problem of monitoring biodiversity. Consequently, a number of the hypotheses in subsequent chapters revolve around methodological questions. I focus on the application of methods designed to quantify biodiversity and explain and predict spatial patterns. I evaluate and compare the effectiveness of these methods when applied to biological records, in the face of their inherent spatial bias. Sources of spatial bias in recording intensity include recorder behaviour (e.g. recording within the vicinity of their home or preferentially visiting sites that are species rich in a given taxonomic group) and variation in recording effort per visit leading to spatial variation in the completeness of species lists (Isaac & Pocock 2015).

In the remainder of this chapter, I briefly outline some of the challenges in measuring biodiversity. I go on to describe the general patterns in biodiversity that ecologists have observed in a variety of taxa and regions and then review some theories of biodiversity that attempt to predict these patterns and the relationships between them, as well as explaining the processes that generate them. Spatial scale emerges as the major obstacle to achieving a unified theory of biodiversity and to addressing useful questions about how best to protect it. I discuss the complexity surrounding the concept of scale-dependence and highlight the ways in which spatial scale can both complicate and facilitate our understanding of biodiversity patterns. I include a discussion of the shortfalls in our knowledge of the distributions and abundances of species, especially at larger spatial scales, a situation that is exemplified by the patchy biological records for the focal taxonomic groups in this thesis: British moths and dragonflies. I finish with a short outline of the specific questions to be addressed in Chapters 2 to 5.

1.2 The challenge of quantifying biodiversity

Biodiversity is the variability among living organisms, but this is a complex concept incorporating all levels of biological organisation from genes to biomes (Gaston & Spicer 2004). The components of biodiversity are varied and include species (taxonomic diversity), traits (functional diversity) and evolutionary history (phylogenetic diversity) to name but a few. There are different levels of biodiversity encompassing local or within-sample variation (*α*-diversity), the spatial or temporal variation between two or more samples (*β*-diversity) or the variation within regions, often comprising multiple, pooled samples (*γ*-diversity) (Whittaker 1960, 1972; Jurasinski *et al.* 2009). This hierarchical framework highlights the scale-dependence of biodiversity. Even once the units and focal scale(s) of biodiversity are defined, the issue of how to quantify the variation remains. There are countless metrics designed to capture the many nuances of biodiversity (Magurran & McGill 2011). For example, are the units of biodiversity to be measured with species presence-absence or abundances? If the latter, how will rare versus common species contribute to the value of the metric? Quantifying biodiversity is not straightforward, but it is essential if we are to explain the distribution and abundance of organisms and provide an evidence base for decision-making to protect biodiversity (Purvis & Hector 2000).

1.3 Large-scale patterns in biodiversity

Ecologists have identified a number of near ubiquitous patterns in the large-scale distribution of biodiversity (Lawton 1999). These are general patterns in the abundance, distribution and diversity of species and the spatial scaling of these variables (Smith *et al.* 2008). Acronyms follow the nomenclature in McGill (2011).

1.3.1 Species-area relationship (SAR)

The first mathematical description of a scaling relationship in ecology was the species-area relationship, modelled as a power law (Arrhenius 1921) and on semi-logarithmic axes (Gleason 1922). The SAR documents the increase in the number of species recorded with the area of nested sampling units and demonstrates that biodiversity is highly dependent on the spatial scale of sampling (Chave 2013a). Moreover, the local slope of the SAR is also scale-dependent with power-law, asymptotic, sigmoidal and triphasic patterns observed depending, empirically, on the range of scales considered. The SAR arises for a number of reasons. Firstly, smaller sample areas contain fewer individuals, which, for statistical reasons, constrains the possible number of species; the number of species cannot exceed the number of individuals. Secondly, species spatial turnover means larger sample areas incorporate larger numbers of species and the faster the rate of turnover, the steeper the slope of the SAR. For example, the accelerating slope of the SAR at coarse spatial grains (e.g. continental) reflects that the sample area approaches species' geographical range sizes, such that an increase in sample area incorporates additional biogeographical regions (Storch *et al.* 2012). As species range sizes underpin the SAR, a number of biological mechanisms would therefore be expected to affect the shape of the SAR including the size of the species pool, interspecific interactions (competition, predation) and minimum area requirements for essential resources. Applications include estimating species extinctions under habitat loss (Pan 2013) and extrapolating species richness from plots to regional spatial scales (Harte & Kitzes 2015).

1.3.2 Endemics-area relationship (EAR)

The endemics-area relationship (EAR) describes the relationship between the number of endemic species (those species restricted to a single sampling unit within the study region) and the area of nested sampling units (Harte & Kinzig 1997). The EAR has been used as an alternative to the SAR for predicting species loss in response to habitat loss, since the SAR has been shown to overestimate extinction rates except in the special (and unrealistic) case where individuals are randomly and independently distributed (Kinzig & Harte 2000; He & Hubbell 2011, but see Axelsen *et al.* 2013).

1.3.3 Occupancy-area relationship (OAR)

Occupancy describes the number of presences of a species in some predefined unit (typically a grid cell) within the study region. This unit may be a habitat patch, a host-plant or a sampling quadrat. Occupancy can be quantified as the number, proportion or area of occupied cells within a study area. The sizes of these grid cells define the grain of the study: sampling many small cells generates fine-grained data, while sampling a few large cells generates coarse-grained data. When occupancy is plotted as a function of the grain of the study, the occupancy-area relationship (OAR) is obtained. This provides a summary of a species' rarity (or commonness) at multiple spatial grains. By summing the occupancies of multiple species at each spatial grain, the expected number of species at a given spatial scale (the SAR) is obtained (Storch *et al.* 2008). Depending on the grain of measurement, occupancy can be a measure of species range extent (coarse sampling grain), regional ubiquity (intermediate sampling grain) or ground cover (fine sampling grain) (Hartley & Kunin 2003, Witte 2003).

By imposing an arbitrary grid cell size on the study area, information about the distribution of organisms within grid cells is lost (Wiegand & Moloney 2004). As the grid cell becomes larger, an increasing amount of uncertainty is introduced as both the number and position of individuals and the amount of unoccupied space within a grid cell is unknown (He & Hubbell 2003). The cells in fine-grained occupancy maps can be merged into coarser-grained cells and so contain all of the information needed to generate a coarse-grained map (Kunin *et al.* 2000). The converse is not true because information about the location of absences is not retained in coarse-grained data. Downscaling models attempt to 'rediscover' some of this lost information by assuming a set of statistical regularities which govern the changing occupancy across scales (Hui *et al.* 2010) and which can guide our estimates of how many absences will be expected within occupied grid cells as the sampling grain becomes finer. When the sampling grain is sufficiently fine that there is, on average, just one individual in each occupied cell, then occupancy begins to approximate total abundance (Kunin 1998; He & Gaston 2000a, 2007; He *et al.* 2002).

1.3.4 Occupancy-abundance relationship (ONR)

The OAR is closely related to the occupancy-abundance relationship (ONR), if we assume a linear relationship between area and abundance (the individual-area relationship: NAR), a relationship that is usually found to apply (Hubbell 2001; Pautasso & Gaston 2006; McGill 2011). There are two forms of the ONR: the intraspecific ONR describes the relationship between the number of sites at which a species is recorded regionally and its mean local abundance where each data point is for a different point in space or time (Borregaard & Rahbek 2010); the interspecific ONR describes the relationship between area of occupancy and local abundance where each data point is a different species (Warren & Gaston 2013). Both relationships are usually positive (Gaston *et al.* 2000; Cowley *et al.* 2001; Blackburn *et al.* 2006; Webb *et al.* 2012, but see Päivinen *et al.* 2005). The mechanisms underlying these well-documented relationships are not well understood, but all models of the ONR assume some pattern of intraspecific aggregation determines the slope of the ONR (Holt *et al.* 2002; Conlisk *et al.* 2007). Like all the patterns we have described here, the ONR is scale-dependent (He & Gaston 2000c). This scale-dependence is unsurprising. At very fine grains occupancy is much lower and begins to equal abundance when each grid cell contains just one individual. At extremely coarse grains, approaching the area of the study region, all species will have equal occupancy. Therefore, steeper ONRs are expected at coarser spatial grains, that is, there is a greater increase in area-of occupancy for a given increase in abundance.

1.3.5 Species abundance distribution (SAD)

The SAD describes the structure of an ecological community in terms of the commonness and rarity of its species. It is usually presented as the frequencies of species within discrete abundance classes and is a way of quantifying the widely observed pattern that an assemblage contains a few common and many rare species (a hollow curve). A large number of models have been developed to describe and explain the SAD (see McGill *et al.* (2007) and Ulrich *et al.* (2010)). The SAD is relevant to conservation practices as it contains information about the dominance, evenness and rarity of species as well as providing a tool to address fundamental ecological questions about the distribution and abundance of species. It has been used to test some of the leading theories about community assembly (Magurran 2005; White *et al.* 2012), although success with this approach is limited as theories of biodiversity predict almost identical patterns in the SAD (Chisholm & Pacala 2010). Like each of the ecological patterns described above, the SAD is highly scale-dependent and there have been numerous attempts to predict the regional SAD from local SADs (Borda-de-Agua *et al.* 2002; Sizling & Storch 2007; Green & Plotkin 2007; Šizling *et al.* 2009; Borda-de-Água *et al.* 2012; Conlisk *et al.* 2012).

1.3.6 Distance-decay of similarity

The distance-decay of similarity describes the decreasing relationship between the similarity of two sites with the geographical distance between them (Nekola & White 1999). The observed pattern (ecological distance) is the aggregate effect of spatial turnover of species along an environmental gradient (environmental distance) and spatial turnover due to stochastic processes such as dispersal limitation (geographical distance). The implication is that species distributions are spatially auto-correlated. Partitioning the distance-decay of similarity into environmental and spatial components and comparing these relationships between regions and taxa has been one approach for ecologists to explore community assembly processes (Fitzpatrick *et al.* 2013). The shape of the distance-decay relationship is central to the spatial scaling of biodiversity as the rate of turnover will determine how local patterns of species diversity will translate to larger spatial extents (Arita & Rodriguez 2002). Unfortunately, the distance-decay relationship is not linear, that is, species turnover is not constant along environmental and geographical gradients (Ferrier *et al.* 2007), which makes extrapolation difficult. A second obstacle to extrapolation is that there are two other concepts of β-diversity: i) pairwise dissimilarity metrics and ii) the ratio of diversity between two nested spatial scales. These concepts are related to the distance decay of similarity, but not equivalent, making mapping of β-diversity on to the distance-decay of similarity somewhat difficult. Moreover, the relationship is highly scale-dependent (Soininen *et al.* 2007b) and varies among taxa (Soininen *et al.* 2007a; Astorga *et al.* 2012).

The functional form of the above biodiversity patterns is often consistent across taxa and spatial scales suggesting a set of general statistical regularities could underpin the relationships we repeatedly observe in very different systems (Nekola & Brown 2007; Storch *et al.* 2012).

1.4 A unified theory of biodiversity

There are a number of general theories of biodiversity that aim to predict multiple biodiversity patterns (Hubbell 2001; Harte *et al.* 2008; Storch *et al.* 2008). Progress towards unifying these theories has focussed on aspects of stochastic geometry. Fuelling the search for such a framework are a multitude of studies that have demonstrated a large number of biodiversity patterns link to and can be derived from other patterns (Harte & Kinzig 1997; Harte *et al.* 2005; McGill 2010b, 2011; Passy 2012), suggesting a set of 'minimally sufficient rules' (McGill 2010b) may underpin each of them. Indeed the distance-decay of similarity and the SAR can be reasonably well predicted in environmentally homogenous tropical forest plots, based on indices of intraspecific aggregation and the regional species abundance distribution (Morlon *et al.* 2008). These same measures can be used to predict the EAR (Green *et al.* 2003a). The SAR can be derived from the OAR by summing the proportion of occupied cells across species at several spatial grains (Sizling & Storch 2004).

The connections between these patterns continue to emerge and the applications associated with predicting one pattern from another have yet to be fully explored. There is the potential to obtain much more information from the large-scale data sets available to us if these relationships can be refined and a set of general principles identified which are able to predict each of these patterns and the links between them. McGill (2010) identified and reviewed six unified theories of biodiversity (neutral, fractal, cluster Poisson point processes, continuum, metapopulation and maximum entropy). Each of these theories can predict two or more patterns out of the global / local species abundance distribution (SAD), the species-area relationship (SAR), the abundance-occupancy relationship (ONR) and the distance decay of similarity. All rest on three common statistical assumptions: intraspecific aggregation, uneven distribution of abundance among species and spatial distributions of species that are mutually independent (McGill 2011), although the latter is unlikely, especially at fine spatial grains (Kissling *et al.* 2011). Intraspecific aggregation is widely documented in ecology at all spatial scales (Kotliar & Wiens 1990; Seidler & Plotkin 2006; Sizling & Storch 2007; Karlson *et al.* 2007; Jovani & Tella 2007; Green & Plotkin 2007). More recently, Azaele *et al.*

(2014) introduced a unified descriptive theory for spatial ecology, which explicitly models intraspecific aggregation using a pair-correlation function (the correlation between species abundances as a function of distance). The theory not only predicts the distance-decay of similarity, species richness and the species abundance distribution but is also able to predict the spatial scaling of these biodiversity patterns.

Existing theories of biodiversity are not yet consistent in the form of the patterns predicted. One explanation may be that the theories emphasise the importance of different processes in structuring species distributions. For example, neutral theory focuses on the role of non-deterministic processes (e.g. demographic stochasticity and dispersal limitation determines community composition), while continuum theory considers the niche as the primary driver of variation in abundance along environmental gradients. If the relative importance of these processes change with spatial scale, then our current suite of theories are only likely to perform well over a limited range of spatial scales. The SAR is known to be triphasic when the full range of scales is considered, from local plots to continental scales (Harte 2011), yet most theories of biodiversity fail to predict this pattern unless the predictions of multiple unified theories are pasted together, but see Azaele *et al.* (2014) and (Rosindell & Cornell 2007). This suggests that theories of biodiversity have yet to fully incorporate spatial scale. McGill (2010) notes that each theory appears to be geared towards characteristic set of scales, perhaps reflecting the sub-discipline from which it emerged. Ecological sub-disciplines tend to be characterised by a subset of patterns and processes, which in turn translates into a characteristic range of spatial scales for studies. For a macroecologist, this is typically continental to global scales with a focus on patterns (e.g. latitudinal gradients in biodiversity) and processes (e.g. climatic and historical drivers) operating at large spatial and temporal scales (Stevens 1989, 2006; Hawkins *et al.* 2007). Biogeographers aim to capture the species-environment relationship using coarse-grain climate data in order to predict current and future species distributions over national or continental extents (Berry *et al.* 2002). Landscape ecology encompasses much finer spatial scales, albeit coarse enough to reflect landscape heterogeneity, connectivity and spatial structure. At this scale key processes are the colonisation, extinction and demography central to metapopulation dynamics (Hanski 1982), the species-habitat associations that can be inferred from landcover data. At a finer scale still, many studies in community ecology are characterised by field- and plot-scale studies where manipulative experiments are possible. At this scale, questions surrounding inter- and intra-specific competition (Gunton & Kunin 2009; Rayburn & Schupp

2013) and the impact of management on local-scale abundance and diversity can be addressed (Woodcock *et al.* 2007). What we are lacking is the framework to link these observations of patterns and process across spatial scales and to join the dots between these ecological sub-disciplines.

The complexity of ecological systems raises the question of whether a general theory of biodiversity is possible. Indeed, the theories of biodiversity discussed above have been evaluated on the basis of their ability to reproduce a core set of biodiversity patterns (e.g. the SAR, SAD, distance-decay of similarity). As discussed above, these observed patterns have been predicted with some success, but almost exclusively over larger spatial extents. Over smaller spatial extents, species differences may not be overpowered by stochastic effects in the way they are at larger spatial extents (Wiegand *et al.* 2012). Species-specific responses to each other and to the environment are clearly important in determining biodiversity patterns, yet these are not explicitly considered in a stochastic geometry framework. In chapters 2, 3 and 5, I use top-down statistical approaches to predict local-scale patterns and attempt to explore the importance of species differences through species-level traits (Chapter 2) and species-environment relationships (Chapters 3 and 5). In chapter 6, I draw on the findings of the chapters in this thesis to discuss the extent to which a unified theory of biodiversity, based on stochastic geometry, can be useful in explaining and predicting biodiversity patterns given species differences, and whether this may depend on spatial scale.

1.5 Scale-dependence

Since the 1980s, the concept of spatial scale has received increasing interest from ecologists (Levin 1992; Schneider 2001; Chave 2013b; Azaele *et al.* 2014; Sandel 2015). Spatial scale is now frequently incorporated into sampling regimes (Fortin & Dale 2005; McMahon & Diez 2007; Sandel & Smith 2009), to capture patterns at multiple spatial scales. Keil *et al.* (2011) used hoverfly species richness at five spatial scales before and after 1980 to examine the scale-dependence of change in species richness: it was negative at fine spatial grains, stable at intermediate grains and positive at coarse grains, indicating the strength and even the sign of temporal trends in biodiversity can change with spatial scale. The implication is that negative changes at fine scales reflect the loss of specialist species from local habitat patches, while positive change at coarse scales reflect the expansion of generalist species (biotic homogenisation). These changes in pattern and process (the form of relationships between variables) with spatial scale have been explicitly studied for a number of other ecological relationships including species-habitat associations (Altmoos & Henle 2010; Cunningham *et al.* 2014), species-environment associations (de Knegt *et al.* 2010), abundance-habitat associations (Holland *et al.* 2004), diversity-stability relationships (Chalcraft 2013), productivity-biodiversity relationships (Chase & Leibold 2002), richness-environment associations (Field *et al.* 2009; Belmaker & Jetz 2011), biotic interactions (Araújo & Rozenfeld 2014), biotic homogenisation (Baiser *et al.* 2012) density-dependence (Gunton & Kunin 2007, 2009) and metapopulation dynamics (Haby *et al.* 2013). As a result, we know that ecological processes tend to operate at characteristic scales (Pearson & Dawson 2003; Wu & Harbin 2006) and that the individuals, species, populations and distributions we study vary in the way they respond to the environment and to each other.

One consequence of this scale-dependence is inconsistent results between studies conducted at different spatial grains and extents (Wiens 1989; Rahbek 2004). A failure to appreciate scale-dependence has perpetuated long-running controversies in ecology including optimising reserve design (Schwartz 1999) and the relative importance of niche and neutral processes in shaping species relative abundances and distributions (Chase 2014; Garzon-Lopez *et al.* 2014). In part this is because scale-dependence is multi-faceted and its measurement is not straightforward. Sandel (2015) identifies three distinct concepts under the umbrella term of scale-dependence, each of which should be explicitly defined by a study. These are 1) the scale component (grain or extent); 2) the subject of scale-dependence (data or model) and 3) the class of scale-dependence (true or perceived). I discuss the implications of these in turn.

The distinction between grain and extent has long been recognised in ecology (Wiens 1989). Spatial grain is the size of the individual sampling units, such as the area of a quadrat or grid cell. Most of ecology makes the implicit assumption of homogeneity within each sampling unit, so the spatial grain defines the resolution at which we can capture spatial variation, like a pixel in a digital image. For example, monthly measures of temperature and rainfall vary rather gradually in space, such that a 25km^2 resolution is quite reasonable for most purposes (see Met Office UKCP09 data used in chapter 3, but see Gillingham *et al.* (2012) for microclimate effects at finer spatial grains), while elevation varies substantially at finer spatial grains. Spatial grain is an important decision in study design as it defines how much variation is contained within samples versus the variation between samples. Any variation within a sampling unit is averaged away under the assumption of homogeneity, thus this information is lost if the chosen grain is too coarse. The spatial extent is the size of the study region of interest, for example a field, a country or a continent (Gunton *et al.* 2014). The spatial extent of a study is a second sampling decision and determines how much of a relationship is visible to an observer. A relevant example here is the triphasic shape of the SAR when the full range of scales is observed (Grilli *et al.* 2012): the slope often appears to decelerate moving from local to regional scales, but to steepen again at continental scales. The grain and extent define the window through which we observe a given pattern or process. The concepts of grain and extent are thus distinct, with different mechanisms unpinning grain- and extent-dependence, as evidenced by the contrasting relationships of β-diversity with grain and extent (Barton *et al.* 2013). Limited resources usually lead to a trade-off in sampling design, such that studies of larger spatial extent tend to have coarser grain sizes. This situation leads to large gaps in our knowledge of the distribution and diversity of species, an issue which I discuss further in section 1.6 of this chapter.

Besides the grain-extent distinction, Sandel (2015) identifies a further distinction between scale-dependent data and scale-dependent models. This can be interpreted as directly measuring the scale-dependence of a single variable or the scale-dependence of a statistical relationship between two or more variables (first-order and second-order scale-dependence, respectively: Sandel & Smith 2009). Examples of scale-dependence in data include changes in species richness, area of occupancy, number of endemics and abundance with spatial grain or extent (e.g. the SAR, EAR, NAR in section 1.3). Scale-dependence of models refers to quantifying the change in statistical descriptors of biodiversity patterns. Examples include parameter estimates (Borda-de-Água *et al.* 2012), effect sizes (Chase & Knight 2013), goodness-of-fit (Gunton & Kunin 2007, 2009), predictive success and the functional form of these relationships (Azaele *et al.* 2014).

Unfortunately, there are a number of pitfalls in measuring scale-dependence that apply to both data and models. The final distinction in Sandel's (2015) taxonomy is between true and perceived scale-dependence. There are two sources of perceived scale-dependence: the observation process (e.g. detectability changing with spatial scale) and imperfect model specification (missing covariates or incorrect functional form of a model). The extent to which scale-dependence is true or perceived can be difficult to pick apart. Consider the OAR in section 1.3. There is a mechanism underpinning the decline in area of occupancy (AOO) with the spatial grain of sampling: intraspecific aggregation leads to more unoccupied cells at finer spatial grains than at coarser spatial grains (Azaele *et al.* 2012). However, the perception of scale dependence is likely to be amplified by the fact that sampling intensity per grid cell also declines with area, such that an unknown proportion of absences at fine spatial scales are artefacts (pseudo-absences or false absences). This kind of perceived scale-dependence can also be generated when important covariates are missing from models (e.g. confounding effects) or by not accounting for spatial autocorrelation among residuals (Sandel 2015).

One implication of scale-dependence is how to match the sampling scale to the characteristic scale at which the process of interest operates (Chase & Knight 2013). Even in studies when sampling has been conducted at a range of scales, measured effect sizes are typically greatest at the finest or coarsest scales, suggesting that sub-optimal sampling scales lead to systematic underestimates of effect sizes (Jackson & Fahrig 2014). This is particularly worrying when the purpose is to quantify the effect of drivers of biodiversity loss and the interventions that will be sufficient to mitigate these impacts. In the UK, drivers of biodiversity loss include land use change related to agricultural intensification, pollution including pesticides and inorganic fertilisers, climate change and the overexploitation of natural resources (Burns *et al.* 2013). Our ability to mitigate these impacts depends on identifying the scale at which these processes have the greatest impact and intervening at the appropriate scale.

Only recently has the precise form of relationships between scale and key measures of diversity, distribution and abundance become a major focus of research (Kunin 1998; Kunin *et al.* 2000; Sizling & Storch 2004; Hartley *et al.* 2004; Storch *et al.* 2007, 2012; Azaele *et al.* 2012). This line of investigation is crucial to developing a multi-scale unified theory of biodiversity. Aside from the theoretical advances made possible by describing how the distribution, abundance and diversity of species (and the parameters quantifying the relationships between these variables) change with spatial scale, the practical applications for biodiversity monitoring are invaluable in providing the tools to interpolate and extrapolate these biodiversity patterns to different spatial grains and extents. One example is that β-diversity determines the local slope of the SAR, providing a means of linking local and regional species richness. We need methods which allow us to extrapolate biodiversity patterns to scales that are unfeasible to sample using traditional field surveys, given the time, money and human resources required for such an endeavour. These are tools with the potential to estimate biodiversity metrics in regions and taxonomic groups where we lack knowledge and to facilitate the discovery of new species and new populations (Townsend Peterson *et al.* 2011). In addition spatial scaling tools could be used to contribute to generating indicators of the status and trends in biodiversity at multiple spatial scales (Collen *et al.* 2013).

1.6 Data and taxonomic groups

The terms Linnaean shortfall and Wallacean shortfall have been coined to describe our lack of knowledge about the diversity and distributions, respectively, of many taxonomic groups (Lomolino & Heaney 2004). These knowledge shortfalls are especially extreme at large scales, that is, national, continental and global patterns of biodiversity are poorly understood (Mora *et al*. 2011; Jetz *et al.* 2012). In the case of the Wallacean shortfall, our sampling design is usually a trade-off between grain and extent and between data quality and data quantity because of the limited resources available for data collection. Data sets covering large spatial extents typically map biodiversity using coarse-grain grids (Robertson *et al.* 2010; Beck *et al.* 2012). Examples include British atlases (Asher *et al.* 2001; Cham *et al.* 2014), which are designed to collect data on species occurrences with national coverage within a defined time-period. Recording is sufficiently patchy that good coverage can only be achieved by mapping the distribution at relatively coarse-grains (usually 100km^2). By contrast, fine-grain data are collected over short time-periods with limited spatial extent or poor spatial coverage (Barbosa *et al.* 2010), but the information content is usually much higher. For example, there may be abundance data for a limited number of grid cells in long-term monitoring schemes like the UK Butterfly Monitoring Scheme, but this level of recording would not be feasible if the spatial coverage were greater. In the case of the Linnaean shortfall, gaps in our knowledge become more extreme with decreasing body size (Whittaker *et al.* 2005). Both the Wallacean and Linnaean shortfalls are especially severe among insect taxa (Cardoso *et al*. 2011).

These data-deficits are obstacles to our theoretical understanding of biodiversity patterns and to addressing more practical and urgent questions in the face of rapid anthropogenic change (Butchart 2010). The UK government is legally required to identify, conserve, protect and enhance biological diversity at a national scale (Convention on Biological Diversity 2020 Aichi targets), which requires the development of methods to monitor progress towards these targets (Mace & Baillie 2007; Jones *et al.* 2011). The scales at which we are able to monitor trends in species abundances and distribution rarely match the scales relevant for reporting and for conservation planning (Miller *et al.* 2004; Araújo *et al.* 2005a; Lengyel *et al.* 2008; Pereira *et al.* 2010; Pelosi *et al.* 2010; Paloniemi *et al.* 2012; Guerrero *et al.* 2013). As such, the Wallacean and Linnaean shortfalls must be addressed (Bini *et al.* 2006; Diniz-Filho *et al.* 2010).

The best-studied taxonomic groups in the UK are undoubtedly birds and butterflies and these would be obvious choices for the study of large-scale biodiversity patterns. However, I focus here on less well-studied groups: the dragonflies (Odonata) and macro-moths (Lepidoptera). There are two reasons for these choices. First, the insights from less-well studied taxonomic groups are potentially more compelling with a greater scope for novel ecological findings. Secondly, aside from the ecological insights, a key focus of this research is to bridge the gap between theoretical models of spatial ecology and monitoring of biodiversity at multiple spatial scales. If the methods I apply in the following chapters are to be useful and widely applicable, the impact of data quality on their performance will be a key consideration. In other words, the data for birds and butterflies could be said to be "too good" for the methodological questions posed in this thesis. Demonstrating the insights that can be derived from patchy biological records for dragonflies and moths is an important step towards harnessing the potential of the datasets that are available for even less well-studied groups. This is particularly timely given the large volumes of biodiversity data currently being generated through citizen science projects (Pocock *et al.* 2014; Silvertown *et al.* 2015; Theobald *et al.* 2015). These data are a rich resource for monitoring biodiversity, but typically lack a standardised protocol for data collection. Examples include the Global Biodiversity Information Facility (GBIF), ebird and iSpot. The major implication of opportunistic recording is that the data contain false absences (when failure to detect a species is wrongly interpreted as the absence of that species). The challenges associated with presence-only data and its associated biases are central to the methodological questions posed in the following chapters. The types of recording behaviour that generate false absences are discussed below.

Isaac *et al.* (2014) identify four classes of bias driving false absences in opportunistic records: 1) temporal variation in recorder effort; 2) spatial variation in recorder effort; 3) variation in sampling effort per visit and 4) spatial and temporal variation in detectability. False-absences are problematic when trying to quantify biodiversity patterns in time and space (Iknayan *et al.* 2014; Isaac & Pocock 2015). One implication of these biases are that maps of species distributions based on opportunistic biological records confound patterns of biodiversity with patterns of recording effort.

Temporal variation in recording effort can be problematic when extracting temporal trends in species distributions (Hickling *et al.* 2006; Powney 2013; van Strien *et al.* 2013). An example of this is the increase in the number of biological records over time (Isaac & Pocock 2015), which can lead to spurious increases in distribution size over time, potentially masking the true trends in stable or declining distributions (Hassall & Thompson 2010). While the focus of this thesis is spatial patterns in biodiversity, temporal variation also has implications for choosing an appropriate time period as a snapshot of the distribution.

Spatial variation in recording activity leads to geographical biases in recording, with a number of potential sources. An example is high intensity recording activity around areas of high quality habitat, or a disproportionate contribution of records by a small number of recorders, focussed in areas around the homes of those individuals. A well-documented example in the UK is the decrease in recording intensity with increasing latitude (Hassall *et al.* 2010; see chapter 2 Appendix 2).

A third source of false absences is the amount of time a recorder has spent in the field on a given visit. In the absence of a standardised protocol for recording, the length of species lists increases asymptotically with time spent in the field (Ugland *et al.* 2003; Szabo *et al.* 2010), therefore grid cells with low recording intensity carry a greater risk of false absences. At the extreme are cells that have never been sampled but are interpreted as absences in opportunistic data sets. A second facet of recording activity within a site is under-recording of common or widespread species. One example of this is incomplete species lists biased towards rare, charismatic or migrant species that are rarely observed in the UK and often excluding less interesting or more common species.

Finally, there is interspecific variation between species in terms of detectability, which can be influenced by factors such as life history stage or flight period. Spatial patterns in detectability can also be driven by habitat characteristics like vegetation structure (Dennis *et al.* 2006).

The effects of uneven recording in space and time can be mitigated to some extent by combining records for consecutive number of years to provide a snapshot with better spatial coverage and / or by aggregating the spatial grain of records to a grain at which fewer grid cells have never been visited. Both approaches are used to generate distribution maps in published atlases, but they discard potentially valuable information about fine grain spatial patterns and temporal dynamics. HoweverAlternative approaches to the problem of false absences are being developed which explicitly model the relationship between recording effort and probability of detection and retain a greater proportion of the information content of the data (Kéry & Royle 2008; Bornand *et al.* 2014; Beale *et al.* 2014). These methods are a promising line of investigation towards the use of biological records for monitoring biodiversity and explaining its structure at multiple spatial scales.

1.7 Thesis outline

In the following chapters my main focus is to explore methods for predicting and explaining large-scale spatial patterns in the distribution and abundance of British dragonflies and moths in a way that explicitly considers issues of spatial scale. When addressing these questions there is certainly a trade-off between the quantity and quality of data used and the quality of the predictions and ecological insights. The statistical approaches used here are chosen as they are less data-hungry than alternative, more mechanistic approaches. This is particularly important when the biodiversity patterns of interest concerns species-rich assemblages and large spatial extents. The species-specific data required to capture the complexity of these interactions and approach these questions in a mechanistic way is not always available. These data-efficient methods have particular relevance for the purposes of biodiversity monitoring for poorly studied regions and taxa. For example, the UK government has a legal obligation to report on progress towards internationally agreed biodiversity targets (Jones *et al.* 2011) and we must find a way to do this even for poorly studied taxonomic groups like macro-moths. A valuable resource for monitoring UK biodiversity is the wealth of opportunistic records collected by volunteer recorders. The methods I employ below are designed to exploit the full potential of these records, so all species can be monitored in a consistent way, regardless of how well-studied they are.

In Chapter 2, I explore area of occupancy as a way of comparing the commonness and rarity of different species. It is one of the IUCN red list criteria for classifying species as threatened and it is, therefore, important to understand how area of occupancy depends on the spatial grain of measurement. We know it is prone to overestimating the distribution size when measured using coarse-grain grids and underestimating it using fine-grain grids. I compare competing models of the OAR in an attempt to obtain an accurate fine-grain metric of distribution size by extrapolating occupancy to fine grains for Odonata species with a range of ecological and distributional traits. Chapters 2 and 3 share a major challenge in overcoming the false-absences in the known distribution of their focal species. In chapter 2, we deal with false-absences by coarsening the data to a spatial grain with far fewer gaps, at a cost of excluding large amounts of information contained in the spatial precision of records.

In Chapter 3, instead of coarsening the data, I apply a method which explicitly models recording effort in each cell. I also introduce environmental information using species distribution modelling techniques, to obtain spatially explicit predictions of probability of occurrence at finer spatial grains than has previously been attempted and to quantify the drivers of the distribution of the Brindled Green moth.

In chapter 4, I move from modelling patterns in single species to considering spatial patterns in multi-species assemblages, specifically, how spatial turnover can best be quantified using abundance-based metrics of β-diversity. I identify a set of criteria and evaluate the performance of 24 abundance-based metrics and five widely used presence-absence metrics for these properties.

In chapter 5, the best-performing metrics of β-diversity are applied to total counts of moths in the Rothamsted Insect Survey and are used to evaluate the independent contributions of climate, landcover and geographical distance in structuring spatial patterns of macro-moth β-diversity.

Chapter 6 discusses the findings of this thesis in relation to the spatial scaling of insect biodiversity, the limitations of the methods used here for explaining biodiversity patterns, the feasibility of a unified theory of biodiversity and the use of biological records in monitoring biodiversity.

1.8 References

Altmoos, M. & Henle, K. (2010). Relevance of multiple spatial scales in habitat models: A case study with amphibians and grasshoppers. *Acta Oecologica*, **36**, 548–560.

Araújo, M.B. & Rozenfeld, A. (2014). The geographic scaling of biotic interactions. *Ecography*, **37**, 1–10.

Araújo, M.B., Thuiller, W., Williams, P.H. & Reginster, I. (2005). Downscaling European species atlas distributions to a finer resolution: implications for conservation planning. *Global Ecology and Biogeography*, **14**, 17–30.

Arita, H.T. & Rodriguez, P. (2002). Geographic range, turnover rate and the scaling of species diversity. *Ecography*, **25**, 541–550.

Arrhenius, O. (1921). Species and area. *Journal of Ecology*, **9**, 95–99.

Asher, J., Warren, M., Fox, R., Harding, P., Jeffcoate, G. & Jeffcoate, S. (2001). *The Millennium Atlas of Butterflies in Britain and Ireland*. Oxford University Press, Oxford.

Astorga, A., Oksanen, J., Luoto, M., Soininen, J., Virtanen, R. & Muotka, T. (2012). Distance decay of similarity in freshwater communities: do macro- and microorganisms follow the same rules? *Global Ecology and Biogeography*, **21**, 365–375.

Axelsen, J.B., Roll, U., Stone, L. & Solow, A. (2013). Species – area relationships always overestimate extinction rates from habitat loss. *Ecology*, **94**, 761–763.

Azaele, S., Cornell, S.J. & Kunin, W.E. (2012). Downscaling species occupancy from coarse spatial scales. *Ecological Applications*, **22**, 1004–1014.

Azaele, S., Maritan, A., Cornell, S.J., Suweis, S., Banavar, J.R., Gabriel, D. & Kunin, W.E. (2014). Towards a unified descriptive theory for spatial ecology : predicting biodiversity patterns across spatial scales. *Methods in Ecology and Evolution*, **6**, 324–332.

Baiser, B., Olden, J.D., Record, S., Lockwood, J.L. & McKinney, M.L. (2012). Pattern and process of biotic homogenization in the New Pangaea. *Proceedings of the Royal Society of London - Series B: Biological Sciences*, **279**, 4772–7.

Barbosa, A.M., Real, R. & Vargas, J.M. (2010). Use of coarse-resolution models of species' distributions to guide local conservation inferences. *Conservation Biology*, **24**, 1378–87.

Barton, P.S., Cunningham, S.A., Manning, A.D., Gibb, H., Lindenmayer, D.B. & Didham, R.K. (2013). The spatial scaling of beta diversity. *Global Ecology and Biogeography*, **22**, 639–647.

Beale, C.M., Brewer, M.J. & Lennon, J.J. (2014). A new statistical framework for the quantification of covariate associations with species distributions. *Methods in Ecology and Evolution*, **5**, 421–432.

Beck, J., Ballesteros-Mejia, L., Buchmann, C.M., Dengler, J., Fritz, S.A., Gruber, B., Hof, C., Jansen, F., Knapp, S., Kreft, H., Schneider, A.-K., Winter, M. & Dormann, C.F. (2012). What's on the horizon for macroecology? *Ecography*, **35**, 673–683.

Belmaker, J. & Jetz, W. (2011). Cross-scale variation in species richness-environment associations. *Global Ecology and Biogeography*, **20**, 464–474.

Berry, P.M., Dawson, T.P., Harrison, P. a & Pearson, R.G. (2002). Modelling potential impacts of climate change on the bioclimatic envelope of species in Britain and Ireland. *Global Ecology and Biogeography*, **11**, 453–462.

Bini, L.M., Diniz-Filho, J.A.F., Rangel, T.F.L.V.B., Bastos, R.P. & Pinto, M.P. (2006). Challenging Wallacean and Linnean shortfalls: knowledge gradients and conservation planning in a biodiversity hotspot. *Diversity and Distributions*, **12**, 475–482.

Blackburn, T.M., Cassey, P. & Gaston, K.J. (2006). Variations on a theme: Sources of heterogeneity in the form of the interspecific relationship between abundance and distribution. *Journal of Animal Ecology*, **75**, 1426–1439.

Borda-de-Água, L., Borges, P.A.V., Hubbell, S.P. & Pereira, H.M. (2012). Spatial scaling of species abundance distributions. *Ecography*, **35**, 549–556.

Borda-de-Agua, L., Hubbell, S.P. & McAllister, M. (2002). Species-area curves, diversity indices, and species abundance distributions: a multifractal analysis. *American Naturalist*, **159**, 138–55.

Bornand, C.N., Kéry, M., Bueche, L. & Fischer, M. (2014). Hide and seek in vegetation: time-to-detection is an efficient design for estimating detectability and occurrence. *Methods in Ecology and Evolution*, n/a–n/a.

Borregaard, M.K. & Rahbek, C. (2010). Causality of the relationship between geographic range size and species abundance. *The Quarterly Review of Biology*, **85**, 3–25.

Burns, F., Eaton, M.A., Gregory, R.D., Al Fulaij, N., August, T.A., Biggs, J., Bladwell, S., Brereton, T., Brooks, D., Clubbe, C., Dawson, J., Dunn, E., Edwards, B., Falk, S., Gent, T., Gibbons, D., Gurney, M., Haysom, K., Henshaw, S., Hodgetts, N., Isaac, N., McLaughlin, M., Musgrove, A., Noble, D., O'Mahony, E., Pacheco, M., Roy, D., Sears, J., Shardlow, M., Stringer, C., Taylor, A., Thompson, P., Walker, K., Walton, P., Willing, M., Wilson, J. & Wynde, R. (2013). State of Nature Report. The State of Nature partnership.

Butchart, S.H.M. (2010). Global Biodiversity : Indicators of Recent Declines. *Science*, **328**, 1164–1169.

Cardoso, P., Erwin, T.L., Borges, P.A. V & New, T.R. (2011). The seven impediments in invertebrate conservation and how to overcome them. *Biological Conservation*, **144**, 2647–2655.

Chalcraft, D.R. (2013). Changes in ecological stability across realistic biodiversity gradients depend on spatial scale. *Global Ecology and Biogeography*, **22**, 19–28.

Cham, S., Nelson, B., Parr, A., Prentice, S., Smallshire, D. & Taylor, P. (2014). *Atlas of Dragonflies in Britain and Ireland*. Field Studies Council, Telford, UK.

Chase, J.M. (2014). Spatial scale resolves the niche versus neutral theory debate. *Journal of Vegetation Science*, **25**, 319–322.

Chase, J.M. & Knight, T.M. (2013). Scale-dependent effect sizes of ecological drivers on biodiversity: why standardised sampling is not enough. *Ecology Letters*, **16 Suppl 1**, 17–26.

Chase, J.M. & Leibold, M.A. (2002). Spatial scale dictates the productivity-biodiversity relationship. *Nature*, **416**, 427–30.

Chave, J. (2013a). The problem of pattern and scale in ecology: what have we learned in 20 years? *Ecology letters*, **16**, 4–16.

Chave, J. (2013b). The problem of pattern and scale in ecology: what have we learned in 20 years? *Ecology Letters*, **2050**.

Chisholm, R.A. & Pacala, S.W. (2010). Niche and neutral models predict asymptotically equivalent species abundance distributions in high-diversity ecological communities. *Proceedings of the National Academy of Sciences of the United States of America*, **107**, 15821–15825.

Collen, B., Pettorelli, N., Baillie, J.E.M. & Durant, S.M. (2013). *Biodiversity Monitoring and Conservation: Bridging the Gap between Global Commitment and Local Action*. Wiley-Blackwell, Oxford, UK.

Conlisk, E., Bloxham, M., Conlisk, J., Enquist, B. & Harte, J. (2007). A new class of models of spatial distribution. *Ecological Monographs*, **77**, 269–284.

Conlisk, J., Conlisk, E., Kassim, A.R., Billick, I. & Harte, J. (2012). The shape of a species' spatial abundance distribution. *Global Ecology and Biogeography*, **21**, 1167–1178.

Cowley, M.J.R., Thomas, C.D., Roy, D.B., Wilson, R.J., Gutiérrez, D., Bulman, C.R., Quinn, R.M., Moss, D. & Gaston, K.J. (2001). Density – distribution relationships in British butterflies . I . The effect of mobility and spatial scale. *Journal of Animal Ecology*, **70**, 410–425.

Cunningham, R.B., Lindenmayer, D.B., Crane, M., Michael, D.R., Barton, P.S., Gibbons, P., Okada, S., Ikin, K. & Stein, J.A.R. (2014). The law of diminishing returns: woodland birds respond to native vegetation cover at multiple spatial scales and over time. *Diversity and Distributions*, **20**, 59–71.

Dennis, R.L.H., Shreeve, T.G., Isaac, N.J.B., Roy, D.B., Hardy, P.B., Fox, R. & Asher, J. (2006). The effects of visual apparency on bias in butterfly recording and monitoring. *Biological Conservation*, **128**, 486–492.

Diniz-Filho, J.A.F., De Marco Jr, P. & Hawkins, B.A. (2010). Defying the curse of ignorance: perspectives in insect macroecology and conservation biogeography. *Insect Conservation and Diversity*, **3**, 172–179.

Ferrier, S., Manion, G., Elith, J. & Richardson, K. (2007). Using generalized dissimilarity modelling to analyse and predict patterns of beta diversity in regional biodiversity assessment. *Diversity and Distributions*, **13**, 252–264.

Field, R., Hawkins, B. a., Cornell, H. V., Currie, D.J., Diniz-Filho, J.A.F., Guégan, J.F., Kaufman, D.M., Kerr, J.T., Mittelbach, G.G., Oberdorff, T., O'Brien, E.M. & Turner, J.R.G. (2009). Spatial species-richness gradients across scales: A meta-analysis. *Journal of Biogeography*, **36**, 132–147.

Fitzpatrick, M.C., Sanders, N.J., Normand, S., Svenning, J.-C., Ferrier, S., Gove, A.D. & Dunn, R.R. (2013). Environmental and historical imprints on beta diversity: insights from variation in rates of species turnover along gradients. *Proceedings of the Royal Society - Series B: Biological Sciences*, **280**, 20131201.

Fortin, M.-J. & Dale, M.R.T. (2005). *Spatial Analysis: A Guide for Ecologists*. Cambridge University Press, Cambridge.

Garzon-Lopez, C.X., Jansen, P. a., Bohlman, S. a., Ordonez, A. & Olff, H. (2014). Effects of sampling scale on patterns of habitat association in tropical trees. *Journal of Vegetation Science*, **25**, 349–362.

Gaston, K.J., Blackburn, T.I.M.M., Greenwood, J.D., Gregory, R.D., Quinn, M. & Lawton, J.H. (2000). Abundance - occupancy relationships. *Journal of Applied Ecology*, **37**, 39–59.

Gleason, H.A. (1922) On the relation between species and area. Ecology, **3**, 158–162.

Green, J.L., Harte, J. & Ostling, A. (2003). Species richness, endemism, and abundance patterns: tests of two fractal models in a serpentine grassland. *Ecology Letters*, **6**, 919–928.

Green, J.L. & Plotkin, J.B. (2007). A statistical theory for sampling species abundances. *Ecology Letters*, **10**, 1037–45.

Grilli, J., Azaele, S., Banavar, J. & Maritan, A. (2012). Spatial aggregation and the species-area relationship across scales. *Journal of Theoretical Biology*, 1–16.

Guerrero, A.M., McAllister, R.R.J., Corcoran, J. & Wilson, K. a. (2013). Scale mismatches, conservation planning, and the value of social-network analyses. *Conservation Biology*, **27**, 35–44.

Gunton, R.M., Klenke, R.A., Paloniemi, R., Gavish, Y., Marsh, C.J., Kunin, W.E. & Henle, K. (2014). The meaning of 'scale'. *Scaling in Ecology and Biodiversity Conservation* (eds K. Henle, S.G. Potts, W.E. Kunin, Y.G. Matsinos, J. Similä, J.D. Pantis, V. Grobelnik, L. Penev & J. Settele), pp. 19–22. Pensoft Publishers, Sofia, Bulgaria.

Gunton, R.M. & Kunin, W.E. (2007). Density effects at multiple scales in an experimental plant population. *Journal of Ecology*, **95**, 435–445.

Gunton, R.M. & Kunin, W.E. (2009). Density-dependence at multiple scales in experimental and natural plant populations. *Journal of Ecology*, **97**, 567–580.

Haby, N.A., Prowse, T.A.A., Gregory, S.D., Watts, M.J., Delean, S., Fordham, D.A., Foulkes, J. & Brook, B.W. (2013). Scale dependency of metapopulation models used to predict climate change impacts on small mammals. *Ecography*, **36**, 832–841.

Hanski, I. (1982). On patterns of temporal and spatial variation in animal populations. *Annales Zoologici Fennici*, **19**, 21–37.

Harte, J. (2011). *Maximum Entropy and Ecology: A Theory of Abundance, Distribution, and Energetics*. Oxford University Press, Oxford, UK.

Harte, J., Conlisk, E., Ostling, A., Green, J.L. & Smith, A.B. (2005). A theory of spatial structure in ecological communities at multiple spatial scales. *Ecological Monographs*, **75**, 179–197.

Harte, J. & Kinzig, A. (1997). On the implications of species-area relationships for endemism, spatial turnover and food web patterns. *Oikos*, **80**, 417–427.

Harte, J. & Kitzes, J. (2015). Inferring Regional-Scale Species Diversity from Small-Plot Censuses. *Plos One*, **10**, e0117527.

Harte, A.J., Zillio, T., Conlisk, E., Smith, A.B. & Harte, J. (2008). Maximum Entropy and the State-Variable Approach to Macroecology. *Ecology*, **89**, 2700–2711.

Hartley, S. & Kunin, W.E. (2003). Scale Dependency of Rarity, Extinction Risk, and Conservation Priority. *Conservation Biology*, **17**, 1559–1570.

Hartley, S., Kunin, W.E., Lennon, J.J. & Pocock, M.J.O. (2004). Coherence and discontinuity in the scaling of species' distribution patterns. *Proceedings of the Royal Society of London - Series B: Biological Sciences*, **271**, 81–8.

Hassall, C. & Thompson, D.J. (2010). Accounting for recorder effort in the detection of range shifts from historical data. *Methods in Ecology and Evolution*, **1**, 343–350.

Hassall, C., Thompson, D.J. & Harvey, I.F. (2010). The impact of climate-induced distributional changes on the validity of biological water quality metrics. *Environmental Monitoring and Assessment*, **160**, 451–456.

Hawkins, B.A., Diniz-Filho, J.A.F., Jaramillo, C.A. & Soeller, S.A. (2007). Climate, niche conservatism, and the global bird diversity gradient. *The American Naturalist*, **170**, S16–27.

He, F. & Gaston, K.J. (2007). Estimating Abundance from Occurrence: An Underdetermined Problem. *The American Naturalist*, **170**, 655–659.

He, F. & Gaston, K.J. (2000a). Estimating Species Abundance from Occurrence. *American Naturalist*, **156**, 553–559.

He, F. & Gaston, K.J. (2000b). Occupancy-abundance relationships and sampling scales. *Ecography*, **23**, 503–511.

He, F., Gaston, K.J. & Wu, J. (2002). On species occupancy-abundance models. *Ecoscience*, **9**, 119–126.

He, F. & Hubbell, S. (2003). Percolation Theory for the Distribution and Abundance of Species. *Physical Review Letters*, **91**, 1–4.

He, F. & Hubbell, S.P. (2011). Species-area relationships always overestimate extinction rates from habitat loss. *Nature*, **473**, 368–71.

Hickling, R., Roy, D.B., Hill, J.K., Fox, R. & Thomas, C.D. (2006). The distributions of a wide range of taxonomic groups are expanding polewards. *Global Change Biology*, **12**, 450–455.

Holland, J.E.Y.D., Bert, D.G. & Fahrig, L. (2004). Determining the Spatial Scale of Species ' Response to Habitat. *BioScience*, **54**, 227–233.

Holt, A.R., Gaston, K.J. & He, F. (2002). Occupancy-abundance relationships and spatial distribution : A review. *Basic and Applied Ecology*, **13**, 1–13.

Hubbell, S.P. (2001). *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University Press, Oxford.

Hui, C., Veldtman, R. & McGeoch, M.A. (2010). Measures, perceptions and scaling patterns of aggregated species distributions. *Ecography*, **33**, 95–102.

Iknayan, K.J., Tingley, M.W., Furnas, B.J. & Beissinger, S.R. (2014). Detecting diversity: Emerging methods to estimate species diversity. *Trends in Ecology and Evolution*, **29**, 97–106.

Isaac, N.J.B. & Pocock, M.J.O. (2015). Bias and information in biological records. **early view**.

Isaac, N.J.B., van Strien, A.J., August, T.A., de Zeeuw, M.P. & Roy, D.B. (2014). Statistics for citizen science: extracting signals of change from noisy ecological data. *Methods in Ecology and Evolution*, **5**, 1052–1060.

Jackson, H.B. & Fahrig, L. (2014). Are ecologists conducting research at the optimal scale? *Global Ecology and Biogeography*, **24**, 52–63.

Jetz, W., McPherson, J.M. & Guralnick, R.P. (2012). Integrating biodiversity distribution knowledge: toward a global map of life. *Trends in Ecology & Evolution*, **27**, 151–9.

Jones, J.P.G., Collen, B., Atkinson, G., Baxter, P.W.J., Bubb, P., Illian, J.B., Katzner, T.E., Keane, A., Loh, J., Mcdonald-Madden, E., Nicholson, E., Pereira, H.M., Possingham, H.P., Pullin, A.S., Rodrigues, A.S.L., Ruiz-Gutierrez, V., Sommerville, M. & Milner-Gulland, E.J. (2011). The Why, What, and How of Global Biodiversity Indicators Beyond the 2010 Target. *Conservation Biology*, **25**, 450–457.

Jovani, R. & Tella, J.L. (2007). Fractal bird nest distribution produces scale-free colony sizes. *Proceedings of the Royal Society of London - Series B: Biological Sciences*, **274**, 2465–9.

Jurasinski, G., Retzer, V. & Beierkuhnlein, C. (2009). Inventory, differentiation, and proportional diversity: a consistent terminology for quantifying species diversity. *Oecologia*, **159**, 15–26. Retrieved August 30, 2011, from http://www.ncbi.nlm.nih.gov/pubmed/18953572

Karlson, R.H., Cornell, H. V & Hughes, T.P. (2007). Aggregation influences coral species richness at multiple spatial scales. *Ecology*, **88**, 170–7.

Keil, P., Biesmeijer, J.C., Barendregt, A., Reemer, M. & Kunin, W.E. (2011). Biodiversity change is scale-dependent: an example from Dutch and UK hoverflies (Diptera, Syrphidae). *Ecography*, **34**, 392–401.

Keith, S.A., Webb, T.J., Böhning-Gaese, K., Connolly, S.R., Dulvy, N.K., Eigenbrod, F., Jones, K.E., Price, T., Redding, D.W., Owens, I.P.F. & Isaac, N.J.B. (2012). What is macroecology? *Biology letters*, **8**, 904–6.

Kéry, M. & Royle, J.A. (2008). Hierarchical Bayes estimation of species richness and occupancy in spatially replicated surveys. *Journal of Applied Ecology*, **45**, 589–598.

Kinzig, A.P. & Harte, J. (2000). Implications of endemics-area relationships for estimates of species extinctions. *Ecology*, **81**, 3305–3311.

Kissling, W.D., Dormann, C.F., Montoya, M., McInerny, G.J. & Ku, I. (2011). Towards novel approaches to modelling biotic interactions in multispecies assemblages at large spatial extents. *Journal of Biogeography*, **39**, 2163–2178.

De Knegt, H.J., van Langevelde, F., Coughenour, M.B., Skidmore, A.K., de Boer, W.F., Heitkönig, I.M.A., Knox, N.M., Slotow, R., van der Waal, C. & Prins, H.H.T. (2010). Spatial autocorrelation and the scaling of species-environment relationships. *Ecology*, **91**, 2455–65. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/20836467

Kotliar, N.B. & Wiens, J.A. (1990). Multiple scales of patchiness and patch structure : a hierarchical framework for the study of heterogeneity. *Oikos*, **59**, 253–260.

Kunin, W.E. (1998). Extrapolating Species Abundance Across Spatial Scales. *Science*, **281**, 1513–1515.

Kunin, W.E., Hartley, S. & Lennon, J.J. (2000). Scaling Down : On the Challenge of Estimating Abundance from Occurrence Patterns. *American Naturalist*, **156**, 560–566.

Lawton, J.H. (1999). Are there general laws in ecology? *Oikos*, **84**, 177–192.

Legendre, P. & Fortin, M.-J. (1989). Spatial pattern and ecological analysis. *Vegetatio*, **80**, 107–138.

Lengyel, S., Déri, E., Varga, Z., Horváth, R., Tóthmérész, B., Henry, P.-Y., Kobler, A., Kutnar, L., Babij, V., Seliškar, A., Christia, C., Papastergiadou, E., Gruber, B. & Henle, K. (2008). Habitat monitoring in Europe: a description of current practices. *Biodiversity and Conservation*, **17**, 3327–3339.

Levin, S.A. (1992). The problem of pattern and scale in ecology. *Ecology*, **73**, 1943–1967.

Lomolino, M. V. & Heaney, L.R. (2004). *Frontiers in Biogeography: New Directions in the Geography of Nature* (M. V. Lomolino & L.R. Heaney, Eds.). Sinauer Associates, Sunderland, Massachusetts.

Mace, G.M. & Baillie, J.E.M. (2007). The 2010 biodiversity indicators: Challenges for science and policy. *Conservation Biology*, **21**, 1406–1413.

Magurran, A.E. (2005). *Measuring Biological Diversity*. Blackwell Science Ltd, Oxford, UK.

Magurran, A.E. & McGill, B.J. (Eds.). (2011). *Biological Diversity: frontiers in measurement and assessment*. Oxford University Press, Oxford, UK.

McGill, B.J. (2011). Linking biodiversity patterns by autocorrelated random sampling. *American Journal of Botany*, **98**, 481–502.

McGill, B.J. (2010). Towards a unification of unified theories of biodiversity. *Ecology Letters*, **13**, 627–42.

McGill, B.J., Etienne, R.S., Gray, J.S., Alonso, D., Anderson, M.J., Benecha, H.K., Dornelas, M., Enquist, B.J., Green, J.L., He, F., Hurlbert, A.H., Magurran, A.E., Marquet, P.A., Maurer, B.A., Ostling, A., Soykan, C.U., Ugland, K.I. & White, E.P. (2007). Species abundance distributions: moving beyond single prediction theories to integration within an ecological framework. *Ecology Letters*, **10**, 995–1015.

McMahon, S.M. & Diez, J.M. (2007). Scales of association: hierarchical linear models and the measurement of ecological systems. *Ecology Letters*, **10**, 437–52.

Miller, J.R., Turner, M.G., Smithwick, E. a. H., Dent, C.L. & Stanley, E.H. (2004). Spatial Extrapolation: The Science of Predicting Ecological Patterns and Processes. *BioScience*, **54**, 310.

Mora, C., Tittensor, D.P., Adl, S., Simpson, A.G.B. & Worm, B. (2011). How many species are there on earth and in the ocean? *PLoS Biology*, **9**, 1–8.

Morlon, H., Chuyong, G., Condit, R., Hubbell, S., Kenfack, D., Thomas, D., Valencia, R. & Green, J.L. (2008). A general framework for the distance-decay of similarity in ecological communities. *Ecology Letters*, **11**, 904–17.

Nekola, J.C. & Brown, J.H. (2007). The wealth of species: ecological communities, complex systems and the legacy of Frank Preston. *Ecology Letters*, **10**, 188–96.

Nekola, J.C. & White, P.S. (1999). The distance decay of similarity in biogeography and ecology. *Journal of Biogeography*, **26**, 867–878.

Päivinen, J., Grapputo, A., Kaitala, V., Komonen, A., Kotiaho, J.S., Saarinen, K. & Wahlberg, N. (2005). Negative density-distribution relationship in butterflies. *BMC Biology*, **3**, 5.

Palmer, M.W. (2007). Species-area curves and the geometry of nature in. *Scaling biodiversity. Cambridge University Press, Cambridge, UK* (eds D. Storch, P.A. Marquet & J.H. Brown), pp. 15–31. Cambridge University Press, New York.

Paloniemi, R., Apostolopoulou, E., Primmer, E., Grodzinska-Jurcak, M., Henle, K., Ring, I., Kettunen, M., Tzanopoulos, J., Potts, S., van den Hove, S., Marty, P., McConville, A. & Simila, J. (2012). Biodiversity conservation across scales: lessons from a science–policy dialogue. *Nature Conservation*, **2**, 7–19.

Pan, X. (2013). Fundamental equations for species-area theory. *Scientific Reports*, **3**, 1334.

Passy, S.I. (2012). A hierarchical theory of macroecology. *Ecology Letters*, **15**, 923–1070.

Pelosi, C., Goulard, M. & Balent, G. (2010). The spatial scale mismatch between ecological processes and agricultural management: Do difficulties come from underlying theoretical frameworks? *Agriculture, Ecosystems & Environment*, **139**, 455–462.

Pereira, H.M., Belnap, J., Brummit, N., Collen, B., Ding, H., Gonzalez-Espinosa, M., Gregory, R.D., Honrado, J., Jongman, R.H.G., Juillard, R., McRae, L., Proenca, V., Rodrigues, P., Opige, M., Rodriguez, J.P., Schmeller, D.S., van Swaay, C. & Vieira, C. (2010). Global biodiversity monitoring. *Frontiers in Ecology and the Environment*, **8**, 458–459.

Pocock, M.J., Chapman, D.S., Sheppard, L.J. & Roy, H.E. (2014). A Strategic Framework to Support the Implementation of Citizen Science for Environmental Monitoring. Final Report to SEPA. Centre for Ecology & Hydrology, Wallingford, Oxfordshire.

Potts, M.D., Davies, S.J., Bossert, W.H., Tan, S. & Nur Supardi, M.N. (2004). Habitat heterogeneity and niche structure of trees in two tropical rain forests. *Oecologia*, **139**, 446–53.

Powney, G.D. (2013). Understanding drivers of species distribution change : a trait-based approach. PhD Thesis. Imperial College London, UK.

Purvis, A. & Hector, A. (2000). Getting the measure of biodiversity. *Nature*, **405**, vol 405 no. 6783.

Rahbek, C. (2004). The role of spatial scale and the perception of large-scale species-richness patterns. *Ecology Letters*, **8**, 224–239.

Rayburn, A.P. & Schupp, E.W. (2013). Effects of community- and neighborhood-scale spatial patterns on semi-arid perennial grassland community dynamics. *Oecologia*, **172**, 1137–1145.

Robertson, M.P., Cumming, G.S. & Erasmus, B.F.N. (2010). Getting the most out of atlas data. *Diversity and Distributions*, **16**, 363–375.

Sandel, B. (2015). Towards a taxonomy of spatial scale-dependence. *Ecography*, **38**, 358–369.

Sandel, B. & Smith, A.B. (2009). Scale as a lurking factor: Incorporating scale-dependence in experimental ecology. *Oikos*, **118**, 1284–1291.

Schneider, D.C. (2001). The Rise of the Concept of Scale in Ecology. *BioScience*, **51**, 545–553.

Schwartz, M.W. (1999). Choosing the Appropriate Scale of Reserves for Conservation. *Annual Review of Ecology and Sytematics*, **30**, 83–108.

Secretariat of the Convention on Biological Diversity. (2010). Biodiversity indicators and the 2010 Target: Experiences and lessons learnt from the 2010 Biodiversity Indicators Partnership. *Technical Series*, **No. 53**.

Seidler, T.G. & Plotkin, J.B. (2006). Seed dispersal and spatial pattern in tropical trees. *PLoS Biology*, **4**, e344.

Silvertown, J., Harvey, M., Greenwood, R., Dodd, M., Rosewell, J., Rebelo, T., Ansine, J. & Mcconway, K. (2015). Crowdsourcing the identification of organisms : A case-study of iSpot. *ZooKeys*, **146**, 125–146.

Sizling, A.L. & Storch, D. (2007). Geometry of species distributions: random clustering and scale invariance. *Scaling Biodiversity* pp. 77–99. Cambridge University Press, Cambridge.

Sizling, A.L. & Storch, D. (2004). Power-law species-area relationships and self-similar species distributions within finite areas. *Ecology Letters*, **7**, 60–68.

Šizling, A.L., Storch, D., Reif, J. & Gaston, K.J. (2009). Invariance in species-abundance distributions. *Theoretical Ecology*, **2**, 89–103.

Smith, F.A., Lyons, S.K., Morgan Ernest, S.K. & Brown, J.H. (2008). Macroecology: more than the division of food and space among species on continents. *Progress in Physical Geography*, **32**, 115–138.

Soberón, J. (2007). Grinnellian and Eltonian niches and geographic distributions of species. *Ecology letters*, **10**, 1115–23.

Soininen, J., Lennon, J.J. & Hillebrand, H. (2007a). A Multivariate Analysis of Beta Diversity across Organisms and Environments. *Ecology*, **88**, 2830–2838.

Soininen, J., McDonald, R. & Hillebrand, H. (2007b). The distance decay of similarity in ecological communities. *Ecography*, **30**, 3–12.

Stevens, R.D. (2006). Historical processes enhance patterns of diversity along latitudinal gradients. *Proceedings of the Royal Society - Series B: Biological Sciences*, **273**, 2283–9.

Stevens, G.C. (1989). The Latitudinal gradient in geographical range - how so many species coexist in the tropics. *American Naturalist*, **133**, 240–256.

Stoll, P. & Prati, D. (2001). Intraspecific Aggregation Alters Competitive Interactions in Experimental Plant Communities. *Ecology*, **82**, 319–327.

Storch, D., Keil, P. & Jetz, W. (2012). Universal species-area and endemics-area relationships at continental scales. *Nature*, **488**, 78–83.

Storch, D., Marquet, P.A. & Brown, J.H. (2007). *Scaling Biodiversity*. Cambridge University Press, Cambridge.

Storch, D., Sizling, A.L., Reif, J., Polechova, J., Sizlingova, E. & Gaston, K.J. (2008). The quest for a null model for macroecological patterns: geometry of species distributions at multiple spatial scales. *Ecology Letters*, **11**, 771–84.

Van Strien, A.J., Termaat, T., Kalkman, V., Prins, M., Knijf, G., Gourmand, A.-L., Houard, X., Nelson, B., Plate, C., Prentice, S., Regan, E., Smallshire, D., Vanappelghem, C. & Vanreusel, W. (2013). Occupancy modelling as a new approach to assess supranational trends using opportunistic data: a pilot study for the damselfly Calopteryx splendens. *Biodiversity and Conservation*, **22**, 673–686.

Szabo, J.K., Vesk, P.A., Baxter, P.W.J. & Possingham, H.P. (2010). Regional avian species declines estimated from volunteer-collected long-term data using List Length Analysis. *Ecological Applications*, **20**, 2157–69.

Theobald, E.J., Ettinger, A.K., Burgess, H.K., DeBey, L.B., Schmidt, N.R., Froehlich, H.E., Wagner, C., HilleRisLambers, J., Tewksbury, J., Harsch, M. a. & Parrish, J.K. (2015). Global change and local solutions: Tapping the unrealized potential of citizen science for biodiversity research. *Biological Conservation*, **181**, 236–244.

Tjørve, E. (2003). Shapes and functions of species – area curves: a review of possible models. *Journal of Biogeography*, **30**, 827–835.

Townsend Peterson, A., Soberon, J., Pearson, R., Anderson, R.P., Martinez-Meyer, E., Nakamura, M. & Araujo, M.B. (2011). *Ecological Niches and Geographical Distributions*. Princeton University Press, Oxford.

Ugland, K.I., Gray, J.S. & Ellingsen, K.E. (2003). The species-accumulation curve and estimation of species richness. *Journal of Animal Ecology*, **72**, 888–897.

Ulrich, W., Ollik, M. & Ugland, K.I. (2010). A meta-analysis of species-abundance distributions. *Oikos*, **119**, 1149–1155.

Warren, P.H. & Gaston, K.J. (2013). Interspecific abundance-occupancy relationships: a test of mechanisms using microcosms. *Journal of Animal Ecology*, **66**, 730–742.

Webb, T.J., Freckleton, R.P. & Gaston, K.J. (2012). Characterizing abundance – occupancy relationships : there is no artefact. *Global Ecology and Biogeography*, **21**, 952–957.

White, E.P., Thibault, K.M. & Xiao, X. (2012). Characterizing species abundance distributions across taxa and ecosystems using a simple maximum entropy model. *Ecology*, **93**, 1772–8.

Whittaker, R.H. (1972). Evolution and Measurement of Species Diversity. *Taxon*, **21**, 213–251.

Whittaker, R.H. (1960). Vegetation of the Siskiyou Mountains , Oregon and California. *Ecological Monographs*, **30**, 280–338.

Whittaker, R.., Araujo, M.B., Jepson, P., Ladle, R.J., Watson, J.E.M. & Willis, K.J. (2005). Conservation biogeography: asessment and prospect. *Diversity and Distributions*, **11**, 3–23.

Wiegand, T. & Moloney, K.A. (2004). Rings , circles , and null-models for point pattern analysis in ecology. *Oikos*, **104**, 209–229.

Wiens, J.. (1989). Spatial scaling in ecology. *Functional Ecology*, **3**, 385–397.

Woodcock, B.A., Potts, S.G., Pilgrim, E., Ramsay, A.J., Tscheulin, T., Parkinson, A., Smith, R.E.N., Gundrey, A.L., Brown, V.K. & Tallowin, J.R. (2007). The potential of grass field margin management for enhancing beetle diversity in intensive livestock farms. *Journal of Applied Ecology*, **44**, 60–69.

Wu, J. & Harbin, L. (2006). Concepts of scale and scaling. *Scaling and Uncertainty analysis in Ecology* (eds J. Wu, K.B. Jones, H. Li & O.L. Loucks), pp. 3–15. Springer, Dordrecht, The Netherlands.

Chapter 2
Can coarse-grain patterns in insect atlas data predict local occupancy?

2.1 Abstract

Species atlases provide an economical way to collect data with national coverage, but are typically too coarse-grained to monitor fine-grain patterns in rarity, distribution and abundance. I test the performance of ten downscaling models in extrapolating occupancy across two orders of magnitude. To provide a greater challenge to downscaling models, I extend previous downscaling tests with plants to highly mobile insect taxa (Odonata) with a life history that is tied to freshwater bodies for reproduction. I investigate the species-level correlates of predictive accuracy for the best performing model to understand whether traits driving spatial structure can cause interspecific variation in downscaling success. Occupancy data for 38 British Odonata species were extracted from the Dragonfly Recording Network (DRN). Occupancy at grains ≥ 100 km2 was used as training data to parameterize ten downscaling models. Predicted occupancy at the 25, 4 and 1 km2 grains was compared to observed data at corresponding grains. Model predictive error was evaluated across species and grains. The Hui model gave the most accurate downscaling predictions across 114 species:grain combinations and the best predictions for 14 of the 38 species, despite being the only model using information at a single spatial grain. The occupancy–area relationship was sigmoidal in shape for most species. Species' distribution type and dispersal ability explained over half of the variation in downscaling predictive error at the species level. Species with a climatic range limit in Britain were poorly predicted compared with other distribution types, and high dispersal ability was associated with relatively poor downscaling predictions. These results suggest that downscaling models, using widely available coarse-grain atlas data, provide reasonable estimates of fine-grain occupancy, even for insect taxa with strong spatial structure. Linking species-level traits with predictive accuracy reveals general principles about when downscaling will be successful.

2.2 Introduction

The lack of fine-grain data over large spatial extents is problematic for accurate monitoring of threatened species and limits our theoretical understanding of biodiversity patterns (McGill 2010a; b; Jetz *et al.* 2012; Beck *et al.* 2012; Keith *et al.* 2012). Species‘ distributions are typically mapped in the form of atlases derived from spatially explicit, opportunistic occurrence records for a specific taxanomic group within a defined geographic extent and time period (Robertson *et al.* 2010). Atlases use coarse grain sizes to minimise pseudo-absences (false absences, or omission errors), at a cost of including large areas where the species is actually absent (commission errors: Boitani *et al*., 2011). However, distribution size is highly scale-dependent (Kunin 1998), such that coarse-grain occupancy is a poor predictor of abundance (Hartley & Kunin 2003).

Recently, ecologists have begun to realise that the scale-dependency of species distributions can be described statistically and even extrapolated across scales (Kunin *et al.* 2000; He & Gaston 2000b; He *et al.* 2002; Hui *et al.* 2006; He & Condit 2007), thus helping to address this fine-grain data deficit and improve our assessment of rarity and extinction risk (Mace *et al.* 2008). Specifically, the occupancy-area relationship (OAR, following the terminology in McGill, 2010b) describes how occupancy (the proportion of grid cells where a species is present) increases with grain size (the area of each grid cell). Elsewhere, closely related relationships are the scale-area curve (Kunin 1998; Veldtman *et al.* 2010), area-area curve (He & Gaston 2000b), range-area curve (Green *et al.* 2003b), scaling pattern of occupancy (Hui *et al.* 2006; Hui 2009) and p-area curve (Storch *et al.* 2008). As the grain used to record species’ presences becomes coarser, empty fine-grain cells merge with neighbouring occupied cells and a greater proportion of the study region appears occupied. There is considerable variation in the shape and slope of the OAR among species, driven by species’ overall abundances, patterns of intraspecific aggregation (Cowley *et al.* 2001b; Storch *et al.* 2008; Conlisk *et al.* 2009; Gaston & He 2011) and the logical constraint that no fewer than one cell can be occupied at a given scale (Fig. 2.1). The local slope of the OAR contains information about intraspecific aggregation: a steep local slope between two spatial grains indicates a species occurs in few fine-grain cells within each occupied coarse grain cell (a sparse, fragmented distribution). A shallow local slope indicates the species is present in many fine-grain cells within each coarse grain cell (an aggregated, contiguous distribution) (Wilson *et al.* 2004; Veldtman *et al.* 2010). Downscaling models have been developed to describe the OAR, mathematically, without reference to any biologically meaningful covariates. As noted above, species occupancy at fine spatial grains is often underestimated when using fine grain data, because there are many false absences in species occurrence records. Downscaling models attempt to provide a solution to this problem, by parameterising the portion of the OAR that is least prone to false absences and identifying a phenomenological relationship between neighbouring spatial grains which can then be extrapolated to finer spatial grains. Although downscaling models do not describe the processes shaping aggregation patterns, they are nonetheless able to capture interspecific variation in the shape of the OAR (Azaele *et al.* 2012).

Downscaling models have been tested (using training data at coarse grains and a test data set at fine grains) for 73 species of rare plants in mainland Britain (Kunin 1998; Kunin *et al.* 2000), 92 species of grasses in mainland Britain (Kunin *et al.* 2000), 301 tree species in a 0.5 km^2 tropical rainforest plot in Barro Colorado Island, Panama (He & Condit 2007), 824 tree species in 0.5 km^2 tropical rainforest plot in Pasoh, Malaysia (He & Gaston 2000b), passerine birds in Bedfordshire (He & Gaston 2000b), 6 large mammalian herbivores in the 13912 km^2 Kruger National Park (Tosh *et al.* 2004) and southern African bird species (Lennon *et al.* 2007; Hui *et al.* 2009). Azaele *et al.* (2012) tested the performance of 9 downscaling models across several orders of magnitude in grain size using multi-scale occupancy data for 16 rare British plant species. The Thomas model, derived from a clustered Poisson point process, provided the most accurate and unbiased estimates of fine-grain occupancy across the 16 species, despite the absence of information about the spatial positions of occupied cells. Virtually all of these tests are for plants and in most cases three or fewer of the available downscaling methods were applied to the data. The range of extrapolation varies greatly among studies from 25-fold (Kunin 1998) to four orders of magnitude (Azaele *et al.* 2012). In the absence of a mechanistic understanding of the OAR (but see McGill & Nekola, 2010; McGill, 2011), it is important to establish whether downscaling models are general enough to describe all observed forms of the OAR and to extend comparative tests of model performance to taxa with a very different set of dispersal abilities, habitat requirements and spatial structures.

I identify four traits, measured at the level of the species, which I predict will lead to interspecific variation in the shape of the OAR (and therefore downscaling success). A species' distribution type (widespread, range limited, local-sparse or local-aggregated) is a broad descriptor of interspecific variation in the number and spatial arrangement of occupied cells (Supplementary Material section 2.7.5). On a more mechanistic level, patterns of intraspecific aggregation depend on the interplay between dispersal ability and the patchy distribution of suitable (micro) climate and habitat (Hubbell 2001; Green & Plotkin 2007; Storch *et al.* 2008; McGill 2010b). The other three traits (dispersal ability, habitat breadth and range change) are chosen for their relationship to those processes influencing intraspecific aggregation and variation in the shape and slope of the OAR (Fig. 2.1). Range change is here defined as a measure of a species' increase or decrease in distribution size within a defined time period. I describe the metric used to measure range change in section 2.3.3.

Here, I present a comparison of downscaling methods applied to coarse-grain records of British Odonata and extrapolate occupancy through two orders of magnitude in spatial grain. These distribution data are used to investigate 1) which downscaling models perform best in predicting fine-grain occupancy from coarse-grain atlas data, and 2) whether species traits can explain interspecific variation in predictive success. These analyses extend knowledge gained in previous downscaling studies by testing for general principles in our ability to predict occupancy at fine spatial grains.

2.3 Methods

2.3.1 Odonata distribution data

Occupancy data for British Odonata were extracted from the Dragonfly Recording Network (DRN) held by the British Dragonfly Society (BDS). The DRN data comprise over 1 million records on 34 510 spatially referenced 1km^2 cells in mainland Britain. OARs based on eight spatial grains were estimated for a total of 38 species, comprising the resident breeding Odonata species in the UK (Supplementary Material section 2.7.1). Spatial variation in recording intensity, geographical biases and pseudo-absences must be acknowledged when estimating species occupancies from presence-only, opportunistic occurrence records (van Strien *et al.* 2013). To address the issue of pseudo-absences, I included only cells in which at least one species had been recorded (as evidence of a visit) and assumed species not recorded in a grid cell were absent. This threshold is intended to address the trade-off between the number of false absences and the exclusion of large amounts of fine-grain data (Supplementary Material section 2.7.3). Cells with < 30% land cover (≥ 70% sea) were excluded at each spatial grain as a trade-off between the total amount of land represented by cells in the analysis and the total number of cells available for analysis at coarse grains. The

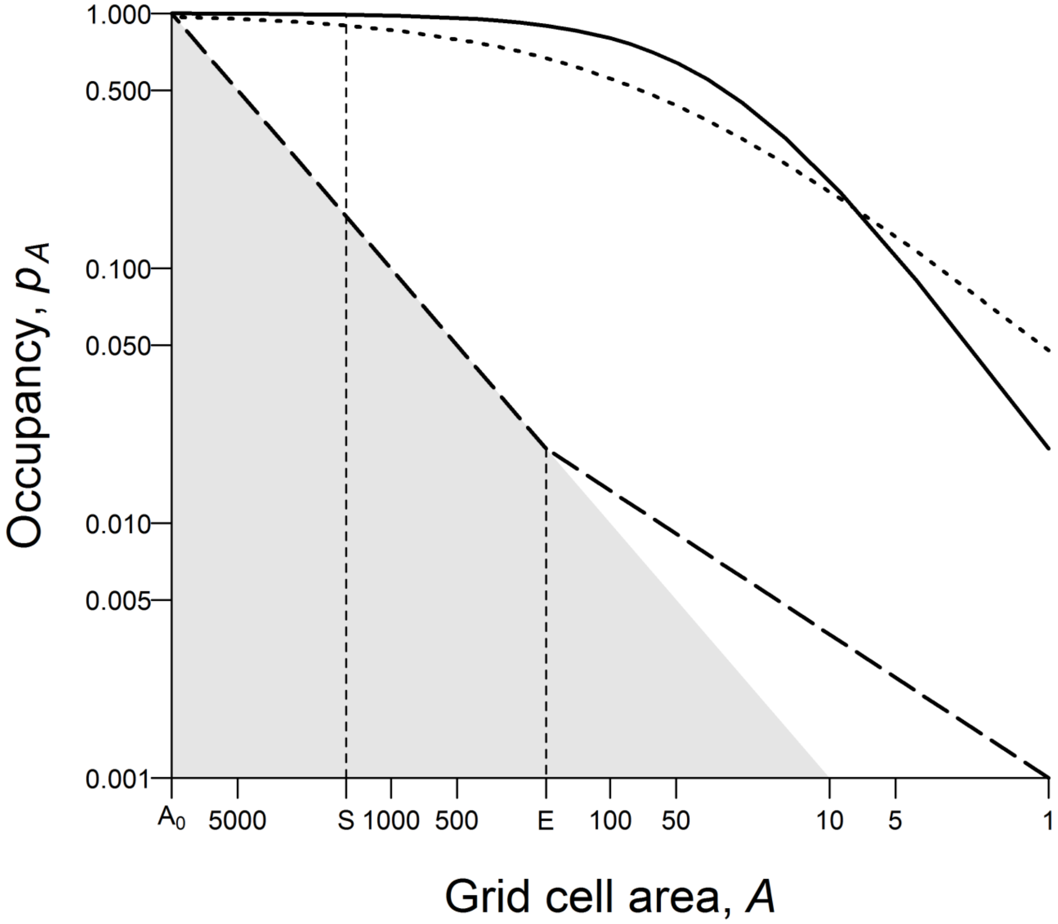

Fig. 2.1 Occupancy-area relationships (OAR) for three hypothetical species.

There are a wide variety of shapes and slopes of the OAR among species, reflecting both the extent of a species' distribution within the study region and the intensity of intraspecific aggregation. Here, the differences in slopes cause the species' curves represented by the solid black line and the dotted black line to cross over, demonstrating that the grain at which occupancy is measured can change our perception of which species is rarest. For widespread species (solid black line) within the study region, the curve becomes shallower as the sampling grain approaches the extent of the study region, A0. At grains coarser than the point of saturation, S, the species represented by the solid black line occurs in all cells (e.g. occupancy = 1). For a species that is restricted to some portion of the study region (dashed line), an inflection point will be seen at the finest grain to contain the entire distribution within a single grid cell (the point of endemism, E). Saturated and endemic grains add no information about the scaling of occupancy for the purposes of downscaling. Occupancy cannot fall within the shaded grey area, which represents the region where occupancy < A/A0 and equates to a species occurring in less than one cell in the study region (adapted from Azaele et al., 2012).

spatial references of occupied grid cells at 1km^2 were coarsened to obtain species' occupancies at the 4, 25, 100, 144, 400, 1600, 6400 km^2 grains to estimate the OAR for each species. A species' occupancy was calculated as the proportion of the total number of sampled grid cells in which the focal species occurs. Data cleaning, manipulation and calculation of species occupancies at multiple scales was performed in R version 2.15.1 (R Core Development Team 2014).

2.3.2 Downscaling

Ten downscaling models (Table 2.1) were fitted to occupancy data at coarse grains ($\geq$ 100km^2) for the 38 British Odonata species. This reflects the typical 100km^2 grain of atlas data in the UK. Models 2 - 9 (Table 2.1) use the shape of the OAR at multiple grains to extrapolate to finer grains (reviewed in Azaele et al 2012). The term Thomas model, as used here, refers to the downscaling formula in Supplementary Material (section 2.7.4), rather than the spatially explicit Thomas point process from which it was derived by Azaele *et al.* (2012). I parameterised these models using occupancy at five coarse spatial grains (100, 144, 400, 1600 and 6400 km^2). Saturated grains contain no information for downscaling purposes (Fig. 2.1). For seven widespread species the OAR was saturated (i.e. reached 100% occupancy) at the coarsest (*Enallagma cyathigerum, Sympetrum striolatum, Pyrrhosoma nymphula, Libellula quadrimaculata and Sympetrum danae*) or two coarsest (*Lestes sponsa*, *Ischura elegans*) grains and so these grains were excluded when parameterising models. Model 1, the Hui model (Hui et al., 2006; Hui, 2009; Table 2.1), uses spatially referenced data from one reference grain size to estimate occupancy at others based on just two pieces of information: the probability that a cell is occupied, P_+, and the conditional probability that neighbouring cells are occupied, $Q_{+/+}$ (an index of spatial aggregation). Bayes' theorem can be used to express all conditional probabilities of occupancy in terms of P_+ and $Q_{+/+}$ and to derive the OAR. I implemented the formulae in Hui (2009), using 100km^2 as the reference grain size.

Mathematica 9.0 Student Edition (Wolfram Research 2013) was used for optimisation of parameter estimates for all models. The parameterised models were used to predict occupancy at 25, 4 and 1km^2 grains. Model predictions were obtained at three grains (25, 4 and 1km^2) for the 38 species, giving a total of 114 predictions for each model. Model predictions were evaluated as the absolute value of the percentage error, $\frac{\left|p_{A,i}^{pred} - p_{A,i}^{ob}\right|}{p_{A,i}^{ob}}.100$, where $p_{A,i}^{ob}$ and $p_{A,i}^{pred}$ are the observed and predicted occupancies at grain *A* for species *i.* I assessed model performance

Table 2.1 Summary of performance for ten downscaling models.

For model formulae and notation, see section 2.7.4. # Params is the number of free parameters. Best is the number of species for which each model gave the best downscaling predictions (the lowest mean percentage error for each species across the three predicted grains). Median, Min and Max are the median, minimum and maximum absolute value of percentage error of downscaling predictions across 114 species: grain combinations, $\frac{\left|p_{A,i}^{pred}-p_{A,i}^{ob}\right|}{p_{A,i}^{ob}} * \mathbf{100}$, where $\boldsymbol{p_{A,i}^{pred}}$ and $\boldsymbol{p_{A,i}^{ob}}$ are the predicted and observed occupancy at grain $\boldsymbol{A}$ for species $\boldsymbol{i}$.

Model	# Params	Best	Median	Min	Max	References
1) Hui	2	14	16.594	0.313	102.467	(Hui *et al.* 2006; Hui 2009)
2) Nachman	2	12	19.480	0.119	85.121	(Nachman 1981)
3) Power Law	2	5	25.196	0.202	126.543	(Kunin 1998)
4) Logistic	2	5	30.107	0.548	93.259	(Hanski & Gyllenberg 1997)
5) Thomas	3	1	59.795	0.457	98.518	(Azaele *et al.* 2012)
6) Finite negative binomial	2	1	73.946	0.835	97.591	(Zillio & He 2010)
7) Generalised negative binomial	3	0	32.561	0.209	99.515	(He *et al.* 2002)
8) Improved negative binomial	3	0	35.009	0.080	89.026	(He & Gaston 2003)
9) Negative binomial	2	0	72.046	0.473	97.863	(He & Gaston 2000b)
10) Poisson	1	0	91.111	46.648	99.132	(Wright 1991)

on a species-by-species basis, as well as across all 114 species:grain combinations. Species level performance was evaluated as the number of species for which each model gave the best overall predictions (the mean absolute value of percentage error across the three predicted grains). The median, minimum and maximum of absolute values of percentage errors were used to evaluate model performance across all 114 species:grain combinations.

2.3.3 Odonata traits

Downscaling errors are most extreme when extrapolated furthest from the fitted region of the OAR. Therefore, the percentage errors at 1km^2 (including the direction of error, + or -) for the overall best performing model were used as the response variable in a species-level trait analysis, calculated as $\frac{\boldsymbol{p_{1,i}^{pred}} - \boldsymbol{p_{1,i}^{ob}}}{\boldsymbol{p_{1,i}^{ob}}}.100$, where $p_{1,i}^{ob}$ and $p_{1,i}^{pred}$ are the observed and predicted occupancies at the 1 km^2 grain for species *i*. Data on two distributional traits (distribution type, range change) and two life-history traits (habitat breadth, dispersal ability) were obtained for the 38 British Odonata species. Distribution type was classified as widespread, range limited, localised-aggregated or localised-sparse, based on the number and spatial arrangement of occupied cells (Supplementary Material, section 2.7.5). Habitat breadth (1 to 6) was obtained from Powney *et al*. (2014). Data for British Odonata range change between 1970 and 2012 were taken from NJB Isaac (unpublished data) as the annual linear trend in the probability of occupancy on a logit scale using a generalised linear mixed effect model (Roy *et al.* 2012). I obtained dispersal ability estimates from Fitt (2013), who inferred dispersal distances from the positions of newly colonised 1 km^2 cells in each year from 1991 to 2012 (2000 to 2012 for the recent colonist *Erythromma viridulum*). Distances of newly colonised cells from the nearest previously occupied 1km^2 cell were weighted by the probability of a species being previously missed in that cell, given the number of times the newly colonised cell was surveyed prior to the first recording of the species (using the list length model; Szabo *et al.* 2010). This method is intended to reduce the error in dispersal distance estimates driven by cells that appear newly colonised, but were in fact merely unrecorded due to low sampling intensity. The 75th percentile of dispersal distances was used as the measure of dispersal ability in the trait analysis (Supplementary Material section 2.7.6).

2.3.4 Statistical analyses

I fitted a phylogenetic generalised least squares model (Supplementary Material section 2.7.7) with normally distributed errors using function *pgls* in R package caper (Orme *et al.* 2012). The dependent variable was the percentage error of downscaling predictions at the 1km^2 grain. In the global model, predictor variables were the dispersal ability (measured as the upper quartile of dispersal distances), habitat breadth, range change and distribution type. Residuals of the model were improved by $\log_{10}$ transformation of dispersal ability. Models were ranked by Akaike Information Criterion with a small sample size correction (AIC_c) using the function *dredge* in R package MuMIn (Barton 2013). Models with Δ (AIC_c difference) < 4 were selected and weighted model averaging across this subset of models was used to estimate the parameters (Burnham & Anderson 2002). Standardised model parameter estimates were used to compare effect sizes between traits. I tested for collinearity between predictor variables using both correlation coefficients between pairs of predictors and variance inflation factors (Supplementary Material section 2.7.9), but found collinearity was not sufficient to warrant exclusion of predictors from the global model. All statistical analyses were performed in R version 2.15.1 (R Core Development Team 2014).

2.4 Results

Observed OARs generally became shallower at the finest grains, resulting in a concave or sigmoidal OAR for many of the 38 Odonata species. The Hui model predictions were also of this shape (Fig. 2.2). The Hui and Power Law models were the only models biased towards over-prediction of occupancy (Fig. 2.2; Supplementary Material section 2.7.8), as indicated by the positive median value of percentage errors (Fig. 2.3). All other models tended to under-predict occupancy. This was particularly severe for the Poisson model, which systematically under-predicted occupancy at all predicted grains for all species (Fig. 2.3). The Hui model had the highest peak in percentage errors surrounding zero, followed by the Nachman and Power Law models. The Hui model also had a lower range of percentage errors (141.6) than

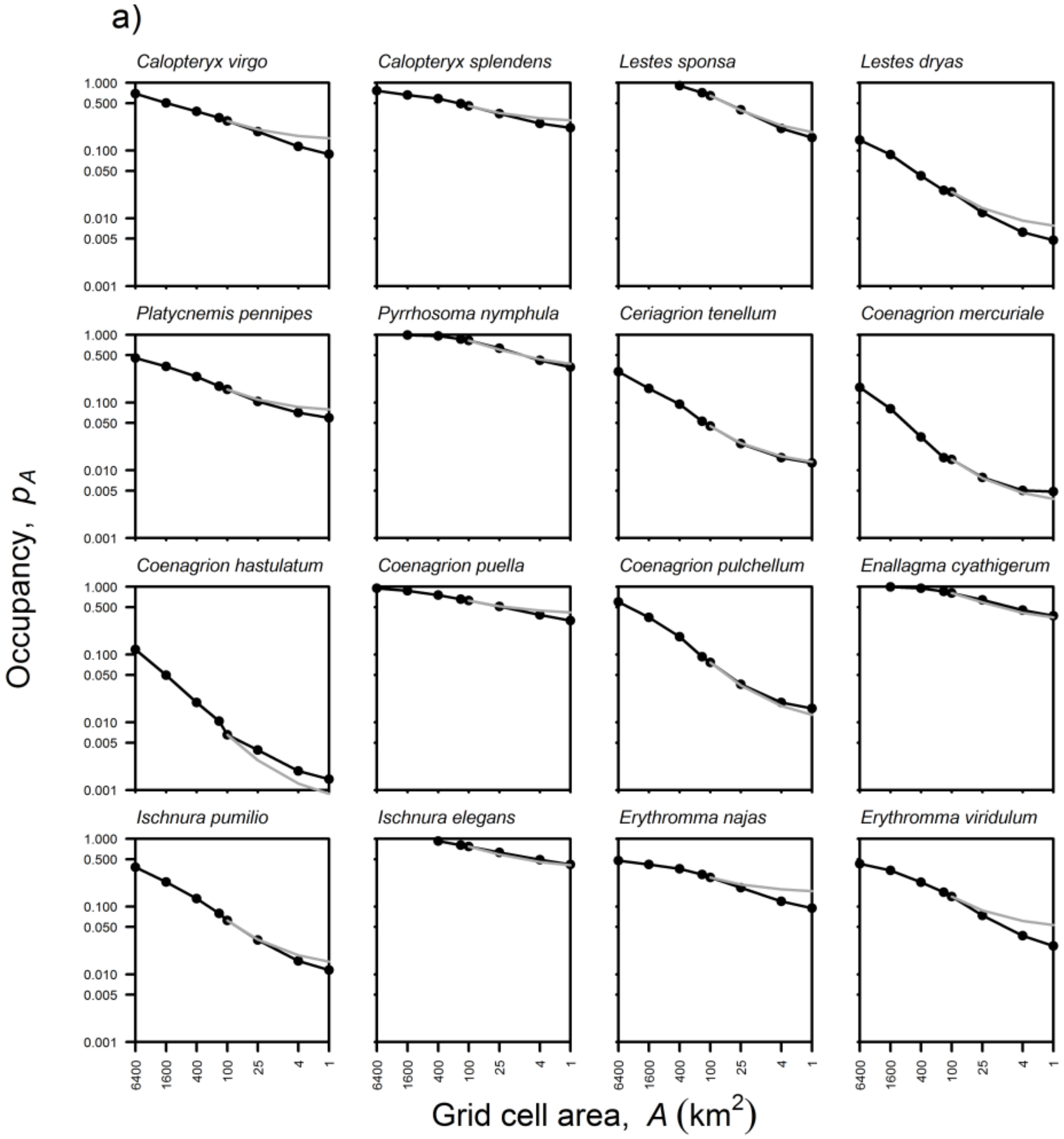

Fig. 2.2 Hui model downscaling predictions for a) 14 species of British Zygoptera (damselflies) and (see overleaf) b) 24 species of British Anisoptera (dragonflies).

The Hui model gave the best overall predictions of the ten downscaling models tested. Black lines and points are the observed occupancies at each spatial grain. Grey lines are the Hui downscaling predictions at the 25, 4 and 1 km2 grains.

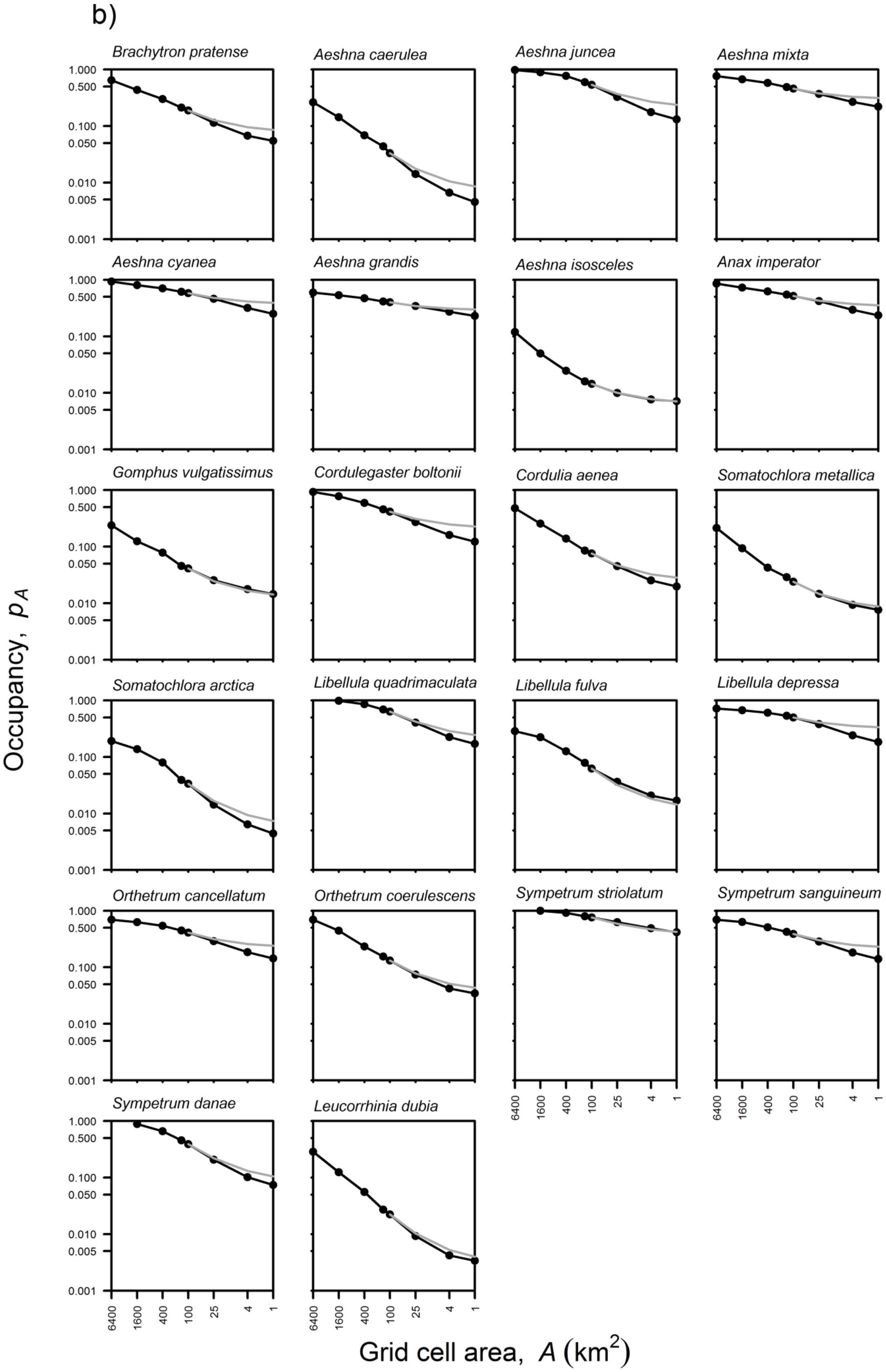

Fig. 2.2 (Continued)

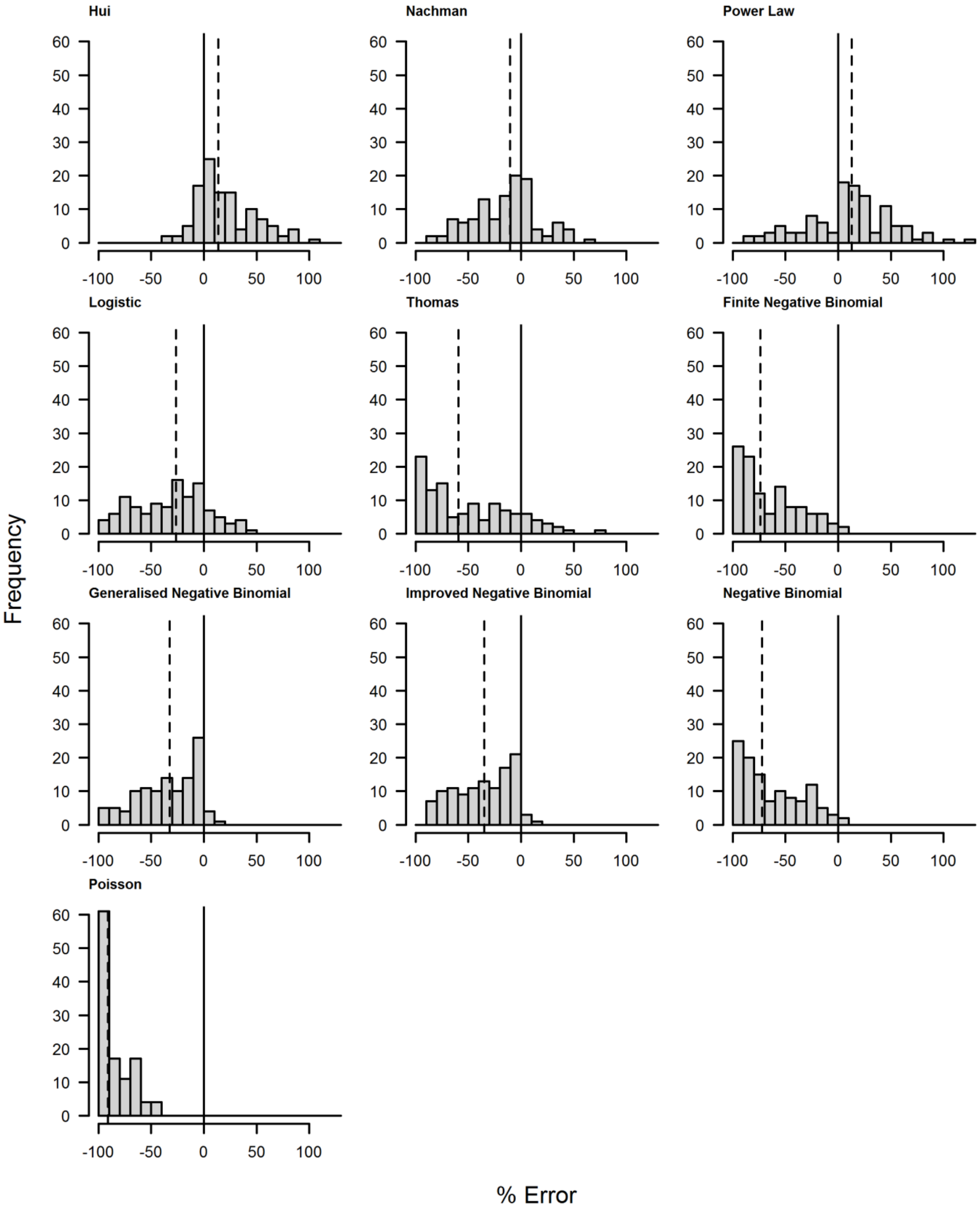

Fig. 2.3 Distribution of errors in downscaling predictions for 114 species:grain combinations.

Percentage errors are calculated as $\frac{\left|p_{A,i}^{pred} - p_{A,i}^{ob}\right|}{p_{A,i}^{ob}} * 100$, where $p_{A,i}^{pred}$ and $p_{A,i}^{ob}$ are the observed and predicted occupancies at grain A for species i. The percentage errors for 114 species:grain combinations are binned into intervals of 10. Vertical solid lines represent zero error in downscaling predictions. Vertical dashed lines are the median % errors. See Table 2.1 for a summary of comparative model performance.

either the Nachman (151.3) or Power Law (210.2) models (Fig. 2.3). Half the Hui model predictions were within 16.6% of the observed occupancy (Table 2.1): the next two best models were the Nachman and Power Law, with comparable figures of 19.5% and 25. 2%, respectively. The Hui model had the lowest median absolute percentage error across species and gave the best predictions for 14 of the 38 species (Fig. 2.4; Table 2.1). The Hui model was never worse than the seventh best model for any species. The relative performance of the Hui model was retained when only predictions at the finest grain were considered; at the 1km^2 grain, the Hui model gave the best predictions for 15 of the 38 species, with 50% of predictions within 36.2% of observed occupancy. By comparison, the Nachman model gave the best predictions for 10 species at the 1km^2 grain with 50% of predictions within 41.1% of observed occupancy and the Power Law model was best for 5 of the 38 species with 50% of predictions within 42.6% of observed occupancy.

Table 2.2 Model selection.

Three models selected from 16 candidate linear models quantifying the effects of species-level traits of British Odonata on the percentage error of downscaling predictions. Downscaling models provide an estimate of fine-grain occupancy, $p_{A,i}^{pred}$, where p is the proportion of grid cells with grain size A in which species i is present. Therefore, the method generates spatially implicit predictions. The global model was Percentage Error ~ Distribution type + log$_{10}$ UQ dispersal ability + Habitat breadth + Range change. Dispersal ability is measured as the upper quartile (UQ) of all distances (km) to newly colonised cells between 1990 and 2012. The symbol • denotes the variables in each candidate model. Models were ranked by AIC$_c$ scores, which applies a correction for small sample sizes to the AIC. R^2 is the amount of variation explained by each model and DF is the number of degrees of freedom. ΔAIC is the difference in AIC$_c$ scores between models. Models with ΔAIC < 4 were selected for weighted model averaging. Akaike weight is the relative likelihood of each model within the subset of models selected. Importance is the relative importance of predictor variables and is the sum of Akaike weights across all models including that predictor.

	Model rank			
	1	**2**	**3**	**Importance**
Distribution type	•	•	•	1
Log$_{10}$ UQ dispersal ability (km)	•	•	•	1
Range change (1970-2012)		•		0.188
Habitat breadth			•	0.147
R^2	0.590	0.596	0.590	-
DF	6	7	7	-
AICc	358.637	361.170	361.660	-
ΔAIC	0	2.533	3.024	-
Akaike weight	0.666	0.188	0.147	-

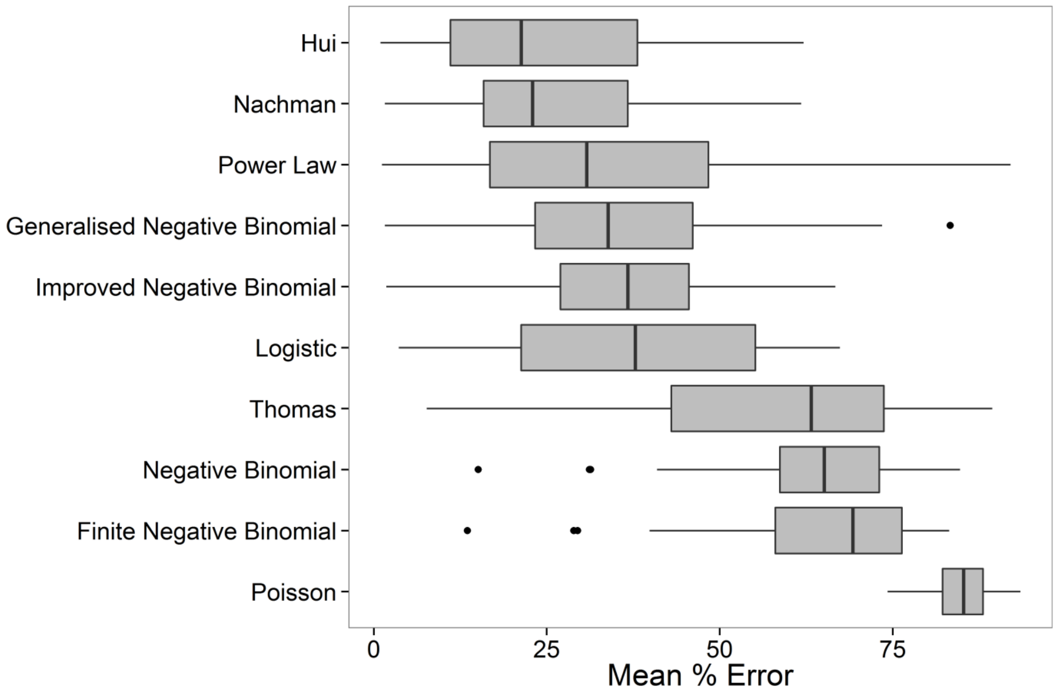

Figure 2.4 Predictive performance of ten downscaling models for 38 British Odonata species.

Each boxplot represents the distribution of mean absolute percentage errors in predictions at 25, 4, and 1 km^2 for 38 species. Mean absolute percentage errors for each species are calculated as $\boldsymbol{\frac{1}{n}\sum_{A=1}^{n}\frac{\left|p_{A,i}^{pred}-p_{A,i}^{ob}\right|}{p_{A,i}^{ob}}.100}$, where $\boldsymbol{p_{A,i}^{pred}}$ and $\boldsymbol{p_{A,i}^{ob}}$ are the predicted and observed occupancy at grain *A* for species $\boldsymbol{i}$ and $\boldsymbol{n}$ is the number of spatial grains for which there are predictions ($\boldsymbol{n = 3}$). The solid line in the centre of the boxes is the median % error and the box is the interquartile range (25th and 75th percentiles). The solid lines are the range of the data and the black points are outliers. Models are ordered by the number of species for which they gave the best overall predictions (Table 2.1).

The percentage errors of Hui model downscaling predictions at the 1km^2 grain were used to investigate species-level trait correlates of downscaling predictive accuracy. The estimate of lambda from the phylogenetically controlled analysis was zero, implying no tendency for closely-related species to have similar downscaling error at the 1km^2 grain. Therefore, I proceeded with model averaging of linear models. The top three models, ranked by AIC$_c$, explained between 0.590 and 0.596 of the variation in downscaling predictions among species (Table 2.2). Distribution type and dispersal ability were the most important predictors of Hui model downscaling error and were present in all three models with ΔAIC < 4 (Table 2.2). Percentage error for species with localised-aggregated distributions, localised- sparse

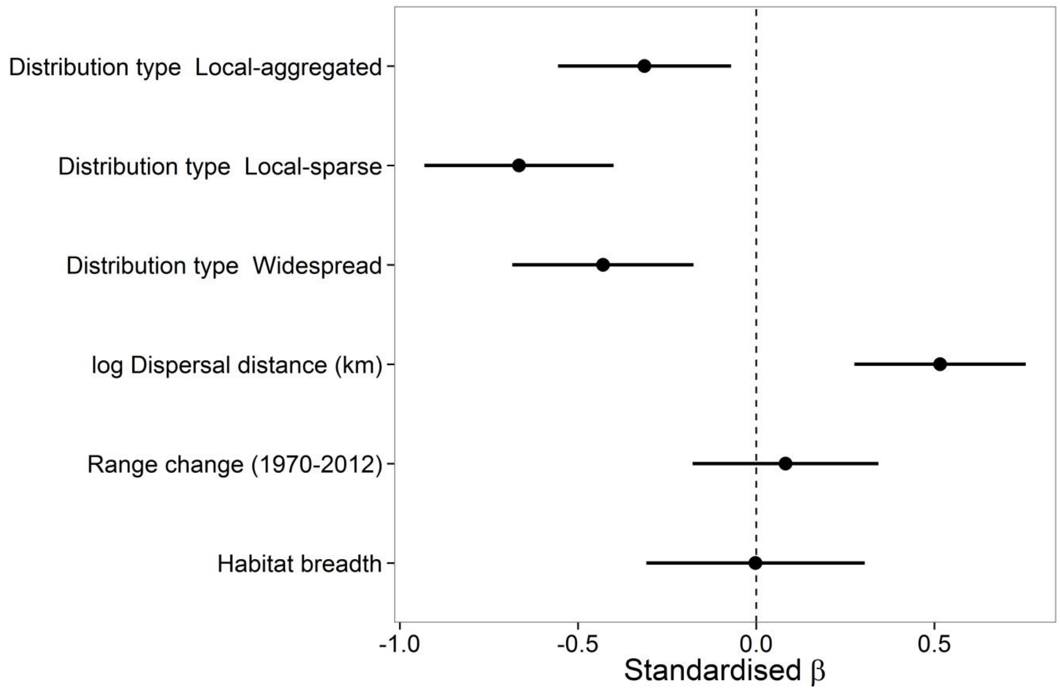

Fig. 2.5 Relative effect sizes of species-level traits on the percentage error of Hui model downscaling predictions.

Standardised β is the standardised parameter estimate derived from weighted model averaging across three linear models with $\Delta AIC_c < 4$. Each variable is rescaled to a mean of 0 and a standard deviation of 1 for comparison of effect sizes among traits. The reference group for Distribution type is Climatic Range Limit, which has a standardised parameter estimate of 0. The percentage error of downscaling predictions was significantly lower for the three distribution types shown than for the species with a climatic range limit. Error bars are the 95% confidence intervals of the mean of the standardised parameter estimates.

distributions and widespread distributions were, on average, 35.6, 52.8 and 36.8 lower than climatic range limited species, respectively. The 95% confidence intervals of the parameter estimates for these three distribution types did not incorporate zero (Fig. 2.5). A unit increase in a species' $\log_{10}$ dispersal ability increased percentage error of downscaling predictions by, on average, 89.8 (Supplementary Material section 2.7.9). The 95% confidence intervals for the dispersal ability parameter estimate did not incorporate zero (Fig. 2.5). Habitat breadth was present in two of the four best models and had lower relative importance in predicting downscaling error. Range change was present in one of the top three ranked models (Table 2.2), increasing the amount of variation in error explained by less than one percent. There was a weak positive effect of range change on the percentage error of downscaling predictions but the 95% confidence intervals for this parameter incorporated zero. Habitat breadth had the lowest relative importance and the effect size was close to zero (Table 2.2; Fig. 2.5).

2.5 Discussion

This comparison of methods for downscaling coarse-grain atlas data has produced four notable results. First, I have observed sigmoidal OARs for many of the 38 species, a shape that has not previously been reported. Second, extrapolating the OAR across two orders of magnitude delivers sensible estimates of fine-grain occupancy, even for highly mobile insects. Third, the Hui model outperforms nine other downscaling models. Finally, I have shown that downscaling accuracy varies systematically with species traits in Odonata. These findings have several implications and applications for how distributional data are used across scales.

The two–parameter Hui model outperforms nine other downscaling models, three of which have an additional parameter. Moreover, it requires data at only one spatial grain. The Hui model has previously given accurate predictions of occupancy for *Drosophila* species in a mesocosm experiment (Hui *et al.* 2006) and predictions of the regional-scale abundance of southern African bird species (Hui *et al.* 2009).

The success of the Hui model reflects that it is the only model tested here to predict an OAR with a slope that becomes shallower at finer grains. The OAR is typically convex at coarse grains for widespread species (approaching saturation) and it is this combination of convex at coarse grains and concave at fine grains that generates the overall sigmoidal relationship. This property indicates that individuals are most aggregated at the finest grain (i.e.1km^2), perhaps reflecting the characteristic grain of British wetlands and the dependence of Odonata on freshwater for reproduction. The fragmented pattern of freshwater bodies in the landscape would also explain the steeper slope of the OAR at intermediate grains. Observed OARs for Barro Colorado Island tree species (He & Condit 2007), Alaskan tree species (Lennon *et al.* 2002) and British plant species (Kunin 1998) do not consistently show the sigmoidal patterns seen here for British Odonata. However successful predictions for Odonata do not imply that the Hui model is constrained to produce sigmoidal OARs, It will be important to investigate the generality of a sigmoidal OAR (and, therefore, the generality of the Hui model's success) among taxa without strong habitat associations.

Variation in the shape of the OAR between studies and taxa (and variation in model performance) could also reflect the window of scales through which the OAR is viewed. Dispersal, biotic interactions, disturbances and habitat availability affect the intensity of intraspecific aggregation (and therefore the slope of the OAR) at characteristic scales (Hortal *et al.* 2010; Procheş *et al.* 2010). It is possible that the range of scales used in this study and those in Kunin (1998a), He & Condit (2007a) and Lennon *et al.* (2002) are not sufficiently broad to capture the full range of variation in the slope of the OAR. My results suggest that the shape of the OAR may be more complex when viewed across the full range of scales. This mirrors the development of theory describing the slope of the SAR. Crawley and Harral (2001) observed multiple phases of increase and plateau in the species-area relationship (SAR) for vascular plants from 0.01m^2 to 110ha. More recently, the assumed shape of the SAR has shifted from power-law to triphasic (Drakare *et al.* 2006; Sizling *et al.* 2011; Storch *et al.* 2012), while the assumed shape of the OAR has developed from linear (reflecting a fractal distribution across scales: Kunin, 1998) to concave down (reflecting saturation in a finite study area: Azaele *et al.*, 2012) to sigmoidal (this study) The theory of OAR and SAR are not merely developing in parallel; the two patterns are linked, conceptually (McGill 2010b). Summing species' occupancies at each grain provides an estimate of the mean number of species for a given area (Sizling & Storch 2007). By varying the area, we therefore obtain the SAR and may be able to infer properties of the SAR from the OAR.

The shape of the predicted OAR depends on each model's depiction of intraspecific aggregation. Spatial structure can be incorporated into OAR models in spatially implicit way (describing spatial variance only) or a spatially explicit way (e.g. pair correlation functions) (Wiens 2000; Hui & McGeoch 2007; Hui *et al.* 2010; McGill 2011). Spatially explicit information has been identified as a key property improving the predictions of several biodiversity patterns (Hui *et al.* 2006; Morlon *et al.* 2008; Conlisk *et al.* 2009; Hui 2009). My results are consistent with this trend: the Hui model is the only candidate model to incorporate information about the relative positions of occupied cells. In fact, the downscaling formula for the Thomas model, as derived in Azaele et al. (2012), can incorporate spatially explicit information, like the Hui model, but here was implemented without using such information. When including spatially explicit information, e.g. by calculating the correlation function, the model might be expected to deliver downscaling predictions that are comparable with the Hui model. A second property of the Hui model likely to be associated with its predictive accuracy is the assumption that intraspecific aggregation is strongest at the finest spatial grains and approaches random at coarse grains, while spatially implict models typically predict the reverse (Hui *et al.*

2006). Empirical evidence is generally consistent with the assumptions of the Hui model (Hartley *et al.* 2004; Wiegand *et al.* 2007; Procheş *et al.* 2010). The shape of the OARs I observed indicate that Odonata species are generally more aggregated at fine grains (higher occupancy) than is assumed by the other downscaling models, all of which consistently under-predict fine-grain occupancy (with the exception of the Power Law). The poorer predictions for range limited species are also consistent with the Hui model assumption of weaker aggregation at coarse grains. Climatic range limits represent strong intraspecific aggregation at the coarsest scales, thus violating one of the assumptions of the Hui model (Hui *et al.* 2006).

While the predictive accuracy of downscaling models is encouraging, there are a number of ways in which my results can inform downscaling improvements. All downscaling models, as fitted here, do not incorporate environmental information from the study region. Although the Hui model uses spatially explicit information, its predictions are spatially-implicit. A potentially useful approach to improving downscaling predictions would be to integrate the concepts used in species distribution modelling (SDM) with downscaling models. The incorporation of climatic or habitat correlates would surely improve the errors associated with Hui model predictions for species with a climatic range limit. Moreover, SDMs would allow us to predict where occupied cells are likely to be. There have been previous attempts to downscale SDMs with varying success (Araújo *et al.* 2005b; McPherson *et al.* 2006; Niamir *et al.* 2011), but only one method has attempted to incorporate the spatial structure captured by the OAR (Keil *et al.* 2012a). The reverse approach, of integrating SDMs into downscaling models, has not been attempted, but offers great potential for deriving accurate predictions that are both fine-grain and spatially explicit.

Accurate downscaling models are one approach to monitoring range change at multiple spatial scales. The slope of the OAR contains information about recent range expansion and contraction (Wilson *et al.* 2004; Pocock *et al.* 2006; Hui 2011). Moreover, time-slicing occurrence data and constructing the OAR for two or more time periods would predict changes in occupancy at multiple scales. My results also suggest that downscaling may be a promising tool for estimating abundance over spatial extents that are too large to sample using traditional methods. If accurate downscaling can be achieved at sufficiently fine grains that each occupied cell contains just one individual, then downscaling methods can be used to predict national-scale abundance (Kunin 1998) and to link population dynamics across scales. However, scaling discontinuities (poor correlations between occupancy at neighbouring spatial grains) have been identified at the grain of human land use and may present an obstacle to downscaling to abundance (Hartley *et al.* 2004; Webb *et al.* 2007). The OARs obtained here do not extend to sufficiently fine grains to confirm whether the same scaling discontinuity can be seen within the Odonata. A useful exercise would be to investigate the degree of correlation between fine-grain occupancy predictions and mean local abundance. If this is sufficiently accurate, downscaling could provide a proxy for multi-site monitoring of populations.

Whilst the DRN records are among the richest available datasets for exploring the OAR over two orders of magnitude, it is worth reflecting on the imperfections in these data. In particular, I have assumed that a single record within a 1 km^2 grid cell reflects evidence that other species are absent. This is probably not the case at 100 km^2, which is the scale at which species atlases are traditionally published (BDS published a new atlas in 2014). In reality, grid cells differ markedly in sampling intensity, and our estimates of occupancy for most species are likely to be systematically under-estimated at the finest grain. It follows that I have over-estimated the performance of eight underpredicting models and under-estimated the downscaling accuracy of the Hui model, which was the best-performing model overall and over-predicted at the finest scales (Fig. 2.2; Fig. 2.3).

I have tested four hypotheses about interspecific variation in the predictive accuracy of downscaling models: collectively these traits explained more than half the observed variation. In particular, dispersal ability and distribution type may be of use for identifying species for which downscaling predictions are unlikely to be successful. Species with a range limit in Britain were less well-predicted than other distribution types. Climatic range limits reflect coarse-scale environmental heterogeneity. In fact, no downscaling model is currently equipped to incorporate information about environmental heterogeneity. The Hui model assumes that intraspecific aggregation becomes weaker at coarse grains, therefore range limited species violate one of the assumptions of the Hui model (Hui *et al.* 2006). A climatic range limit also generates species OARs that approach the scale of endemism (as defined in Fig. 2.1), which contains little information for the purposes of downscaling. One way to address this would be to calculate the Hui parameters, P_+ and $Q_{+/+}$, while excluding cells outside of the range margin, thereby avoiding the portion of the OAR that approaches the scale of endemism. Downscaling predictions were more successful for species with limited dispersal abilities, and relatively poor for the most mobile species. One reason could be that mobility reduces aggregation at the finer scales, thus violating the Hui model assumption that spatial structure is random at the coarsest grains and increasingly patchy at fine spatial grains. Alternatively dispersive species experience higher rates of population turnover (Simmons & Thomas 2004; Pöyry *et al.* 2009; Hill *et al.* 2011; Hof *et al.* 2012; Jaeschke *et al.* 2013) and vagrancy (individuals recorded during migration between suitable habitat patches), such that records collated over many years overestimate the average number of occupied fine-grain cells in any one year. Like many of the predictions that emerge from macroecological theory, I have assumed the data are static and do not incorporate temporal dynamics (Fisher *et al.* 2010; White *et al.* 2010).

Describing species' spatial structure is central to understanding and linking biodiversity patterns and informing our conservation efforts, but atlas data is typically too coarse to address these issues effectively. I have demonstrated that downscaling models can provide accurate estimates of fine-grain occupancy for highly mobile insects, observed a sigmoidal OAR for many species and found the Hui model to provide the most accurate downscaling estimates. In doing so, I have identified some properties that explain the success and failure of downscaling models and which will contribute to their development and future application to a range of theoretical and conservation issues.

2.6 References

Araújo, M.B., Thuiller, W., Williams, P.H. & Reginster, I. (2005). Downscaling European species atlas distributions to a finer resolution: implications for conservation planning. *Global Ecology and Biogeography*, **14**, 17–30.

Azaele, S., Cornell, S.J. & Kunin, W.E. (2012). Downscaling species occupancy from coarse spatial scales. *Ecological Applications*, **22**, 1004–1014.

Barton, K. (2013). MuMIn: Multi-model inference. R package version 1.9.13. http://CRAN.R-project.org/package=MuMIn.

Beck, J., Ballesteros-Mejia, L., Buchmann, C.M., Dengler, J., Fritz, S.A., Gruber, B., Hof, C., Jansen, F., Knapp, S., Kreft, H., Schneider, A.-K., Winter, M. & Dormann, C.F. (2012). What's on the horizon for macroecology? *Ecography*, **35**, 673–683.

Boitani, L., Maiorano, L., Baisero, D., Falcucci, A., Visconti, P. & Rondinini, C. (2011). What spatial data do we need to develop global mammal conservation strategies? *Philosophical transactions of the Royal Society of London. Series B, Biological Sciences*, **366**, 2623–32.

Burnham, K.P. & Anderson, D.R. (2002). *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*, 2nd edn. Springer, New York.

Conlisk, E., Conlisk, J., Enquist, B., Thompson, J. & Harte, J. (2009). Improved abundance prediction from presence-absence data. *Global Ecology and Biogeography*, **18**, 1–10.

Cowley, M.J.R., Thomas, C.D., Wilson, R.J., Gutiérrez, D. & Bulman, C.R. (2001). Density – distribution relationships in British butterflies . II . An assessment of mechanisms. *Journal of Animal Ecology*, **70**, 426–441.

Crawley, M.J. & Harral, J.E. (2001). Scale Dependence in Plant Biodiversity. *Science*, **291**, 864–868.

Drakare, S., Lennon, J.J. & Hillebrand, H. (2006). The imprint of the geographical, evolutionary and ecological context on species-area relationships. *Ecology Letters*, **9**, 215–227.

Fisher, J.A.D., Frank, K.T. & Leggett, W.C. (2010). Dynamic macroecology on ecological time-scales. *Global Ecology and Biogeography*, **19**, 1–15.

Fitt, R. (2013). Range expansion under climate change in UK Odonata. MSc Thesis. University of York, UK.

Gaston, K.J. & He, F. (2011). Species occurrence and occupancy. *Biological Diversity: frontiers in measurement and assessment* (eds A.E. Magurran & B.J. McGill), pp. 141–151. Oxford University Press, New York.

Green, J.L., Harte, J. & Ostling, A. (2003). Species richness, endemism, and abundance patterns: tests of two fractal models in a serpentine grassland. *Ecology Letters*, **6**, 919–928.

Green, J.L. & Plotkin, J.B. (2007). A statistical theory for sampling species abundances. *Ecology Letters*, **10**, 1037–45.

Hanski, I. & Gyllenberg, M. (1997). Uniting Two General Patterns in the Distribution of Species. *Science*, **275**, 397–400. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/8994039

Hartley, S. & Kunin, W.E. (2003). Scale Dependency of Rarity, Extinction Risk, and Conservation Priority. *Conservation Biology*, **17**, 1559–1570.

Hartley, S., Kunin, W.E., Lennon, J.J. & Pocock, M.J.O. (2004). Coherence and discontinuity in the scaling of species' distribution patterns. *Proceedings of the Royal Society of London - Series B: Biological Sciences*, **271**, 81–8.

He, F. & Condit, R. (2007). The distribution of species: occupancy, scale, and rarity. *Scaling Biodiversity* (eds D. Storch, P.A. Marquet & J.H. Brown), pp. 32–50. Cambridge University Press, New York.

He, F. & Gaston, K.J. (2000). Estimating Species Abundance from Occurrence. *American Naturalist*, **156**, 553–559.

He, F. & Gaston, K.J. (2003). Occupancy, spatial variance, and the abundance of species. *American Naturalist*, **162**, 366–375. Retrieved October 6, 2011, from http://www.ncbi.nlm.nih.gov/pubmed/16689947

He, F., Gaston, K.J. & Wu, J. (2002). On species occupancy-abundance models. *Ecoscience*, **9**, 119–126.

Hill, J.K., Griffiths, H.M. & Thomas, C.D. (2011). Climate change and evolutionary adaptations at species' range margins. *Annual Review of Entomology*, **56**, 143–59.

Hof, C., Brändle, M., Dehling, D.M., Munguía, M., Brandl, R., Araújo, M.B. & Rahbek, C. (2012). Habitat stability affects dispersal and the ability to track climate change. *Biology Letters*, **8**, 639–643.

Hortal, J., Roura-Pascual, N., Sanders, N.J. & Rahbek, C. (2010). Understanding (insect) species distributions across spatial scales. *Ecography*, **33**, 51–53.

Hubbell, S.P. (2001). *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University Press, Oxford.

Hui, C. (2011). Forecasting population trend from the scaling pattern of occupancy. *Ecological Modelling*, **222**, 442–446.

Hui, C. (2009). On the scaling patterns of species spatial distribution and association. *Journal of Theoretical Biology*, **261**, 481–7.

Hui, C. & McGeoch, M.A. (2007). Capturing the ‘ droopy-tail ’ in the occupancy-abundance relationship. *Ecoscience*, **14**, 103–108.

Hui, C., McGeoch, M.A., Reyers, B., le Roux, P.C., Greve, M. & Chown, S.L. (2009). Extrapolating population size from the occupancy-abundance relationship and the scaling pattern of occupancy. *Ecological Applications*, **19**, 2038–48.

Hui, C., McGeoch, M.A. & Warren, M. (2006). A spatially explicit approach to estimating species occupancy and spatial correlation. *Journal of Animal Ecology*, **75**, 140–147.

Hui, C., Veldtman, R. & McGeoch, M.A. (2010). Measures, perceptions and scaling patterns of aggregated species distributions. *Ecography*, **33**, 95–102.

Jaeschke, A., Bittner, T., Reineking, B. & Beierkuhnlein, C. (2013). Can they keep up with climate change? - Integrating specific dispersal abilities of protected Odonata in species distribution modelling. *Insect Conservation and Diversity*, **6**, 93–103.

Jetz, W., McPherson, J.M. & Guralnick, R.P. (2012). Integrating biodiversity distribution knowledge: toward a global map of life. *Trends in Ecology & Evolution*, **27**, 151–9.

Keil, P., Belmaker, J., Wilson, A.M., Unitt, P. & Jetz, W. (2012). Downscaling of species distribution models: a hierarchical approach. *Methods in Ecology and Evolution*, **4**, 82–94.

Keith, S.A., Webb, T.J., Böhning-Gaese, K., Connolly, S.R., Dulvy, N.K., Eigenbrod, F., Jones, K.E., Price, T., Redding, D.W., Owens, I.P.F. & Isaac, N.J.B. (2012). What is macroecology? *Biology letters*, **8**, 904–6.

Kunin, W.E. (1998). Extrapolating Species Abundance Across Spatial Scales. *Science*, **281**, 1513–1515.

Kunin, W.E., Hartley, S. & Lennon, J.J. (2000). Scaling Down : On the Challenge of Estimating Abundance from Occurrence Patterns. *American Naturalist*, **156**, 560–566.

Lennon, J.J., Kunin, W.E. & Hartley, S. (2002). Fractal species distributions do not produce power-law species-area relationships. *Oikos*, **97**, 378–386.

Lennon, J.J., Kunin, W.E., Hartley, S. & Gaston, K.J. (2007). Species distribution patterns, diversity scaling and testing for fractals in southern African birds. *Scaling Biodiversity* (eds D. Storch, P.A. Marquet & J.H. Brown), pp. 32–50. Cambridge University Press, Cambridge.

Mace, G.M., Collar, N.J., Gaston, K.J., Hilton-Taylor, C., Akçakaya, H.R., Leader-Williams, N., Milner-Gulland, E.J. & Stuart, S.N. (2008). Quantification of extinction risk: IUCN's system for classifying threatened species. *Conservation Biology*, **22**, 1424–42.

McGill, B.J. (2011). Linking biodiversity patterns by autocorrelated random sampling. *American Journal of Botany*, **98**, 481–502.

McGill, B.J. (2010a). Matters of scale. *Science*, **328**, 575–6.

McGill, B.J. (2010b). Towards a unification of unified theories of biodiversity. *Ecology Letters*, **13**, 627–42.

McGill, B.J. & Nekola, J.C. (2010). Mechanisms in macroecology: AWOL or purloined letter? Towards a pragmatic view of mechanism. *Oikos*, **119**, 591–603.

McPherson, J., Jetz, W. & Rogers, D. (2006). Using coarse-grained occurrence data to predict species distributions at finer spatial resolutions—possibilities and limitations. *Ecological Modelling*, **192**, 499–522.

Morlon, H., Chuyong, G., Condit, R., Hubbell, S., Kenfack, D., Thomas, D., Valencia, R. & Green, J.L. (2008). A general framework for the distance-decay of similarity in ecological communities. *Ecology Letters*, **11**, 904–17.

Nachman, G. (1981). A mathematical model of the functional relationship between density and spatial distribution of a population. *Journal of Animal Ecology*, **50**, 453–460.

Niamir, A., Skidmore, A.K., Toxopeus, A.G., Muñoz, A.R. & Real, R. (2011). Finessing atlas data for species distribution models. *Diversity and Distributions*, 1–13.

Orme, D., Freckleton, R., Thomas, G., Petzoldt, T., Fritz, S., Isaac, N. & Pearse, W. (2012). The caper package: comparative analyses of phylogenetics and evolution in R. R package version 0.5.2. http://CRAN.R-project.org/package=caper.

Pocock, M.J.O., Hartley, S., Telfer, M.G., Preston, C.D. & Kunin, W.E. (2006). Ecological correlates of range structure in rare and scarce British plants. *Journal of Ecology*, **94**, 581–596.

Powney, G., Brooks, S., Barwell, L., Bowles, P., Fitt, R., Pavitt, A., Spriggs, R. & Isaac, N. (2014). Morphological and Geographical Traits of the British Odonata. *Biodiversity Data Journal*, **2**, e1041.

Pöyry, J., Luoto, M., Heikkinen, R.K., Kuussaari, M. & Saarinen, K. (2009). Species traits explain recent range shifts of Finnish butterflies. *Global Change Biology*, **15**, 732–743.

Procheş, Ş., Warren, M., McGeoch, M.A. & Marshall, D.J. (2010). Spatial scaling and transition in pneumatophore arthropod communities. *Ecography*, **33**, 128–136.

R Core Development Team. (2014). R: A language and environment for statistical computing. Version 3.1.1. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/.

Robertson, M.P., Cumming, G.S. & Erasmus, B.F.N. (2010). Getting the most out of atlas data. *Diversity and Distributions*, **16**, 363–375.

Roy, H.E., Adriaens, T., Isaac, N.J.B., Kenis, M., Onkelinx, T., Martin, G.S., Brown, P.M.J., Hautier, L., Poland, R., Roy, D.B., Comont, R., Eschen, R., Frost, R., Zindel, R., Van Vlaenderen, J., Nedvěd, O., Ravn, H.P., Grégoire, J.-C., de Biseau, J.-C. & Maes, D. (2012). Invasive alien predator causes rapid declines of native European ladybirds. *Diversity and Distributions*, **18**, 717–725.

Simmons, A.D. & Thomas, C.D. (2004). Changes in dispersal during species' range expansions. *American Naturalist*, **164**, 378–95.

Sizling, A.L., Kunin, W.E., Sizlingová, E., Reif, J. & Storch, D. (2011). Between geometry and biology: the problem of universality of the species-area relationship. *American Naturalist*, **178**, 602–11.

Sizling, A.L. & Storch, D. (2007). Geometry of species distributions: random clustering and scale invariance. *Scaling Biodiversity* pp. 77–99. Cambridge University Press, Cambridge.

Storch, D., Keil, P. & Jetz, W. (2012). Universal species-area and endemics-area relationships at continental scales. *Nature*, **488**, 78–83.

Storch, D., Sizling, A.L., Reif, J., Polechova, J., Sizlingova, E. & Gaston, K.J. (2008). The quest for a null model for macroecological patterns: geometry of species distributions at multiple spatial scales. *Ecology Letters*, **11**, 771–84.

Van Strien, A.J., Termaat, T., Kalkman, V., Prins, M., Knijf, G., Gourmand, A.-L., Houard, X., Nelson, B., Plate, C., Prentice, S., Regan, E., Smallshire, D., Vanappelghem, C. & Vanreusel, W. (2013). Occupancy modelling as a new approach to assess supranational trends using opportunistic data: a pilot study for the damselfly Calopteryx splendens. *Biodiversity and Conservation*, **22**, 673–686.

Szabo, J.K., Vesk, P.A., Baxter, P.W.J. & Possingham, H.P. (2010). Regional avian species declines estimated from volunteer-collected long-term data using List Length Analysis. *Ecological Applications*, **20**, 2157–69.

Tosh, C.A., Reyers, B. & Jaarsveld, A.S. (2004). Estimating the abundances of large herbivores in the Kruger National Park using presence–absence data. *Animal Conservation*, **7**, 55–61.

Veldtman, R., Chown, S.L. & McGeoch, M.A. (2010). Using scale-area curves to quantify the distribution, abundance and range expansion potential of an invasive species. *Diversity and Distributions*, **16**, 159–169.

Webb, T.J., Noble, D. & Freckleton, R.P. (2007). Abundance-occupancy dynamics in a human dominated environment: linking interspecific and intraspecific trends in British farmland and woodland birds. *Journal of Animal Ecology*, **76**, 123–34.

White, E.P., Ernest, S.K.M., Adler, P.B., Hurlbert, A.H. & Lyons, S.K. (2010). Integrating spatial and temporal approaches to understanding species richness. *Philosophical Transactions of the Royal Society of London - Series B: Biological Sciences*, **365**, 3633–3643.

Wiegand, T., Gunatilleke Savitri, C. V, Gunatilleke Nimal, I.A.U. & Huth, A. (2007). How individual species structure diversity in tropical forests. *Proceedings of the National Academy of Sciences of the United States of America*, **104**, 19029–19033.

Wiens, J.A. (2000). Ecological heterogeneity: an otongeny of concepts and approaches. *The Ecological Consequences of Heterogeneity* (eds M.J. Hutchings, E.A. John & A.J.A. Stewart), pp. 9–31. Blackwell Science, Oxford.

Wilson, R.J., Thomas, C.D., Fox, R., Roy, D.B. & Kunin, W.E. (2004). Spatial patterns in species distributions reveal biodiversity change. *Nature*, **432**, 393–396.

Wolfram Research. (2013). Mathematica 9.0 Student Edition. Wolfram Research, Champagne, Illinois.

Wright, D.H. (1991). Correlations Between Incidence and Abundance are Expected by Chance. *Journal of Biogeography*, **18**, 463.

Zillio, T. & He, F. (2010). Modeling spatial aggregation of finite populations. *Ecology*, **91**, 3698–706.

2.7 Supplementary Material

2.7.1 Odonata species

Table S2.1 The 38 resident British Odonata species

Latin name	Common name	Authority	Sub-order	Family
Calopteryx splendens	Banded Demoiselle	Harris	Zygoptera	Calopterygidae
Calopteryx virgo	Beautiful Demoiselle	Linnaeus	Zygoptera	Calopterygidae
Lestes sponsa	Emerald Damselfly	Fabricius	Zygoptera	Lestidae
Lestes dryas	Scarce Emerald Damselfly	Kirby	Zygoptera	Lestidae
Platycnemis pennipes	White-legged Damselfly	Pallas	Zygoptera	Platycnemididae
Pyrrhosoma nymphula	Large Red Damselfly	Schmidt	Zygoptera	Coenagrionidae
Ceriagrion tenellum	Small Red Damselfly	Villers	Zygoptera	Coenagrionidae
Coenagrion mercuriale	Southern Damselfly	Charpentier	Zygoptera	Coenagrionidae
Coenagrion hastulatum	Northern Damselfly	Charpentier	Zygoptera	Coenagrionidae
Coenagrion puella	Azure Damselfly	Linnaeus	Zygoptera	Coenagrionidae
Coenagrion pulchellum	Variable Damselfly	Lohmann	Zygoptera	Coenagrionidae
Enallagma cyathigerum	Common Blue Damselfly	Charpentier	Zygoptera	Coenagrionidae
Ischnura pumilio	Scarce Blue-tailed Damselfly	Charpentier	Zygoptera	Coenagrionidae
Ischnura elegans	Blue-tailed damselfly	Vander Linden	Zygoptera	Coenagrionidae
Erythromma najas	Red-eyed Damselfly	Hansemann	Zygoptera	Coenagrionidae
Erythromma viridulum	Small Red-eyed Damselfly	Charpentier	Zygoptera	Coenagrionidae
Brachytron pratense	Hairy Dragonfly	Müller	Anisoptera	Aeshnidae
Aeshna caerulea	Azure Hawker	Strom	Anisoptera	Aeshnidae
Aeshna juncea	Common Hawker	Linnaeus	Anisoptera	Aeshnidae
Aeshna mixta	Migrant Hawker	Latreille	Anisoptera	Aeshnidae
Aeshna cyanea	Southern Hawker	Müller	Anisoptera	Aeshnidae
Aeshna grandis	Brown Hawker	Linnaeus	Anisoptera	Aeshnidae
Aeshna isosceles	Norfolk Hawker	Müller	Anisoptera	Aeshnidae
Anax imperator	Emperor Dragonfly	Leach	Anisoptera	Aeshnidae
Gomphus vulgatissimus	Club-tailed Dragonfly	Linnaeus	Anisoptera	Gomphidae
Cordulegaster boltonii	Golden-ringed Dragonfly	Selys	Anisoptera	Cordulegastridae
Cordulia aenea	Downy Emerald	Linnaeus	Anisoptera	Corduliidae
Somatochlora metallica	Brilliant Emerald	Vander Linden	Anisoptera	Corduliidae
Somatochlora arctica	Northern Emerald	Zetterstedt	Anisoptera	Corduliidae
Libellula quadrimaculata	Four-spotted Chaser	Linnaeus	Anisoptera	Libellulidae
Libellula fulva	Scarce Chaser	Müller	Anisoptera	Libellulidae
Libellula depressa	Broad-bodied Chaser	Linnaeus	Anisoptera	Libellulidae
Orthetrum cancellatum	Black-tailed Skimmer	Linnaeus	Anisoptera	Libellulidae
Orthetrum coerulescens	Keeled Skimmer	Fabricius	Anisoptera	Libellulidae
Sympetrum striolatum	Common Darter	Charpentier	Anisoptera	Libellulidae
Sympetrum sanguineum	Ruddy Darter	Muller	Anisoptera	Libellulidae
Sympetrum danae	Black Darter	Sulzer	Anisoptera	Libellulidae
Leucorrhinia dubia	White-faced Darter	Vander Linden	Anisoptera	Libellulidae

2.7.2 Threshold species list length for inclusion of cells

There are a number of sources of bias when estimating the occupancy-area relationship (OAR) from unstructured records of species' occurrences. It is important to acknowledge that the species recorded in a cell are not always a complete list of those species present. A single species may have been recorded because it is particularly charismatic or rare, while a number of more common species present are not recorded. As such, common species tend to be under-represented, while rare species are over-represented. One method of addressing this bias is to exclude cells with a species list length falling below some threshold, hence excluding cells which are likely to be an incomplete list of the species present. However, this is also problematic as the number of cells available for the analysis declines steeply as the threshold species list length becomes higher. The list length results in large losses of cells at fine-grains and very little loss of cells at coarse grains (Fig. S2.1), therefore proportion occupancy at the finest spatial grains increases rapidly as the list length threshold gets higher. For some species this results in a spurious non-monotonic OAR when the list length threshold is high (e.g. *Somatochlora metallica* at list length 6, Fig. S2.2). Moreover, the cells excluded are not spatially random. In fact, cells that are poorly sampled and those that are less speciose are more likely to be lost as the threshold species list length is increased. Odonata diversity decreases from South to North in Britain, as does sampling intensity. Therefore, higher list length thresholds for inclusion of cells introduce spatial biases into our estimates of distribution size: cells are more likely to be excluded in the North, so the distribution size will be heavily influenced by the most species-rich and well-sampled regions in the south-east (Fig. S2.3). The choice of the threshold species list length for including cells is, therefore, a trade-off between these two sources of bias (under-recording of common species and spatial bias in estimates of distribution size). Our choice of a list length of >= 1 for inclusion of cells in the analysis reflects this trade-off. In any case, the choice of list length does not substantially affect the observed OARs for any species in our analysis (Table S2.1).

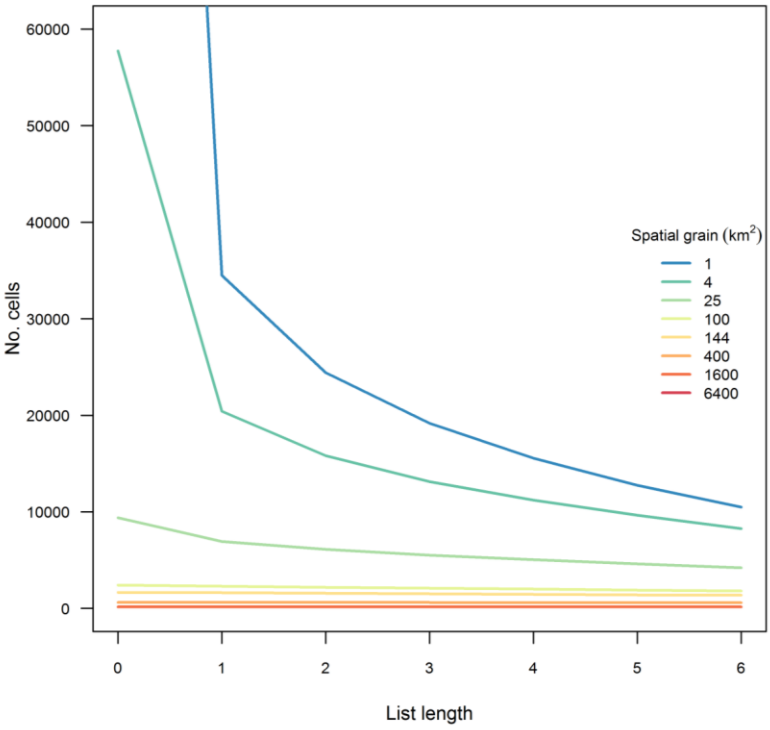

Fig. S2.1 Decline in the number of cells available for analysis as the species list length threshold increases.

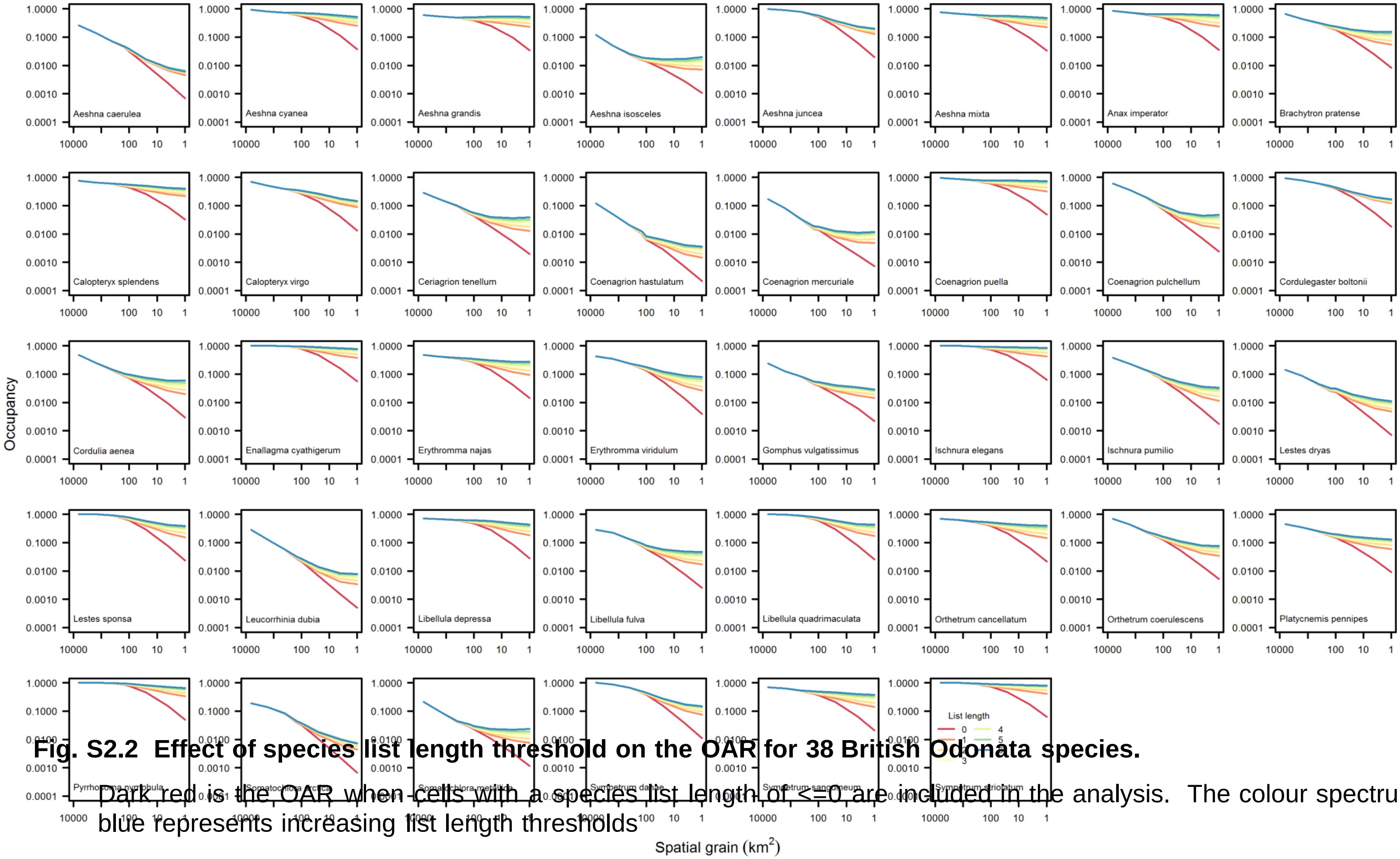

Fig. S2.2 Effect of species list length threshold on the OAR for 38 British Odonata species. Dark red is the OAR when cells with a species list length of <=0 are included in the analysis. The colour spectrum towards blue represents increasing list length thresholds

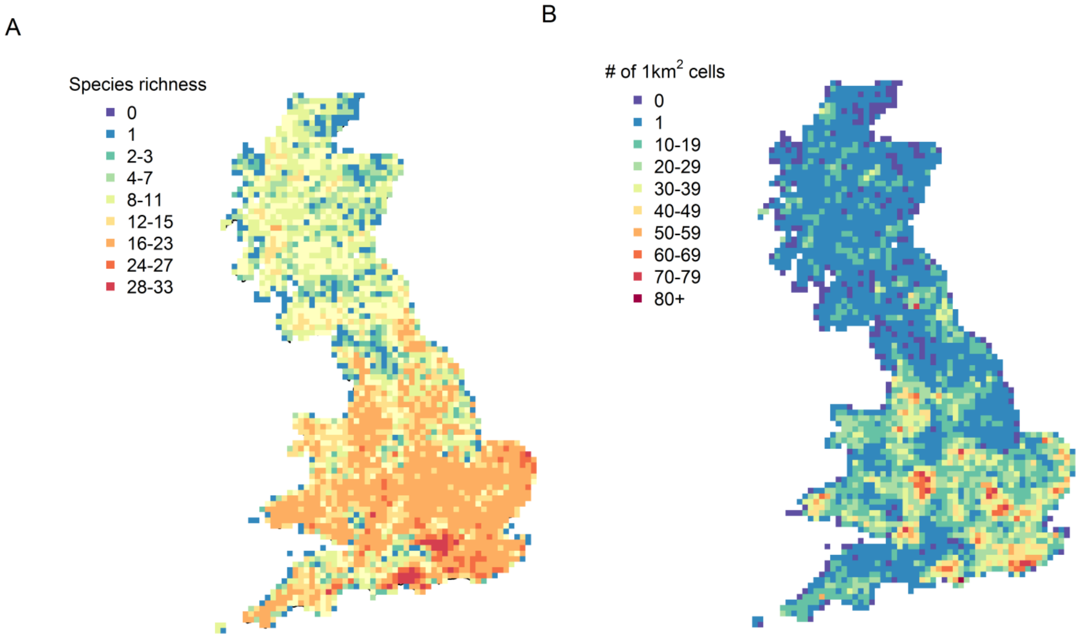

Fig. S2.3 Spatial patterns of A) species richness and B) sampling intensity in British Odonata records at the 100km^2 grain.

Species richness is the number of species recorded in each 100km^2 cell between 1990 and 2012. Sampling intensity (# 1km^2 cells) is measured as the number of 1km^2 cells visited within each 100km^2 cell between 1990 and 2012.

Table S2.2 Correlations between OARs estimated using a list length of 1 and six other list length thresholds for the 38 British Odonata species

	List length threshold						
Species	**0**	**1**	**2**	**3**	**4**	**5**	**6**
Aeshna caerulea	0.999901	1	0.999997	0.999972	0.999971	0.999904	0.999888
Aeshna cyanea	0.993162	1	0.998907	0.996996	0.993226	0.987672	0.979178
Aeshna grandis	0.982596	1	0.992985	0.973081	0.919701	0.798752	0.486339
Aeshna isosceles	0.998582	1	0.999777	0.999285	0.998532	0.997285	0.99517
Aeshna juncea	0.999029	1	0.999938	0.999916	0.999937	0.99987	0.999819
Aeshna mixta	0.990633	1	0.998336	0.995696	0.990177	0.981692	0.966379
Anax imperator	0.991143	1	0.997349	0.9899	0.97193	0.935577	0.861896
Brachytron pratense	0.998318	1	0.999754	0.999303	0.998424	0.997019	0.995226
Calopteryx splendens	0.99186	1	0.999436	0.998632	0.997245	0.99469	0.992184
Calopteryx virgo	0.996661	1	0.999799	0.999416	0.998547	0.997343	0.996147
Ceriagrion tenellum	0.999394	1	0.999906	0.999711	0.999366	0.998862	0.998133
Coenagrion hastulatum	0.99994	1	0.999992	0.999979	0.999953	0.999925	0.999914
Coenagrion mercuriale	0.999724	1	0.999965	0.999886	0.999782	0.999643	0.99954
Coenagrion puella	0.989157	1	0.995866	0.985878	0.965299	0.930885	0.871851
Coenagrion pulchellum	0.999804	1	0.999978	0.999944	0.999875	0.999762	0.999667
Cordulegaster boltonii	0.997676	1	0.999941	0.999915	0.999885	0.999869	0.99991
Cordulia aenea	0.999402	1	0.999903	0.999703	0.999359	0.998824	0.998085
Enallagma cyathigerum	0.997772	1	0.999742	0.999729	0.999288	0.998402	0.997047
Erythromma najas	0.996892	1	0.999445	0.998407	0.995899	0.991167	0.983815
Erythromma viridulum	0.999388	1	0.999934	0.999835	0.999605	0.999199	0.99889
Gomphus vulgatissimus	0.9987	1	0.999843	0.99959	0.999304	0.999029	0.998785
Ischnura elegans	0.991948	1	0.996968	0.991903	0.985556	0.978561	0.96907
Ischnura pumilio	0.999736	1	0.999968	0.999919	0.999814	0.999656	0.999538
Lestes dryas	0.999667	1	0.999967	0.999907	0.999802	0.999651	0.999527
Lestes sponsa	0.999345	1	0.999954	0.999857	0.999534	0.998907	0.99801
Leucorrhinia dubia	0.999953	1	0.999995	0.999986	0.999977	0.999956	0.999939
Libellula depressa	0.997274	1	0.999492	0.998307	0.995429	0.989021	0.977838
Libellula fulva	0.999266	1	0.999922	0.999786	0.999538	0.999115	0.998809
Libellula quadrimaculata	0.998981	1	0.999923	0.999861	0.999679	0.999218	0.998999
Orthetrum cancellatum	0.997004	1	0.999541	0.998794	0.997107	0.994206	0.990095
Orthetrum coerulescens	0.99931	1	0.999936	0.999832	0.999721	0.999543	0.999488
Platycnemis pennipes	0.996231	1	0.99937	0.998478	0.997396	0.996251	0.995777
Pyrrhosoma nymphula	0.998674	1	0.999712	0.999385	0.998523	0.99724	0.995775
Somatochlora arctica	0.999882	1	0.999988	0.999976	0.999919	0.999886	0.999902
Somatochlora metallica	0.999502	1	0.999918	0.999726	0.999401	0.998885	0.998081
Sympetrum danae	0.999462	1	0.999972	0.999913	0.99977	0.999705	0.999653
Sympetrum sanguineum	0.996054	1	0.999247	0.997869	0.994942	0.989709	0.98292
Sympetrum striolatum	0.991396	1	0.998239	0.996886	0.99492	0.993721	0.992534

2.7.3 Threshold proportion land for inclusion of cells

An additional source of bias is the inclusion of cells with large proportions of sea. Following the species-area relationship, fewer species will be present in a cell containing a greater proportion of sea. This introduces a negative bias in distribution size. This can be addressed by excluding cells with the proportion of land below a specified threshold. However, the number of cells included in the analysis declines rapidly as the threshold of land required increases, particularly at coarse grains, where large proportions of cells in the North and South West are sea. When the threshold land is set very high, the disproportionate loss of coarse grain cells leads to a positive bias in coarse-grain occupancy. Our choice of 0.3 as the threshold proportion of land required for inclusion of a cell is a trade-off between the total number of cells in the analysis at each spatial grain and the total amount of land represented by these cells (Fig. S2.4).

The threshold proportion of land and the threshold species list length for inclusion of a cell can also drive different patterns of bias at different spatial grains. In particular, if disproportionately more cells are excluded at fine grains due to the chosen thresholds, then occupancy at fine grains can be spuriously higher than at coarser grains, generating a non-monotonic OAR. This is clearly not possible and cannot be fitted by downscaling models.

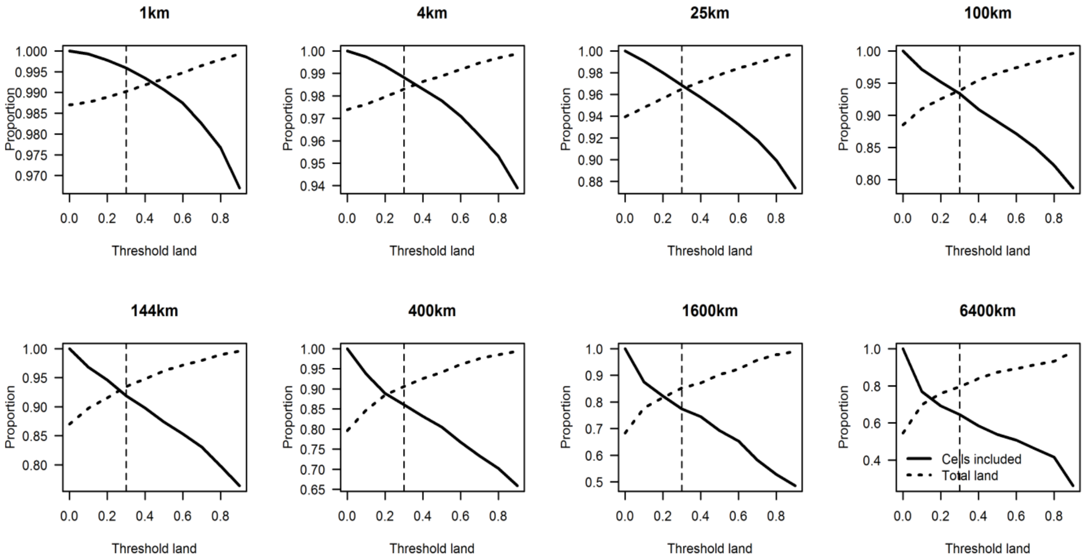

Fig. S2.4 Trade-off between the total proportion land in the study region and proportion of cells included in the analysis.

The vertical dashed lines are the threshold proportion of land we required to include cells in the analysis (0.3). The same threshold was used for cells at all spatial grains.

2.7.4 Details of downscaling models

The formulae and notation of the ten downscaling models are defined below. The Hui model (model 1) uses information at single spatial grain, while Models 2 to 9 are fitted to multiple coarse grains to estimate scale invariant parameters from which the OAR is extrapolated to finer grains. Consequently, models 2 to 9 are expressed in terms of p_A, the proportion of occupied cells at grain A in a study region of size A_0. Following Azaele et al. (2012), the free parameters of downscaling models 2 to 9 (shown in bold after each formula) were estimated for each species by numerical minimisation of the Euclidean norm of predicted occupancy in log space, $\frac{1}{N}\sum_{A=1}^{g}\left(\log p_{A,i}^{pred} - \log p_{A,i}^{ob}\right)^2$, where $p_{A,i}^{pred}$ and $p_{A,i}^{ob}$ are the predicted and observed occupancy at grain A for species i and g is the number of grains used to parameterise the model. To estimate the parameters of the Thomas model, a simulated annealing optimisation algorithm was specified to ensure a robust search for the global minimum (Bolker 2008). All optimisation was carried out in Mathematica 9.0 Student Edition. It should be noted that the Thomas model, like the Hui model, can be used to downscale with occupancy data at a single spatial grain, provided that information about the positions of occupied cells is used to parameterise the model.

1) Hui

The Hui model (Hui et al. 2006; Hui 2009) was developed by to describe the spatial scaling of species occupancy. The scaling pattern uses conditional probabilities (joint-count statistics) as well as probability of presence to describe the distribution of a species within a presence-absence grid. The scaling pattern describes how these probabilities depend on a percolation process as neighbouring fine-grain cells are combined into larger coarse-grain cells. Here, we use the model to predict the probability of occupancy at fine grains (the target grain), using observed occupancy data at a coarser reference grain. The relationships between these probabilities can be defined using Bayes' theorem, such that all conditional probabilities can be expressed in terms of two pieces of information estimated from spatially referenced occurrence data at the reference grain: in this case, species atlas data at 10km x 10km (100km^2). The first piece of information required is occupancy, the probability that a randomly chosen cell is occupied; the second, a measure of spatial aggregation, is the conditional probability that, given a cell is occupied, a randomly chosen cell adjacent to it is also occupied. The notation for these probabilities and the joint-count statistics are defined below, along with the relationships between them. We use upper case letters to refer to observed probabilities at the reference grain and lower case letters to refer to estimated probabilities at the target (fine) grain.

$\boldsymbol{P_+}$: observed probability of presence, obtained at the reference grain of the data (100 km^2)

$\boldsymbol{Q_{+|+}}$**:** observed conditional probability, obtained at the reference grain of the data, that a randomly chosen cell adjacent to a given occupied cell is also occupied.

$\boldsymbol{P_0}$**:** observed probability of absence at the reference grain. $P_0 = 1 - P_+$

$\boldsymbol{Q_{0|0}}$**:**, observed conditional probability that a randomly chosen cell adjacent to an empty cell is also empty. This can be calculated from $Q_{+|+}$ and P_+ using Bayes' theorem $Q_{0|0} = 1 - ((1 - Q_{+|+})\, P_+ / (1 - P_+)$

$\boldsymbol{p_+}$: estimated probability of presence at the finer, target grain

$\boldsymbol{q_{+|+}}$**:** estimated conditional probability at the finer, target grain that a randomly chosen cell adjacent to a given occupied cell is also occupied

$\boldsymbol{p_0}$**:** estimated probability of absence at the finer, target grain, $1 - p_+$

$\boldsymbol{q_{0|0}}$ **:** estimated conditional probability, at the finer target grain, that a randomly chosen cell adjacent to an empty cell is also empty

$\boldsymbol{q_{0|+}}$**:** estimated conditional probability, at the finer target grain, that a randomly chosen cell adjacent to an occupied cell is empty

$\boldsymbol{q_{+|0}}$**:** estimated conditional probability, at the finer target grain, that a randomly chosen cell adjacent to an empty cell is occupied

$\boldsymbol{b_0}$**:** conditional probability that a cell with two empty neighbours is also empty at the finer, target grain

***n* :** an index of spatial grain (or the linear grain size). One cell at the reference grain has an area of n^2 cells at the finer, target grain (e.g. to estimate occupancy at 2km x 2km using the reference grain of 10km x 10km, n = 10/2 = 5). The value of n does not need to be an integer.

The formula we use to estimate occupancy with the Hui model is derived from equations 6 and 7 in Hui (2009):

$P_0 = p_0 . {q_{0|0}}^{2(n-1)} . {b_0}^{(n-1)^2}$ (Eqn. A)

$$Q_{0|0} = {q_{0|0}}^{n}.{b_0}^{n(n-1)} \quad \text{(Eqn. B)}$$

The two unknown terms, $q_{0|0}$ and b_0 can be expressed in terms of p_0, P_0 and $Q_{0|0}$. This is achieved for the term $Q_{0|0}$ by rearranging equations 6 and 7 equal to b_0 (and hence to each other). This equation can then be expressed in terms of the unknown term:

$$q_{0|0} = {p_0}^{-\frac{1}{n-1}}.{P_0}^{\frac{1}{n-1}}.{Q_{0|0}}^{\frac{-1}{n}} \quad \text{(Eqn. C)}$$

By substituting equation C into Bayes' theorem relating the conditional probabilities we can express the conditional probability $q_{0|+}$ in terms of p_0, P_0 and $Q_{0|0}$:

$$q_{0/+} = \frac{p_0(1-{p_0}^{-\frac{1}{n-1}}{P_0}^{\frac{1}{n-1}}{Q_{0|0}}^{\frac{-1}{n}})}{1-p_0} \quad \text{(Eqn. D)}$$

We can now express b_0 in terms of p_0, P_0 and $Q_{0|0}$, using equation 3 in Hui (2009):

$$b_0 = \frac{{q_{0|0}}^2.p_0}{{q_{0|0}}^2.p_0 + {q_{0|+}}^2.p_+} \quad \text{(Eqn. E)}$$

Equations C and D are substituted into equation D to estimate the unknown b_0:

$$b_0 = \frac{\left({p_0}.^{1-\frac{2}{n-1}}.{P_0}^{\frac{2}{n-1}}.{Q_{0|0}}^{\frac{-2}{n}}\right)}{\left({p_0}^{1-\frac{2}{n-1}}.{P_0}^{\frac{2}{n-1}}.{Q_{0|0}}^{\frac{-2}{n}} + \frac{{p_0}^2.\left(1-{p_0}^{-\frac{1}{n-1}}.{P_0}^{\frac{1}{n-1}}.{Q_{0|0}}^{\frac{-1}{n}}\right)^2}{1-p_0}\right)}$$

Finally, the Hui model scaling relationship in Eqn. A can be rewritten, substituting in $q_{0|0}$ and b_0 as defined in equations C and E to obtain:

$$P_0 = p_0.\left({p_0}^{-\frac{1}{n-1}}.{P_0}^{\frac{1}{n-1}}.{Q_{0|0}}^{\frac{-1}{n}}\right)^{2(n-1)}\left(\frac{\left({p_0}^{1-\frac{2}{n-1}}.{P_0}^{\frac{2}{n-1}}.{Q_{0|0}}^{\frac{-2}{n}}\right)}{\left({p_0}^{1-\frac{2}{n-1}}.{P_0}^{\frac{2}{n-1}}.{Q_{0|0}}^{\frac{-2}{n}} + \frac{{p_0}^2.\left(1-{p_0}^{-\frac{1}{n-1}}.{P_0}^{\frac{1}{n-1}}.{Q_{0|0}}^{\frac{-1}{n}}\right)^2}{1-p_0}\right)}\right)^{(n-1)^2} \quad \text{(Eqn. F)}$$

Note that p_0 in equation F is the only unknown variable. In the absence of an analytical solution, the value of p_0 is estimated by finding the numerical root of the above equation, using an iterative algorithm to find successively better approximations to the root. The predicted value of p_0 is that which satisfies the relationship above for the observed values of P_0 and $Q_{0|0}$ at the reference grain. Predicted occupancy is then $p_+ = 1 - p_0$.

2) Nachman

$p_A = 1 - e^{-cA^z}$

c **:** constant

z **:** constant

3) Power Law

$p_A = cA^z$

c **:** constant

z **:** constant

4) Logistic

$p_A = \frac{cA^z}{1+ cA^z}$,

c **:** constant

z **:** constant

5) Thomas

$p_A = 1 - \exp\left\{-\rho \int \left[1 - \exp\left(-\mu \int_A \; k(||\vec{c} - \vec{x}||)\, d\vec{x}\right)\right] d\vec{c}\right\}$

ρ **:** intensity of the Poisson distribution of cluster centres in a Thomas spatial point process

***σ*²:** variance of the bivariate normal distribution of points around cluster centres

μ **:** mean number of points around each cluster centre

6) Finite Negative Binomial

$p_A = 1 - \frac{\Gamma\left(N+\frac{A_0k}{A}-k\right)\Gamma\left(\frac{A_0k}{A}\right)}{\Gamma\left(N+\frac{A_0k}{A}\right)\Gamma\left(\frac{A_0k}{A}- k\right)}$

N **:** total number of individuals

A₀ **:** total area of study region

7) Generalised Negative Binomial

$p_A = 1 - \left(1 + \frac{cA^z}{k}\right)^{-k}$

c **:** constant

z **:** constant

***k*:** overdispersion parameter of a negative binomial distribution

8) Improved negative binomial

$p_A = 1 - \left[c(\gamma A)^{b-1}\right]^{\frac{\gamma A}{1-c(\gamma A)^{b-1}}}$

γ: mean density

***b*:** constant

***c*:** constant

9) Negative Binomial

$p_A = 1 - \left(1 + \frac{\gamma A}{k}\right)^{-k}$

γ: mean density

***k*:** overdispersion parameter of the negative binomial distribution

10) Poisson

$p_A = 1 - e^{-\gamma A}$

γ: mean density

2.7.5 Species distribution type

In the trait analysis, the predictor distribution type is intended to capture two components of species' distributions: the size of the distribution and the spatial arrangement of occupied cells. Distribution type was initially classified by eye, using distribution maps of British Odonata at the 100km^2 grain. Four discrete categories were identified: Climatic Range Limit (a large range size with a Northern, Southern, Continental (South Easterly) or Oceanic (Westerly) distribution), Widespread (a large range size with a distribution throughout British mainland), Local-aggregated (a small range size, with a largely contiguous distribution), and Local-sparse (a small range size with a disjunct distribution). In order to confirm that these categories were borne out in the data, we plotted each species on two axes quantifying the distribution size (area of occupancy) and spatial arrangement of occupied cells (residuals of the relationship between occupancy and fractal dimension (Wilson *et al.* 2004) for grains 100km^2 and 10000km^2). Seven species changed category (Fig. S5).

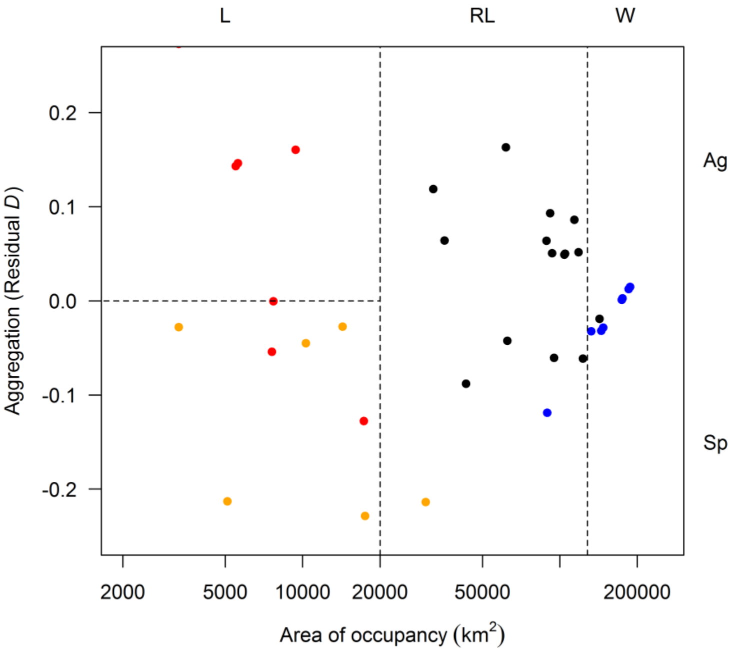

Fig. S2.5 Classification of species' distribution type for the trait analysis.

The colour of circles indicates the initial classification of distribution type. Blue = widespread, black = climatic range limit, red = local-aggregated, yellow = local-sparse. The dashed lines denote the revised division of species into the four categories of distribution type, based on quantifying distribution size and the spatial arrangement of occupied cells. The labels in the margins define the four categories, L = local (occupancy < 20 000 km^2), RL = range limited (20 000 km^2 < occupancy < 125 000 km^2), W = widespread (occupancy > 125 000 km^2), Ag = aggregated (residual D > 0), Sp = sparse (residual D < 0).

2.7.6 Upper quartile of dispersal distances

In the absence of field-based dispersal estimates for many species of British Odonata, dispersal estimates were taken from R Fitt. Dispersal distances were inferred from the distances of newly colonised 1km^2 cells in each year from the nearest previously occupied cell. The 75th percentile of all dispersal distances between 1991 and 2012 was used as the measure of species-level dispersal in the trait analysis (75% of newly colonised cells for the focal species were within this distance of the nearest occupied cell). False absences can lead to overestimates of dispersal from distribution data when high percentiles from the dispersal kernel are used to infer dispersal. However, lower percentiles conceal much of the interspecific variation in dispersal, because most individuals of any species will disperse very short distances, while only a few individuals will disperse far. Our use of the 75th percentile of the dispersal kernal reflects this trade-off between the stronger signal (more interspecific variation) and greater noise (less certainty in the estimates of dispersal) at the highest percentiles of the dispersal kernel (see Fig. S2.6).

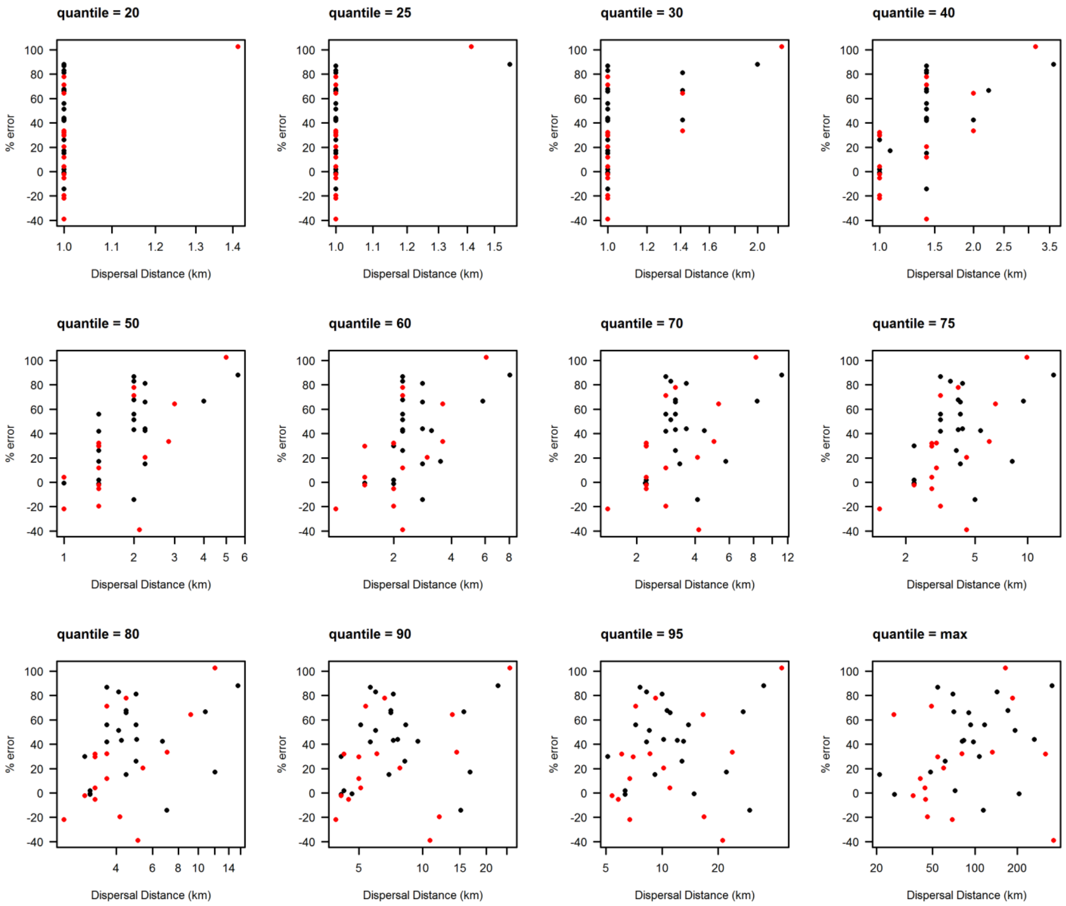

Fig. S2.6 Effect of species' dispersal on the percentage error of downscaling predictions using different quantiles of the dispersal kernel as the estimate of dispersal distance

Red circles are Zygoptera (damselflies) and black circles are Anisoptera (dragonflies), indicating there is no clear phylogenetic signal in dispersal distance, despite the body size differences between dragonflies and damselflies.

2.7.7 Odonata phylogeny

To control for phylogenetic non-independence among the traits of related taxa, we attempted to build a phylogeny based on genetic distances for all 38 British Odonata species in the analysis. Due to a lack of suitable genetic data for a large number of Odonata species and low confidence in alignments, we instead used a phylogeny based on species taxonomy. We converted the taxonomy (Suborder, Family, Genus, Species) into a tree with polytomies at each node and branch lengths set to 1 using the *as.phylo* function from the R package *ape* (Paradis *et al.* 2004).

Table S2.3 Summary of percentage errors and absolute percentage errors of downscaling predictions

Median, min and max are the absolute percentage error of downscaling predictions at three spatial grains. Best is the number of species for which each model gave the best predictions (the lowest mean percentage error for each species).

	% errors											
Spatial Grain (km^2)	**25**				**4**				**1**			
Model	**Median**	**Min**	**Max**	**Best**	**Median**	**Min**	**Max**	**Best**	**Median**	**Min**	**Max**	**Best**
Hui	2.946	-29.347	24.097	12	22.548	-34.342	64.685	12	32.737	-39.094	102.467	15
Nachman	-0.299	-35.276	35.974	8	-13.044	-67.252	49.709	9	-36.33	-85.121	66.136	10
Power Law	10.716	-34.304	43.698	4	16.924	-66.161	105.869	7	14.429	-83.639	126.543	5
Logistic	-8.188	-36.218	30.889	5	-40.254	-77.808	36.904	5	-62.254	-93.259	42.914	4
Thomas	-27.166	-75.158	44.877	2	-72.386	-94.513	74.985	1	-90.219	-98.518	28.74	3
Finite Negative Binomial	-35.67	-60.819	5.274	1	-78.67	-91.12	-0.835	2	-92.945	-97.591	-34.52	1
Generalised Negative Binomial	-7.142	-57.789	14.412	3	-34.711	-93.37	2.101	0	-58.524	-99.515	-2.521	0
Improved Negative Binomial	-9.629	-38.587	10.817	2	-37.629	-72.525	1.561	2	-62.436	-89.026	-3.476	0
Negative Binomial	-30.189	-64.27	4.584	1	-74.42	-92.094	-3.166	0	-90.989	-97.863	-37.531	0
Poisson	-67.962	-84.497	-46.648	0	-91.111	-96.759	-82.29	0	-97.181	-99.132	-93.859	0

	Absolute value of % errors											
Spatial Grain (km^2)	**25**				**4**				**1**			
Model	**Median**	**Min**	**Max**	**Best**	**Median**	**Min**	**Max**	**Best**	**Median**	**Min**	**Max**	**Best**
Hui	5.566	0.313	29.347	12	24.314	1.663	64.685	12	36.231	0.739	102.467	15
Nachman	7.562	0.234	35.974	8	23.371	0.197	67.252	9	41.090	0.119	85.121	10
Power Law	14.632	0.434	43.698	4	29.901	0.202	105.869	7	42.649	2.930	126.543	5
Logistic	14.501	0.548	36.218	5	40.254	2.053	77.808	5	62.254	6.367	93.259	4
Thomas	28.164	0.457	75.158	2	73.663	6.213	94.513	1	90.219	2.254	98.518	3
Finite Negative Binomial	35.670	2.191	60.819	1	78.670	0.835	91.120	2	92.945	34.520	97.591	1
Generalised Negative Binomial	7.416	0.240	57.789	3	34.711	0.209	93.370	0	58.524	2.521	99.515	0
Improved Negative Binomial	10.725	0.363	38.587	2	37.629	0.080	72.525	2	62.436	3.476	89.026	0
Negative Binomial	30.189	0.473	64.270	1	74.420	3.166	92.094	0	90.989	37.531	97.863	0
Poisson	67.962	46.648	84.497	0	91.111	82.290	96.759	0	97.181	93.859	99.132	0

2.7.8 Comparison of downscaling models for British Odonata

Model performance was assessed using the absolute values of percentage errors and the raw percentage errors of downscaling predictions for 114 species:grain combinations are shown in Table S2.3. Absolute values of percentage errors are a better measure of overall predictive accuracy, as they avoid averaging across positive and negative errors with a model and cancelling out predictive error. However, raw percentage errors are also useful as they provide information about positive or negative bias in downscaling predictions.

2.7.9 Trait analysis

Table S2.4 Unstandardised parameter estimates for the trait analysis.

We tested for an effect of four species-level traits on the predictive error of the Hui downscaling model using a linear model. The global model was Percentage Error ~ Distribution type + $\log_{10}$ Dispersal ability + Range change+ Habitat breadth. Weighted model averaging was used to obtain parameter estimates for each trait with the lower and upper 95% confidence intervals. Parameter estimates are averaged across three models with ΔAIC < 4, weighted by the Akaike weights of each model. The reference group of the factor distribution type is Climatic Range Limit. The trait variables are ordered by decreasing relative importance.

Parameter	Estimate	Lower 95% CI	Upper 95% CI
Intercept	0.725	-21.341	35.851
Distribution type local-aggregated	-35.626	-63.257	-7.995
Distribution type local-sparse	-52.763	-73.807	-31.719
Distribution type widespread	-36.795	-58.572	-15.017
Log_{10} Dispersal ability (km)	89.792	0.222	0.752
Range change (1970-2012)	68.007	-146.781	282.794
Habitat breadth	-0.042	-7.925	7.842

Table S2.5 Generalised variance inflation factors (GVIF) for each of the predictor variables included in the global model of predictive downscaling error.

GVIFs were obtained using the function *vif* in R package car (Fox & Weisberg 2011). All GVIF values are < 4 indicating collinearity does not severely inflate the variance associated with parameter estimates.

Predictor	Generalised variance inflation factor (GVIF)	Df	GVIF $^{(1/(2*Df))}$
Distribution type	2.276139	3	1.14692
$\log_{10}$ Dispersal distance (km)	1.203343	1	1.09697
Range change (1970-2012)	1.312466	1	1.145629
No. habitat types	1.790005	1	1.33791

Table S2.6 Correlation matrix between pairs of traits included the global linear model of predictive downscaling error.

Predictor	Distribution type	$\log_{10}$ Dispersal distance (km)	Range change	No. habitat types
Distribution type	1	0.28265	0.39481	0.655771
$\log_{10}$ Dispersal distance (km)	0.28265	1	0.122213	-0.18865
Range change	0.39481	0.122213	1	0.179419
No. habitat types	0.655771	-0.18865	0.179419	1

2.7.10 Supplementary References

Azaele, S., Cornell, S.J. & Kunin, W.E. (2012). Downscaling species occupancy from coarse spatial scales. *Ecological Applications*, **22**, 1004–1014.

Bolker, B.M. (2008). *Ecological Models and Data in R*. Princeton University Press, Oxford.

Fox J. & Weisberg S (2011) *An R Companion to Applied Regression*. Sage Publications, Thousand Oaks, CA, USA

Hui, C. (2009). On the scaling patterns of species spatial distribution and association. *Journal of Theoretical Biology*, **261**, 481–7.

Hui, C., McGeoch, M.A., Reyers, B., le Roux, P.C., Greve, M. & Chown, S.L. (2009). Extrapolating population size from the occupancy-abundance relationship and the scaling pattern of occupancy. *Ecological Applications*, **19**, 2038–48.

Hui, C., McGeoch, M.A. & Warren, M. (2006). A spatially explicit approach to estimating species occupancy and spatial correlation. *Journal of Animal Ecology*, **75**, 140–147.

Paradis E., Claude J. & Strimmer K. (2004) Analyses of phylogenetics and evolution in R language. *Bioinformatics*, **20**, 289-290

Wilson, R.J., Thomas, C.D., Fox, R., Roy, D.B. & Kunin, W.E. (2004). Spatial patterns in species distributions reveal biodiversity change. *Nature*, **432**, 393–396.

Chapter 3

Filling in the gaps in the fine-grain distribution of the Brindled Green moth

3.1. Abstract

There are many uncertainties in our knowledge of species distributions. Absences in opportunistic biological records can constitute a true absence or a failure to detect a species that was present. These false absences limit our ability to identify threatened species, to plan networks of protected areas and to understand the drivers of species distributions. The Beale observer effort model fills in these gaps in species distributions by estimating the probability of detecting a species, given observer effort, species-environment associations and residual spatial autocorrelation. Here, I apply this model to biological records of the Brindled Green moth (a species whose distribution is widespread but under-recorded in the British Isles) at two spatial grains (100 and 25 km^2) and compare the predictions to an independent data set. Residual spatial autocorrelation had higher relative importance in predicting probability of occurrence than any of the environmental predictors at both the fine and coarse grains, but its effect on the distribution of the Brindled Green declined with latitude. Predictions of probability of occurrence, evaluated against an independent dataset, were slightly better at the finer 25 km^2 grain (AUC = 0.680 ± 0.075) compared to the coarser 100 km^2 grain (AUC = 0.600 ± 0.173). The Beale observer effort model identified sites with high probability of occurrence for the Brindled Green but no records. It is therefore a promising tool for targeting visits to these sites. Relationships between predicted probability of occurrence and mean local abundance in an independent data set were positive but weak and will require finer grain predictions to evaluate to the degree to which predicted habitat suitability can be used as proxy for abundance. The results have highlighted that the scale of sampling and the characteristic scale of ecological processes are critical considerations for accurate modelling of species distributions.

3.2 Introduction

Species distributions are often poorly known, and the data used to estimate them are biased in space (Whittaker *et al*. 2005). This lack of information is termed the Wallacean Shortfall (Lomolino & Heaney 2004). Two sources of error in our knowledge of species distributions are false absences and false presences. This uncertainty limits our understanding of the drivers of species distributions (Diniz-Filho *et al.* 2010; Jetz *et al.* 2012; Keith *et al.* 2012; Beck *et al.* 2013a) and is an obstacle to assessing species conservation status (Sousa-Silva *et al.* 2014) and monitoring temporal trends (Burns *et al*. 2013; Isaac *et al*. 2014b), both of which are needed to categorise extinction risk (IUCN, 2001). Poorly known species distributions prevent the optimal design of reserve networks (Bini *et al.* 2006; Lessmann *et al.* 2014) and make it difficult to evaluate the success of conservation initiatives at large spatial scales (Pereira *et al*. 2010; García-Roselló *et al.* 2015).

Several solutions to the Wallacean shortfall have been proposed. These include investing in standardised sampling methods to obtain unbiased estimates of presence *and* absence (Aranda *et al*. 2011). Unfortunately, the time, resources and financial requirements to sample with sufficient intensity to eliminate sampling bias are usually unfeasible. By definition, knowledge of species distributions requires data over large spatial extents. In most cases, the viable option is to collate unstructured opportunistic records of species occurrences (Schmeller *et al.* 2009). Examples include citizen science projects and volunteer collected data used to generate species atlases.

A second tool to address the Wallacean shortfall is species distribution modelling (SDM). One of the primary applications of SDMs has been to facilitate the discovery of previously unrecorded populations, through characterising the relationship between the abiotic environment and the presence or abundance of a species (Raxworthy *et al.* 2003; Townsend Peterson *et al.* 2011; Hill *et al.* 2014). These species-environment relationships can be used to make predictions about the suitability of unrecorded sites for a focal species, to fill in the gaps in our knowledge or to target areas requiring increased recording intensity. One problem for SDMs is that two different processes can generate the absence of a species from a grid cell: true absence (the cell is unoccupied) and false absence, in which the species has not been detected (e.g. because the cell has not been surveyed intensively). It is difficult to distinguish true absences from false absences in presence-only data, which can lead to biased estimates of the species-environment relationship (Lahoz-Monfort *et al.* 2014). One solution is to generate artificial absences (background or pseudo-absence data), but the methods of selecting these absences vary and the choice of method can have a large impact on model predictions (Lobo *et al.* 2010; Barbet-Massin *et al.* 2012).

Species' distributions can be measured as the extent of occurrence or the area of occupancy (Jetz *et al.* 2008; Gaston & Fuller 2009). Extent of occurrence is defined as a polygon encompassing all known presences, while area of occupancy refines the distribution by identifying regions within the extent of occurrence where the species is absent (Gaston 1991). There is a trade-off here between commission errors, which are greatest in extent of occurrence, and omission errors, which become more common as the grain used to measure area of occupancy becomes finer (Rondinini *et al.* 2006). One approach to dealing with omission errors in area of occupancy is to coarsen spatially referenced point samples to a grain where false absences are deemed to be acceptably small. Analyses of British atlas data traditionally use 10x10km grid cells (Powney & Isaac 2015), but for most parts of the world a much larger grain size would be required (Meyer *et al.* 2015). One problem with this approach is that coarse-grain predictions can severely overestimate the area of occupancy or the area of suitable habitat (Seo *et al.* 2009). Downscaling models address this issue by extrapolating coarse-grain area of occupancy to finer grains using spatial scaling laws (Kunin 1998; He & Gaston 2000; Zillio & He 2010; see Chapter 2). These methods have had some success in predicting fine-grain occupancy (Azaele *et al.* 2012; Barwell *et al.* 2014), but the predictions are not spatially explicit and do not incorporate environmental information. This limits their application in reserve design, and tracking movement in species distributions (e.g. with climate change).

SDMs incorporate environmental information, but face another problem: the mismatch between fine-grain environmental information and the coarse-grain of species data. Fine-grain variation is averaged away when environmental data is coarsened to that of the species data. More recently, methods have been proposed to link fine grain environmental data to coarse-grain species occurrences (Keil *et al.* 2012a; Keil & Jetz 2014). These 'downscaling SDMs' are a promising avenue to address the Wallacean shortfall when environmental data is available at a finer grain size than the species' data, but discard information when coarsening species records, which are typically spatially referenced at grains ≤ 1km. The species data are coarsened as the downscaling SDMs assume that all absences are true absences. By coarsening the data, there is much greater certainty that absences are true absences.

To model both environment and species data at fine grains, it is necessary to model explicitly the data collection process, which generates data with false absences through the spatial variation in recording intensity. Directly modelling the relationship between some measure of sampling intensity (e.g. number of visits) and detection probability allows species occurrence records to be modelled at the scale they are collected (Beale *et al.* 2014). Consequently, occupancy models have become a focus of many studies using presence-only data to examine the distribution status, and / or trends therein (Kéry & Royle 2008; Chen *et al.* 2013; McCarthy *et al.* 2013; Comte & Grenouillet 2013; Guillera-Arroita *et al.* 2014; Lahoz-Monfort *et al.* 2014).

Beale *et al.* (2014) introduced a Bayesian approach to species distribution modelling which quantifies nonlinear species-environment associations and incorporates a spatial random effect to quantify unexplained variation in species distributions. A possible extension of the model is described in the supplementary methods of Beale *et al.* (2014), in which an additional hierarchical level (a data model of cell-specific observer effort) is incorporated into the model. This approach offers a solution to the problem of false absences at fine spatial grains. Instead of coarsening fine-grain records to deal with false absences, the method estimates the relationship between recording intensity and detection probability during the modelling process, allowing us to estimate which absences are true absences and which are false absences. I call this the Beale observer effort model.

I apply the Beale observer effort model to the Brindled Green moth, a species whose distribution is widespread but under-recorded in the British Isles, with many gaps in the known distribution at grains <100 km^2 (e.g. 10 km x 10 km). The species was selected as it is widely distributed in England, but patchy in Wales and especially at higher latitudes, suggesting its distribution is climatically limited. The Brindled Green also uses oak as its sole host-plant, so broadleaved woodland cover, as defined in landcover maps, is a good candidate for predicting its distribution. The purpose of this research is to model the distribution of the Brindled Green moth using patchy data and I do not expect to produce a perfect model of the species' distribution. The inclusion of a spatial random effect will help to account for spatial autocorrelation in the distribution of the Brindled Green moth, for example unmeasured environmental covariates, spatial processes and other stochastic factors. There is evidence for opposing and synergistic effects of climate and landcover on moth distributions (Fox *et al.* 2014). Models fitted at finer grains are expected to better capture the scale of effect of predictors such as elevation and land cover (Pearson *et al.* 2004), which can vary at much finer grains than is captured in coarser grain models. Climatic variables such as temperature and rainfall are predicted to influence distribution patterns at much coarser spatial grains, (but see Gillingham *et al.* 2012 for strong effects of microclimatic variation). Predictions at two spatial grains are used to investigate 1) the environmental drivers of distribution of the Brindled Green moth in Britain, 2) whether modelling species distributions at finer spatial grains can provide more accurate predictions of the pattern of occurrence than the coarser grains we typically use for species distribution modelling, 3) if the predictions can be used as a tool to target recording towards areas with high suitability, but no records of the focal species and 4) if fine scale predictions of habitat suitability can be used to infer local presence and abundance in light traps.

3.3 Methods

I fit the Beale observer effort model (Beale *et al.* 2014) at two spatial scales, using Brindled Green occurrence data in the National Moth Recording Scheme as my training data set. I compare these predictions with observed patterns of presence-absence and abundance of the Brindled Green moth in the Rothamsted Insect Survey (RIS), a network of light traps distributed around Britain. I do not expect the RIS to fully validate the model predictions, as the RIS traps sample only a small area within the grid cells for which I have predictions. The implication of this is that predicting a low probability of occurrence in cells with an RIS record, or conversely, predicting high probability of occurrence in cells with no records need not invalidate the model. RIS traps located within a landcover type or elevation that are unusual compared with the rest of the grid cell could lead to these mismatches between predicted and observed distribution. However, I would still predict a correlation between these data that should be stronger when the NMRS data are modelled at finer spatial grains.

3.3.1 Distribution and recording intensity data

Estimates of recording intensity and distribution data for the Brindled Green moth were obtained from the National Moth Recording Scheme (NMRS) led by Butterfly Conservation. The NMRS data comprise over 17 million records of >900 macro-moths: a record comprises a spatial reference, a date and a species identity. I extracted all moth records collected in mainland Britain between 2000 and 2011 with a precision of ≤ 1km^2. To ensure the independence of the NMRS and RIS datasets, I excluded from the analyses any NMRS records in 1km^2 cells where Rothamsted light traps are located, and records for which “Rothamsted Light Trap” was the stated sampling method. The remaining NMRS dataset comprised > 8.5 million records of 994 species across 40759 spatially referenced 1km cells: from these records I derived measures of sampling intensity and the training dataset of Brindled Green records at two grain sizes: 25 km^2 and 100 km^2. Sampling intensity was estimated for each 1km^2 cell as the number of visits to that cell. A visit is defined as a unique combination of site and date (Van Strien *et al.* 2013). Cells with no moth records were given a value of 0 for the number of visits. To calculate sampling effort at 25 km^2 and 100 km^2 grains I simply summed the number of visits within each 1km^2 cell. There were 0 visits in 1816 out of the 9082 25 km^2 cells in mainland Britain and in 71 out of 2422 100 km^2 grain cells. Presence-only training data for the Brindled Green moth comprised 8451 records across 1788 1km^2 cells.

3.3.2 Environmental predictors

I used four environmental variables to predict the British distribution of the Brindled Green moth at 100 km^2 and 25 km^2 grains (henceforth called hectads and quadrants) grains. For each 1km^2 cell, I derived the percentage cover of broadleaved woodland (WDCV) from the Landcover Map 2007 (Morton *et al.* 2011), digital elevation (ELV) data from NextMap Britain (Intermap Technolologies 2007) and mean annual temperature (MAT) and mean annual rainfall (MAR) from the monthly Met Office UKCP09 datasets (Perry & Hollis 2005). Data at the 1 km^2 grain were coarsened to larger grains by aggregating 1km^2 cells and taking the mean of the contributing 1km^2 cells. Data cleaning and preparation for all distribution and environmental data were performed in R 3.0.3 (R Core Development Team 2014).

3.3.3 Model fitting

I model the Brindled Green presence-only data at hectad and quadrant grains. I also attempted to fit the model at finer grains but this proved too computationally intensive to be practical at grains $\leq$ 4 km^2. I used the hierarchical Bayesian model described in Beale *et al.* (2014) and fitted the model using OpenBUGS 3.2.3 (Lunn *et al.* 2009), called from an R script using package R2OpenBUGS (Sturtz *et al.* 2005). BUGS code was taken from the original implementation of the model in Beale *et al.* (2014). The model consists of a basic species distribution model (SDM) in the form of a generalised additive model with probability of occurrence as the dependent variable, modelled as a function of the four environmental variables and a spatially explicit random effect, which captures the spatial dependence of each cell on the surrounding eight cells. All environmental variables were rescaled to a mean of 0 and standard deviation of 1 to avoid numerical overflow and convergence problems during MCMC sampling. Following the procedure described in Beale *et al.* (2014), smooth functions were estimated for each of the environmental covariates using penalised spline regression with two knots. Each of these spline bases were included as an additive term in the generalised linear model of probability of occurrence of the Brindled Green moth. Observed presences are linked to the underlying pattern of true presence-absence (the latent variable), by modelling the probability of observing a species as conditional on presence and the probability of detection (Beale *et al.* 2014). I assume that the probability of detection, P_{det}, increases asymptotically with the number of visits to a cell, following the increasing form of an exponential decay function,

$$P_{det} = 1 - \exp(-\beta_{obs} * v),$$

where β_{obs} is a constant and v is recording intensity measured as the number of visits to a grid cell.

Uninformative priors were used for all environmental variables with a mean of 0 and variance of 1000. β_{obs} was given an uninformative normal prior with a mean of 0.3, a variance of 100 and constrained to be ≥ 0. The prior for the spatial random effect was defined by an intrinsic conditional autoregressive model (iCAR), based on a sparse matrix of neighbours derived from the spatially referenced environmental data. Initial values for each chain should be over-dispersed with respect to the prior distribution. To obtain initial values, I modelled observed presence-absence as a function of the four environmental predictors using a generalised linear model with a binomial error structure. For each chain, the initial value was drawn from a normal distribution with the mean taken as the parameter estimate for that environmental variable and a variance of 100.

I ran four chains, each with 20000 iterations and discarded 15000 as burnin. Only every tenth iteration was kept to avoid autocorrelation in MCMC samples. Convergence was assessed using the Gelman and Rubin convergence diagnostic, inspection of the Gelman-Rubin-Brooks plot in R package coda (Plummer *et al.* 2006) and by visual inspection of traceplots to ensure the four chains were well-mixed. Parameter estimates for environmental and spatial predictors, detection probability and the latent variable, probability of occurrence, were calculated as the median of MCMC samples with upper and lower credible intervals calculated as the 0.025 and 0.975 quantiles, drawn from the posterior distribution for each parameter, including a total of 20000 iterations (5000 iterations from each of the four chains).

3.3.4 Quantifying the relative importance of covariates

The overall contributions of each predictor (MAT, MAT, EL, WDCV) and residual spatial autocorrelation were quantified as the absolute difference between predicted probabilities of occurrence for each cell and the probabilities when the contribution of each predictor was partitioned into individual components, following the method suggested in Beale *et al.* (2014). These components were expressed as the ratio of each component to the contribution of all components, providing a measure of the relative importance of each covariate (bounded between 0 and 1). All relative importance estimates include estimates of uncertainty derived from the 95% credible intervals of posterior distributions of all monitored parameters.

3.3.5 Model evaluation

I also compared model predictions (predicted probability of occurrence) to independent data in the Rothamsted Insect Survey (RIS) using the area under the receiver operating characteristic (ROC: Fielding & Bell (1992)) curve (AUC). To compare continuous predicted probabilities of occurrence with observed presence absence, predicted probability of occurrence must first be converted to categorical presence-absences. The AUC is a threshold-independent measure, summarising overall model performance using the full range of possible thresholds of probability of occurrence to classify presences and absences. It quantifies the relationship between sensitivity (true presences) and 1-specificity (false presences). I used a subset of the RIS comprising 148 light traps running between 2000 and 2011 for comparability with the time period of the distribution data extracted from the NMRS. Presence-absence and total abundances (summed across all years between 2000 and 2011) from the RIS data were available for 53 quadrants and 24 hectads in the NMRS and were used to test if the predictions could be used as a proxy for habitat quality (e.g. do predictions correlate with the abundances of the Brindled Green moth in light traps)? I used variance component analysis under hierarchical sampling (Crawley 2013) to quantify the variation in predicted probability of occurrence between and within hectads.

3.4 Results

3.4.1 Species-environment associations

Marginal effects of the four environmental predictors on the probability of occurrence of the Brindled Green moth did not differ substantially between quadrant

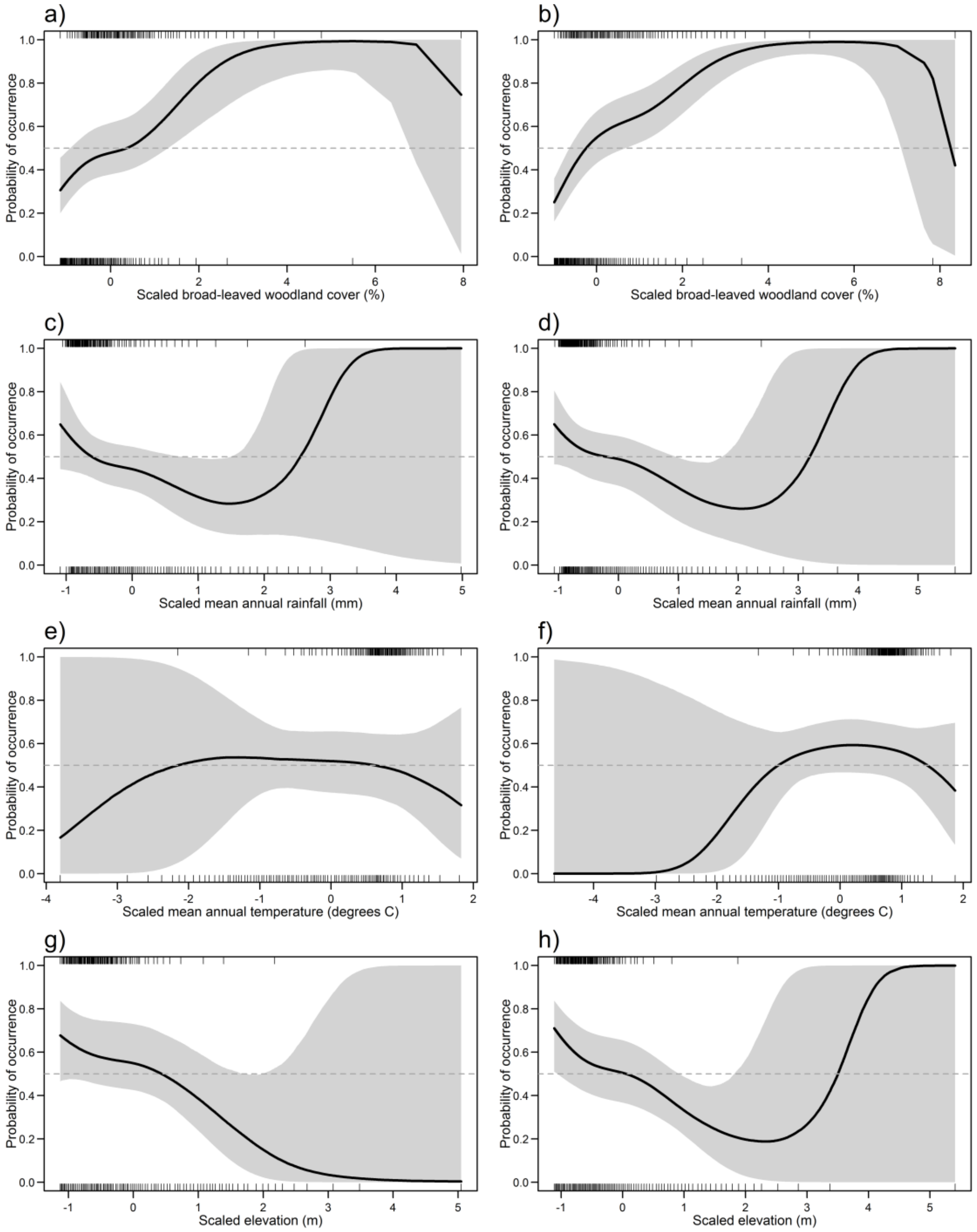

Fig. 3.1 Marginal effects

Marginal effects of broad-leaved woodland cover (a, b), mean annual rainfall (c, d), mean annual temperature (e, f) and elevation (g, h) on the probability of occurrence of the Brindled Green moth at 100km^2 (a, c, e, g) and 25km^2 grains (b, d, f, h). Predictions are based on multiplying the regression spline bases by their respective parameter estimates and adding the variance from the intercept parameter, all derived from a generalised additive model. Solid black lines are the median of 20000 Markov Chain Monte Carlo simulations. Grey areas are the 95% credible intervals. Quantile distributions of the observed data are shown above (presences) and below (absences) each plot.

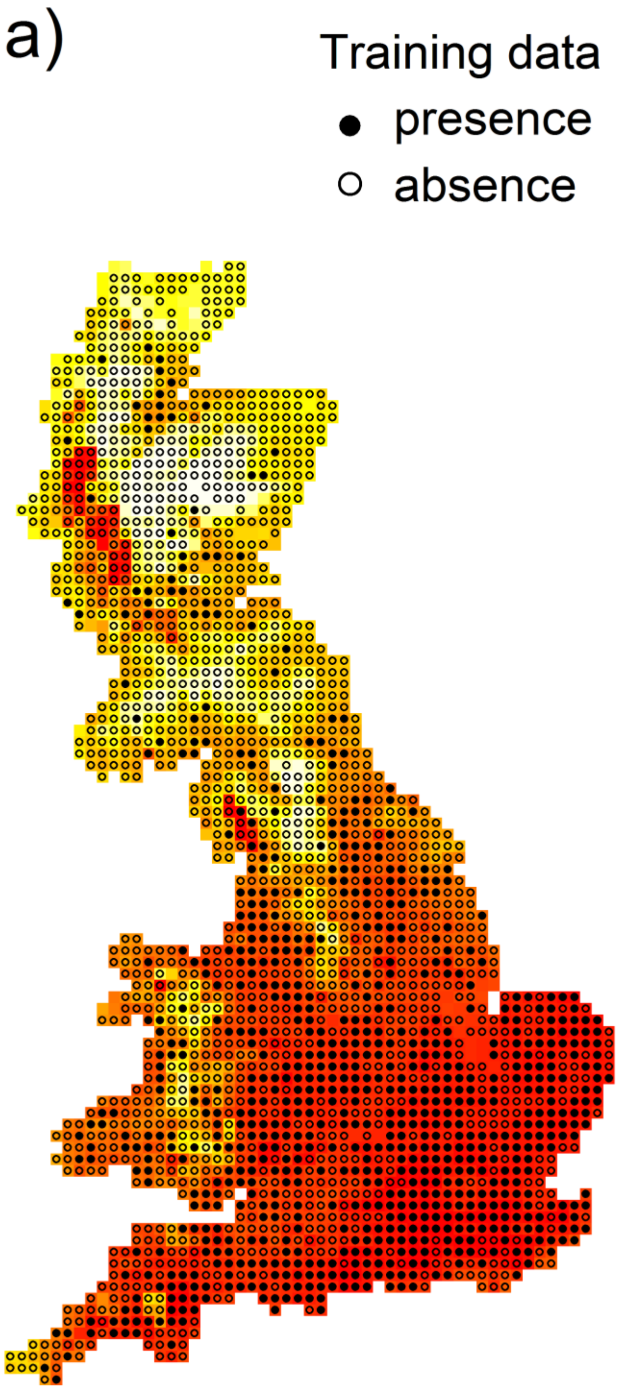

Fig. 3.2 Predicted probability of occurrence for the Brindled Green moth, as predicted by the Beale model fitted at a) hectad (100km^2) and b) quadrant (25km^2) grains.

Empty circles are cells that have been visited (defined as having a record for at least one macromoth between 2000 and 2011), but with no record of the Brindled Green moth. Filled circles are cells with one or more records for the Brindled Green. No circle indicates cells that have received no visits (no moths have been recorded in the National Moth Recording Scheme).

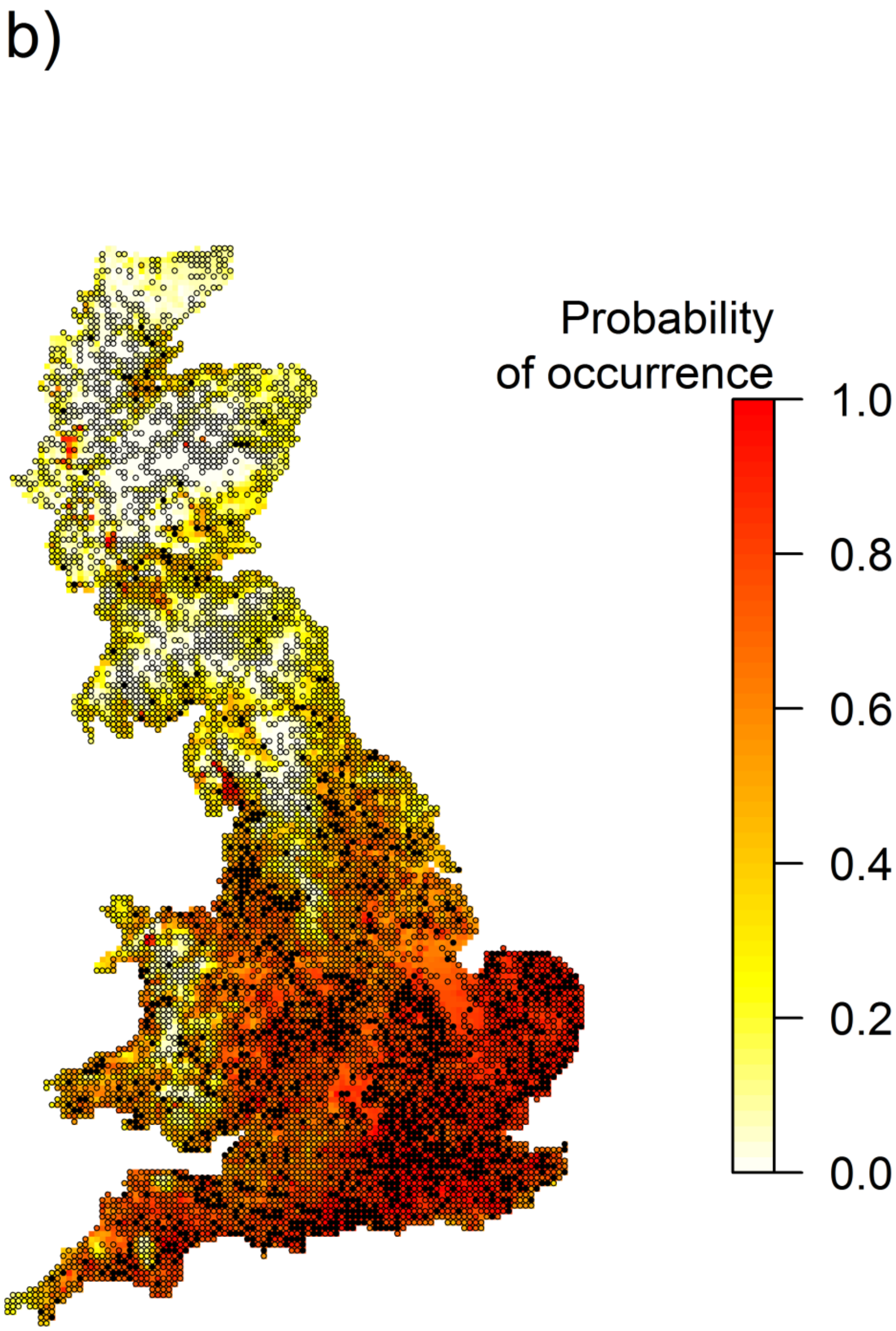

Fig. 3.2 continued

and hectad grains (Fig. 3.1). Probability of occurrence was positively related to WDCV (Fig. 3.1 a and b). MAR (Fig. 3.1 c and d) and ELV (Fig. 3.1 g and h) showed very similar marginal effects, especially at the quadrant grain, both having a negative relationship with probability of occurrence over most of the range of observed values (note that the deviation from this trend at high values is accompanied by large credible intervals indicate high uncertainty). Low probabilities of occurrence are clearly associated with high ELV as evidenced by the predictions for Exmoor, Dartmoor, Snowdonia, the Pennines and the Scottish Highlands (Fig. 3.2). There was some evidence for a hump-shaped relationship between MAT and probability of occurrence, with highest probability of occurrence at intermediate temperatures (Fig. 3.1 e and f). Predictions for extreme values of all four environmental predictors were associated with high levels of uncertainty: 95% credible intervals spanned the full range of possible values of probability of occurrence, presumably because of limited data for extreme values.

Within each spatial grain the overall relative importance of residual spatial autocorrelation was higher than for the four measured environmental covariates. Differences in the overall relative importance of ELV, MAR, MAT and WDCV within each spatial grain were negligible with all components having very similar relative importance. It is not surprising that each of the environmental predictors had high relative importance as they were selected based on a priori knowledge about the Brindled Green moth. MAT had the lowest impact on probability of occurrence at both spatial grains. Relative importance of the covariates did not differ substantially between spatial grains (Table 3.1).

The Beale observer effort model estimates a spatially explicit error term for each grid cell in the analysis. This parameter captures residual spatial autocorrelation (RSA) which may be driven by unmeasured environmental variables, poor specification of the species-environment relationship, spatial processes (e.g. dispersal limitation and source-sink dynamics) and stochastic events (e.g.

Table 3.1 Overall relative importance of the covariate effects and the spatially explicit error term in predicting probability of occurrence of the Brindled Green at two spatial grains.

The values are calculated as the median value of relative importance across all grid cells with 95% credible intervals, following the procedure described in Beale *et al.* (2014).

	Overall relative importance (95% CI)	
	Hectad (100 km^2)	Quadrant (25 km^2)
Mean annual temperature (MAT)	0.756 (0.657, 0.934)	0.776 (0.647, 0.953)
Mean annual rainfall (MAR)	0.792 (0.682, 0.949)	0.780 (0.689, 0.946)
Elevation (ELV)	0.815 (0.690, 0.974)	0.790 (0.654, 0.961)
% Broadleaved woodland cover (WDCV)	0.787 (0.723, 0.948)	0.793 (0.701, 0.945)
Residual spatial autocorrelation (RSA)	0.880 (0.656, 0.970)	0.894 (0.695, 0.977)

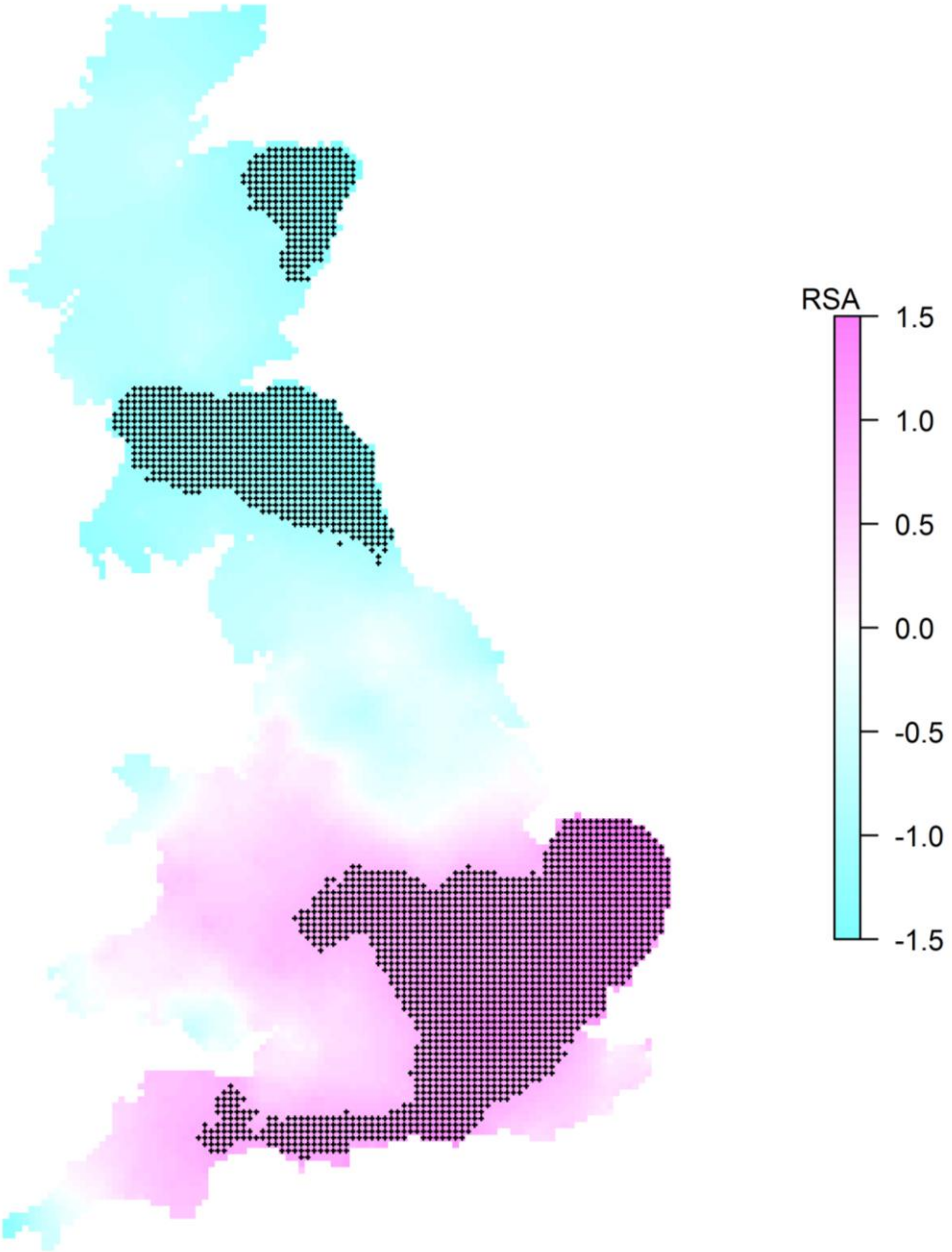

Fig. 3.3 Residual spatial autocorrelation (RSA) in UK quadrants (25 km^2 grain) for the Brindled Green moth

RSA is a spatially explicit error term estimated using an intrinsic conditional autoregressive model (iCAR). Values of RSA are the median of 20000 Markov Chain Monte Carlo simulations. White areas with RSA close to zero indicate regions where environmental variables (temperature, rainfall, broad-leaved woodland cover and elevation) predict well the probability of occurrence. Pink areas indicate regions where the probability of presence is much higher than predicted by environmental variables and blue areas where the probability of presence is much lower than predicted by environmental variables. Black cross symbols indicate quadrants where the 95% credible intervals (0.025 and 0.975 quantiles) of RSA do not overlap 0.

unpredictable disturbance events). Mapping RSA identified a latitudinal gradient in the effect of unmeasured variables on probability of occurrence, with RSA being positive in the southern portion of Britain, close to zero in the region north of the Wash and transitioning to negative at higher latitudes and towards Western peninsulas in Wales and Cornwall (Fig. 3.3). Median RSA was positive and the 95% credible interval (CI) did not overlap zero in an large contiguous area including Norfolk, Suffolk, most of the South east, parts of the west midlands and an area parallel to the south coast, extending as far West as Devon (Fig. 3.3). In the north, there are two regions where median RSA was negative and the 95% CI did not overlap zero. One region incorporates Aberdeenshire, the Grampians and surrounding areas. A second area is the region extending from Glasgow and surrounding areas into Lothian and the borders.

3.4.2 Targeting recording

Comparing the NMRS data with predictions of suitability for the Brindled Green moth highlights areas that have not been visited by recorders, but which are predicted to have high probability of occurrence for the Brindled Green (Fig. 3.2). One such area is south and east of the Wash, comprising parts of South Lincolnshire and Cambridgeshire. Another is largely in Oxfordshire. These gaps in recording are much larger at the quadrant grain. The predictions also highlight a number of isolated hotspots of high probability of occurrence in Western Scotland.

3.4.3 Model performance

Overall model predictive success was slightly better at the quadrant grain (AUC = 0.680 ± 0.075 SD) compared to the hectad grain (0.600 ± 0.173 SD) when compared to the observed presence and absence of the Brindled Green, although predictive success was poor at both spatial grains when evaluated against an independent data set (RIS). Quadrant predictions were able to pick up some variation in suitability within hectads (Fig. 3.4a), although percentage variance components indicated most variation in predicted probability of occurrence was common to both spatial grains (between hectad variance component = 84%). A smaller but substantial amount of variation was between quadrants nested within hectads (within hectad variance component = 16%). Variance in predicted probability of occurrence was most strongly associated with within-hectad variance in WDCV (r^2 = 0.286), while variance in MAR, MAT and ELV had low explanatory power ($r^2 < 0.05$: Fig. 3.4b).

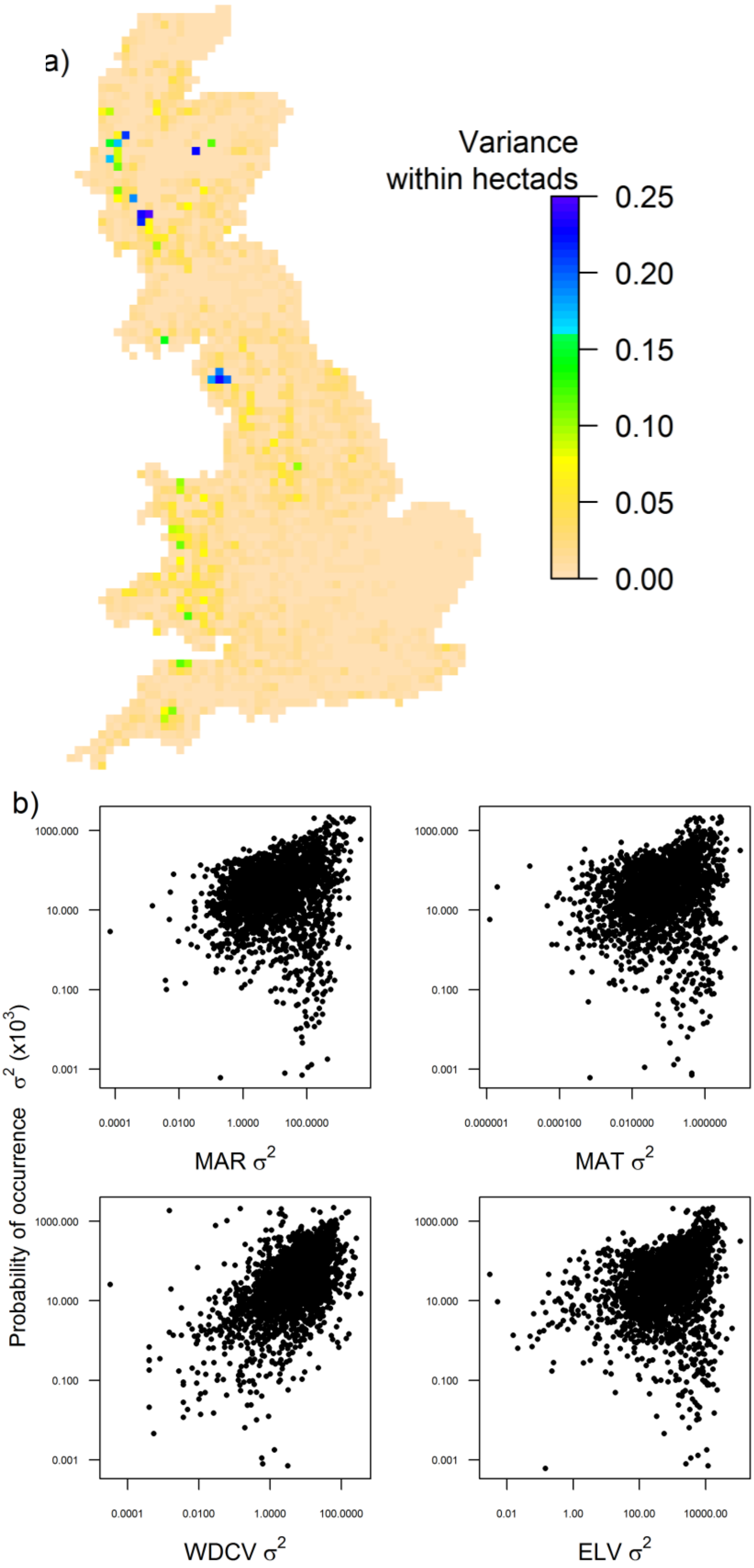

Fig. 3.4 Variance within hectads

Variance of a) predicted probability of occurrence of the quadrants within each hectad and b) the relationship between variance in each of the climate and land cover variables and variance in probability of occurrence within each hectad.

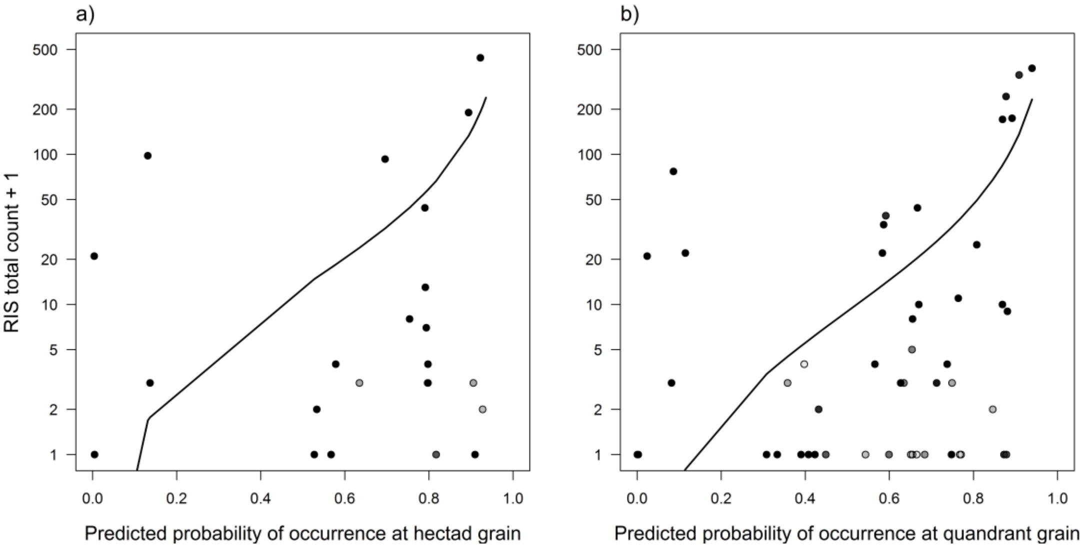

Fig. 3.5 Relationship between predicted probability of occurrence and total annual counts of the Brindled Green moth in RIS light traps.

Predictions are shown in a) 24 hectads (100 km^2 grain) and b) 53 quadrants (25 km^2 grain). Solid black lines are the fitted values for a generalised linear model with poisson error structure and logit transformed probability of occurrence as the dependent variable. Points are shaded according to sampling effort (how many years light traps were operating in that grid cell between 2000 and 2011), with darker points indicating higher sampling effort.

There was a weak but positive relationship between predicted probability of occurrence and the local abundance of Brindled Green moths in the Rothamsted Light Trap Network (Fig. 3.5).

3.5 Discussion

The application of the Beale observer effort species distribution model to the known distribution of the Brindled Green moth has highlighted five key results. Firstly, I have characterised the marginal effects of four environmental factors whose impact on the species' distribution would be expected, a priori, to be felt at different spatial scales. Second, I have identified a latitudinal gradient in the extent to which probability of occurrence deviates from that predicted purely by the environmental associations modelled, suggesting additional unmeasured variables or spatial processes are important in shaping the distribution of the Brindled Green. Third, a species distribution model accounting for observer effort produced marginally better predictions at a finer spatial grain. Fourth, the Beale observer effort model has generated fine grain (i.e. sub-hectad scale) predictions of probability of occurrence for areas of the distribution that have never been sampled, which provides a potential tool for targeting future activity towards under-recorded areas. Finally, I identify a weak positive association between total counts in RIS light traps and the predicted probability of occurrence of the Brindled Green moth suggesting the application of these methods at finer spatial grains could provide a proxy for local abundance estimates.

3.5.1 What is driving the distribution of the Brindled Green moth?

Like any species distribution model, these marginal effects are associations and not causal effects on the distribution of Brindled Green. At both grains, WDCV had a positive association with probability of occurrence. Higher probability of occurrence in cells with greater broad-leaved woodland cover is consistent with the dependence of the Brindled Green on oak species as the larval foodplant (Waring & Townsend 2009). Greater woodland coverage is also likely to support higher densities of woodland-associated moth species (Fuentes-Montemayor *et al.* 2012) leading to a higher probability of observing the species. The negative association between both MAR and ELV and the probability of occurrence are consistent with patterns in the garden tiger moth (Conrad *et al.* 2002), and UK butterfly species (Roy *et al.* 2001). MAT appeared to have negligible association with the distribution of the Brindled Green, contrary to many of the findings for butterflies (Warren *et al.* 2001) and moths (Pollard 1988) at their northern range limits. One reason for the absence of a relationship could be that MAT masks seasonal and diurnal temperature variation. For example, adult night-flying moths such as the Brindled Green moth are likely to be more affected by mild nights rather than the warm days that influence day-flying butterflies and moths. Warm summer temperatures are known to positively influence butterfly abundance in Britain (Roy *et al.* 2001), while warm, wet Winter temperatures have a negative effect on moth over wintering survival in Britain (Conrad *et al.* 2002). Brindled Green ecology is not sufficiently well-known to speculate on which months it might be most temperature-sensitive, but models more sophisticated than fitted here would be insightful.

Relative importance of WDCV, ELV, MAT and MAR, and the marginal effects of these covariates on the distribution of the Brindled Green moth, were broadly similar at quadrant and hectad grains. I predicted that the species-environment relationship would be stronger at finer grains, especially for those variables that vary substantially within hectads (i.e. ELV and WDCV, but not MAR or MAT), but this was not the case. One reason for this may be that a quadrant is not especially fine-grained relative to the biological scale of interest when mapping species distributions (the "population-scale"). If this is the case the model would need to be fitted to data at an even finer range of spatial grains in order to pin-point the scale of effect (the grain at which elevation and broadleaved woodland cover are most strongly associated with the presence of the Brindled Green). By predicting at finer grains, the issue of recorder effort becomes increasingly important. For the purposes of species atlases in Britain, we usually assume there are no false absences in hectad-grain datasets, yet these results at hectad grain identify a substantial number of hectads with high predicted probability of occurrence but no recorded presences (Fig. 3.2a). This is consistent with a number of studies that have demonstrated the pitfalls of ignoring imperfect detection in species distribution modelling, even at coarser grain sizes (Rota *et al.* 2011; Dorazio 2014; Lahoz-Monfort *et al.* 2014). As noted above, I tried and failed to fit the Beale observer effort model at 4 km^2 grain. Beale (pers. comm.) has suggested Integrated Nested Laplace Approximation (INLA) as a viable tool for efficiently approximating the posterior distributions of hierarchical Bayesian models with large datasets (see Bivand *et al.* 2015 for implementation in R), although this has yet to be applied to hierarchical model structures.

The map of median RSA indicates that there are large regions of Britain in which the four measured environmental variables substantially under- or over-predict the probability of occurrence of the Brindled Green (Fig. 3.3). Positive and negative RSA values indicates that probability of occurrence is higher and lower, respectively, than would be predicted based on measured environmental covariates, while an RSA close to zero indicates the environmental variables capture well the probability of occurrence.

Unfortunately, there are limitations when interpreting these patterns in RSA: it is not possible to unpick whether it is stochastic processes (e.g. neutral) or unmeasured environmental covariates that are driving RSA. One plausible explanation for the decreasing RSA with latitude is spatial patterns of colonisation and extinction, as described in metapopulation theory (Hanski 1994). Dispersal rates can be different at the range limit compared to the core. The decreasing values of RSA at higher latitudes and towards peninsulas in Wales and Cornwall may reflect more fragmented and lower quality habitat with increasing latitude or on peninsulas. If these are population sinks, supporting smaller populations, dispersal may be selected against (Gaston 2009). Limited dispersal from these populations would translate into lower probability of occurrence than expected based on habitat suitability alone, consistent with the negative RSA observed towards the fringes of the British distribution of the Brindled Green. By contrast, predicted probability of occurrence at lower latitudes tends to be greater than would be predicted by habitat suitability based on the four environmental predictors I have used to model the species-environment relationship. Some of this positive RSA may be explained by WDCV failing to capture the effect of solitary oaks on the distribution of the Brindled Green, or due to the exclusion of broad-leaved woodland habitat not dominated by trees > 5m high or with tree cover > 20% in the Land Cover Map 2007 (see Morton *et al.* 2011). There is evidence that solitary trees and hedgerows can act as stepping stones between forest fragments for other macro-moth species with affinity to woodland (Slade *et al.* 2013). Indeed, the Brindled Green has been recorded in parkland and gardens, presumably where there are solitary oaks that can be larval hosts. These solitary oaks are likely to be much more common in more urbanised areas in southern Britain. Moreover, broadleaved woodlands themselves are much more fragmented in the southern lowlands (54 % of woodlands are < 100 ha in England compared to 18 % in Scotland: Watts 2006). Together, the large numbers of solitary oaks and the greater movement of individuals between networks of fragmented woodland in the south would lead to greater occurrence of the Brindled Green moth at lower latitudes than would be predicted by the species-environment relationship captured here.

The iCAR model requires that a decision is made *a priori* about the distance over which neighbouring cells are able to influence one another (e.g. the assumed scale of spatial autocorrelation). It isn’t obvious what distance would be appropriate to capture the influence of neighbouring grid cells in a given dataset (Yen *et al.* 2013). Increasing the size of this neighbourhood would take into account processes operating over larger spatial scales and would allow grid cells with high quality habitat to influence the probability of occurrence in cells further afield (Beale *et al.* 2010). Matching the chosen distance to the characteristic scale of processes captured by RSA (which will themselves differ) is difficult and could greatly affect the magnitude of RSA. My chosen neighbourhood of grid cells allows only the habitat suitability of the eight grid cells directly neighbouring the focal cell to influence it. Unfortunately, there is very little information about dispersal processes of the Brindled Green which could be used to guide the decision about the neighbourhood of grid cells that would be appropriate to capture spatial processes. One approach would be to estimate mobility based on traits including wing morphology adult and larval feeding guild and forest affinity as evidenced by Slade *et al.* (2013) for other macro-moths. There is some evidence to suggest that moth species in general have high mobility and are unlikely to be dispersal limited.

3.5.2 Identifying false absences

The predictions identify areas with high probability of occurrence that have not been sampled or have experienced low numbers of visits in the period 2000-2011. A potential application for this feature of the model would be to target recording activity to these grid cells. Such an approach could better capture the underlying distribution without any increase in overall recording activity. It would also provide a direct validation of the model predictions.

3.5.3 Model performance

As predicted, overall model performance was better at the quadrant grain than the hectad grain. This suggests that finer spatial grains could yield better species distribution models, provided the observation process is modelled. However, the improvement in performance was small. One reason for this may be that improvements associated with finer grain size are limited by the amount of within-hectad variation. My results indicate that just 16% of the total variation was between quadrants (within hectads), meaning the remaining 84% of variation is common to both scales. One reason for this may be the limited number of hectads containing more than one light trap with which to distinguish variation within cells.

Overall model predictive success, evaluated against an independent data set was still poor at both spatial grains. One source of discrepancy between model predictions and observed data in the RIS is for those cells where the model predicts high probability of occurrence for the Brindled Green moth but where it is absent from RIS light traps. One explanation would be that the model is over-predicting probability of occurrence in these cells. However, it may be that RIS traps sample only a small fraction of a quadrant and an even smaller fraction of a hectad. Estimates for the range of attraction of light traps have varied from 3 m to ~ 200 m, depending on the type of light trap used, with most finding moths are attracted primarily from short distances (van Grunsven *et al.* 2014 and references therein). RIS light traps are standardised and have a known detection radius. By contrast NMRS data come from a range of lights traps (along with many other methods of sampling). Of the 53 quadrant cells with RIS data to validate the predictions, 28 were predicted high probability of occurrence (> 0.6) for the Brindled Green, but the species was absent from 9 of these. Of these 9 RIS absences, only 1 grid cell had Brindled Green records in the NMRS, lending evidence to the explanation that the model appears to over-predict the distribution of the Brindled Green. However, NMRS recording activity in these cells was substantially lower (median 7 visits in 12 years) than in cells where the Brindled Green had been recorded (median 209 visits in 12 years). If the RIS is undersampling the quadrant grain, model validation with the RIS data would require model predictions at spatial grains substantially finer than a quadrant, and probably finer even than $1km^2$. Alternatively, resurveying (or surveying) those grid cells with no records would provide a proper validation of the model predictions.

A second discrepancy is between model predictions and the NMRS data. This is apparent in cells where low probability of occurrence is predicted, but the NMRS data show a record of the Brindled Green (see Fig. 3.2). One explanation for these errors could be poor model performance (e.g. missing environmental covariates). Alternatively the migration of individuals between suitable habitat patches could generate these patterns. As explained above, the spatial autocorrelation captured by the RSA parameter may be operating over larger spatial scales than I specified when fitting the model, which would mean the full influence of spatial autocorrelation would not be captured by the RSA parameter. Isolated records in areas of low probability of occurrence may be fed by movement from grid cells with high quality habitats, but those cells may be outside the neighbourhood I have specified. Alternatively, as noted above, the larval hosts (pedunculate and sessile oaks) are likely to be present in land cover types outside of broad-leaved woodland (e.g. parks, gardens or fields with isolated oak trees). In fact, the Brindled Green is found in parkland and some gardens and suburban areas (Waring & Townsend 2009). Maps of the NMRS data and predicted probability of occurrence also indicate that records of the Brindled Green in cells with low predicted probability of occurrence are generally isolated from neighbouring records (see Fig. 3.2). Long-distance movements between sites of high probability of occurrence may result in these isolated records.

3.5.4 Do the predictions correlate with local abundance estimates for the Brindled Green?

There is a large body of evidence that habitat quality is positively associated with abundance (Matter & Roland 2002; Oliver *et al.* 2012; Howard *et al.* 2014; Curtis & Isaac 2015). The results presented here indicate a weak correlation between probabilities of occurrence and total counts of the Brindled Green in light traps. The limited sample area of RIS light traps explored in the previous section also has implications for the observed relationship between predicted probability of occurrence and abundance in RIS light traps. As I note in Chapter 1, abundance scales allometrically with the spatial extent sampled (Pautasso & Gaston 2006), therefore total counts in RIS light traps would be expected to severely underestimate the abundance in a 25 km^2 cell. Once it is possible to fit the Beale observer effort model at 1 km^2 or finer, it will be possible to start assessing the relationship between predicted probability of occurrence (as a proxy for habitat quality) and local abundance.

3.5.5 Conclusions

By modelling under-recorded species distributions at fine spatial grains, using information about species-environment associations, probability of detection and accounting for spatial autocorrelation, I have shown that the Beale observer effort model is a promising tool for addressing the Wallacean shortfall, with applications in quantifying the environmental covariates of species distributional patterns, exploring their characteristic the scales of effect and for focusing recording activity towards those sites that are more likely to yield undiscovered populations. These results have highlighted that the scale of sampling (in both training and test data) and the characteristic scale of the ecological processes shaping species distributions are critical considerations for accurate modelling of species distributions. Key challenges to matching the scale of effect and the scale of sampling include estimating the scale at which ecological processes like dispersal operate and the further development of statistical and efficient computational methods to address biases in fine grain data.

3.6 References

Aranda, S.C., Gabriel, R., Borges, P.A. V., de Azevedo, E.B. & Lobo, J.M. (2011). Designing a survey protocol to overcome the Wallacean shortfall: a working guide using bryophyte distribution data on Terceira Island (Azores). The Bryologist, 114, 611–624.

Azaele, S., Cornell, S.J. & Kunin, W.E. (2012). Downscaling species occupancy from coarse spatial scales. Ecological Applications, 22, 1004–1014.

Barbet-Massin, M., Jiguet, F., Albert, C.H. & Thuiller, W. (2012). Selecting pseudo-absences for species distribution models: how, where and how many? Methods in Ecology and Evolution, no–no.

Barwell, L.J., Azaele, S., Kunin, W.E. & Isaac, N.J.B. (2014). Can coarse-grain patterns in insect atlas data predict local occupancy? Diversity and Distributions, 20, 895–907.

Beale, C.M., Brewer, M.J. & Lennon, J.J. (2014). A new statistical framework for the quantification of covariate associations with species distributions. Methods in Ecology and Evolution, 5, 421–432.

Beale, C.M., Lennon, J.J., Yearsley, J.M., Brewer, M.J. & Elston, D. a. (2010). Regression analysis of spatial data. Ecology Letters, 13, 246–264.

Beck, J., Ballesteros-Mejia, L., Nagel, P. & Kitching, I.J. (2013). Online solutions and the 'Wallacean shortfall': what does GBIF contribute to our knowledge of species' ranges? Diversity and Distributions, 19, 1043–1050.

Bini, L.M., Diniz-Filho, J.A.F., Rangel, T.F.L.V.B., Bastos, R.P. & Pinto, M.P. (2006). Challenging Wallacean and Linnean shortfalls: knowledge gradients and conservation planning in a biodiversity hotspot. Diversity and Distributions, 12, 475–482.

Bivand, R.S., Virgilio, G.-R. & Havard, R. (2015). Spatial Data Analysis with R - INLA with Some Extensions. Journal of Statistical Software, 63.

Burns, F., Eaton, M.A., Gregory, R.D., Al Fulaij, N., August, T.A., Biggs, J., Bladwell, S., Brereton, T., Brooks, D., Clubbe, C., Dawson, J., Dunn, E., Edwards, B., Falk, S., Gent, T., Gibbons, D., Gurney, M., Haysom, K., Henshaw, S., Hodgetts, N., Isaac, N., McLaughlin, M., Musgrove, A., Noble, D., O'Mahony, E., Pacheco, M., Roy, D., Sears, J., Shardlow, M., Stringer, C., Taylor, A., Thompson, P., Walker, K., Walton, P., Willing, M., Wilson, J. & Wynde, R. (2013). State of Nature Report. The State of Nature partnership.

Chen, G., Kéry, M., Plattner, M., Ma, K. & Gardner, B. (2013). Imperfect detection is the rule rather than the exception in plant distribution studies. Journal of Ecology, 101, 183–191.

Comte, L. & Grenouillet, G. (2013). Species distribution modelling and imperfect detection: comparing occupancy versus consensus methods. Diversity and Distributions, 19, 996–1007.

Conrad, K.F., Woiwod, I.P. & Perry, J.N. (2002). Long-term decline in abundance and distribution of the garden tiger moth (Arctia caja) in Great Britain. Biological Conservation, 106, 329–337.

Crawley, M.J. (2013). Th R Book, 2nd edn. John Wiley & Sons, Chichester.

Curtis, R.J. & Isaac, N.J.B. (2015). The effect of temperature and habitat quality on abundance of the Glanville fritillary on the Isle of Wight: implications for conservation management in a warming climate. Journal of Insect Conservation.

Diniz-Filho, J.A.F., De Marco Jr, P. & Hawkins, B.A. (2010). Defying the curse of ignorance: perspectives in insect macroecology and conservation biogeography. Insect Conservation and Diversity, 3, 172–179.

Dorazio, R.M. (2014). Accounting for imperfect detection and survey bias in statistical analysis of presence-only data. Global Ecology and Biogeography, 23, 1472–1484.

Fielding, A.H. & Bell, J.F. (1992). A review of methods for the assessment of prediction errors in conservation presence / absence models. Environmental Conservation, 24, 38–49.

Fox, R., Oliver, T.H., Harrower, C., Parsons, M.S., Thomas, C.D. & Roy, D.B. (2014). Long-term changes to the frequency of occurrence of British moths are consistent with opposing and synergistic effects of climate and land-use changes. Journal of Applied Ecology, 51, 949–957.

Fuentes-Montemayor, E., Goulson, D., Cavin, L., Wallace, J.M. & Park, K.J. (2012). Factors influencing moth assemblages in woodland fragments on farmland: Implications for woodland management and creation schemes. Biological Conservation, 153, 265–275.

García-Roselló, E., Guisande, C., Manjarrés-hernández, A., González-dacosta, J., Heine, J., Pelayo-villamil, P., González-vilas, L., Vari, R.P., Vaamonde, A., Granado-lorencio, C. & Lobo, J.M. (2015). Can we derive macroecological patterns from primary Global Biodiversity Information Facility data ? Global Ecology and Biogeography, 24, 335–347.

Gaston, K.J. (2009). Geographic range limits: achieving synthesis. Proceedings of the Royal Society - Series B: Biological Sciences, 276, 1395–1406.

Gaston, K.J. (1991). How large is a species ' Geographic Range? Oikos, 61, 434–438.

Gaston, K.J. & Fuller, R. a. (2009). The sizes of species' geographic ranges. Journal of Applied Ecology, 46, 1–9.

Gillingham, P.K., Palmer, S.C.F., Huntley, B., Kunin, W.E., Chipperfield, J.D. & Thomas, C.D. (2012). The relative importance of climate and habitat in determining the distributions of species at different spatial scales: A case study with ground beetles in Great Britain. Ecography, 35, 831–838.

Van Grunsven, R.H. a., Lham, D., van Geffen, K.G. & Veenendaal, E.M. (2014). Range of attraction of a 6-W moth light trap. Entomologia Experimentalis et Applicata, 152, 87–90.

Guillera-Arroita, G., Lahoz-Monfort, J.J., MacKenzie, D.I., Wintle, B. a & McCarthy, M. a. (2014). Ignoring imperfect detection in biological surveys is dangerous: a response to 'fitting and interpreting occupancy models'. PloS one, 9, e99571.

Hanski, I. (1994). A Practical Model of Metapopulation Dynamics. Journal of Animal Ecology, 63, 151–162.

He, F. & Gaston, K.J. (2000). Occupancy-abundance relationships and sampling scales. Ecography, 23, 503–511.

Hill, N.A., Lucieer, V., Barrett, N.S., Anderson, T.J. & Williams, S.B. (2014). Filling the gaps: Predicting the distribution of temperate reef biota using high resolution biological and acoustic data. Estuarine, Coastal and Shelf Science, 147, 137–147.

Howard, C., Stephens, P. a., Pearce-Higgins, J.W., Gregory, R.D. & Willis, S.G. (2014). Improving species distribution models: The value of data on abundance. Methods in Ecology and Evolution, 5, 506–513.

Intermap Technolologies. (2007). Intermap Product Handbook and Quick Start Guide, Standard Edition, version 4.0.

Isaac, N.J.B., van Strien, A.J., August, T. a., de Zeeuw, M.P. & Roy, D.B. (2014). Statistics for citizen science: extracting signals of change from noisy ecological data. Methods in Ecology and Evolution.

IUCN International Union for the Conservation of Nature. (2001). IUCN Red List Categories and Criteria: Version 3.1.

Jetz, W., McPherson, J.M. & Guralnick, R.P. (2012). Integrating biodiversity distribution knowledge: toward a global map of life. Trends in Ecology & Evolution, 27, 151–9.

Jetz, W., Sekercioglu, C.H. & Watson, J.E.M. (2008). Ecological correlates and conservation implications of overestimating species geographic ranges. Conservation Biology, 22, 110–119.

Keil, P., Belmaker, J., Wilson, A.M., Unitt, P. & Jetz, W. (2012). Downscaling of species distribution models: a hierarchical approach. Methods in Ecology and Evolution, 4, 82–94.

Keil, P. & Jetz, W. (2014). Downscaling the environmental associations and spatial patterns of species richness. Ecological Applications, 24, 823–831.

Keith, S.A., Webb, T.J., Böhning-Gaese, K., Connolly, S.R., Dulvy, N.K., Eigenbrod, F., Jones, K.E., Price, T., Redding, D.W., Owens, I.P.F. & Isaac, N.J.B. (2012). What is macroecology? Biology letters, 8, 904–6.

Kéry, M. & Royle, J.A. (2008). Hierarchical Bayes estimation of species richness and occupancy in spatially replicated surveys. Journal of Applied Ecology, 45, 589–598.

Kunin, W.E. (1998). Extrapolating Species Abundance Across Spatial Scales. Science, 281, 1513–1515.

Lahoz-Monfort, J.J., Guillera-Arroita, G. & Wintle, B. a. (2014). Imperfect detection impacts the performance of species distribution models. Global Ecology and Biogeography, 23, 504–515.

Lessmann, J., Muñoz, J. & Bonaccorso, E. (2014). Maximizing species conservation in continental Ecuador: A case of systematic conservation planning for biodiverse regions. Ecology and Evolution, 4, 2410–2422.

Lobo, J.M., Jiménez-Valverde, A. & Hortal, J. (2010). The uncertain nature of absences and their importance in species distribution modelling. Ecography, 33, 103–114.

Lomolino, M. V. & Heaney, L.R. (2004). Frontiers in Biogeography: New Directions in the Geography of Nature. Sinauer Associates, Sunderland, Massachusetts.

Lunn, D., Spiegelhalter, D., Thomas, A. & Best, N. (2009). The BUGS project: Evolution, critique and future directions (with discussion). Journal of the American Statistical Association, 28, 3049–3082.

Matter, S.F. & Roland, J. (2002). An experimental examination of the effects of habitat quality on the dispersal and local abundance of the butterfly Parnassius smintheus. Ecological Entomology, 27, 308–316.

McCarthy, M.A., Moore, J.L., Morris, W.K., Parris, K.M., Garrard, G.E., Vesk, P. a., Rumpff, L., Giljohann, K.M., Camac, J.S., Bau, S.S., Friend, T., Harrison, B. & Yue, B. (2013). The influence of abundance on detectability. Oikos, 122, 717–726.

Meyer, C., Kreft, H., Guralnick, R. & Jetz, W. (2015). Global priorities for an effective information basis of biodiversity distributions. PeerJ PrePrints, 3, e1057.

Morton, D., Rowland, C., Wood, C., Meek, L., Marston, C., Smith, G., Wadsworth, R. & Simpson, I. (2011). Final Report for LCM2007 - the new UK land cover map. Countryside Survey Technical Report No 11/07 logy and Hydrology (CEH Project Number: CO3259).

Oliver, T.H., Gillings, S., Girardello, M., Rapacciuolo, G., Brereton, T.M., Siriwardena, G.M., Roy, D.B., Pywell, R. & Fuller, R.J. (2012). Population density but not stability can be predicted from species distribution models. Journal of Applied Ecology, 49, 581–590.

Pautasso, M. & Gaston, K.J. (2006). A test of the mechanisms behind avian generalized individuals-area relationships. Global Ecology and Biogeography, 15, 303–317.

Pearson, R.G., Dawson, T.P. & Liu, C. (2004). Modelling species distribution in Britain: a hierarchical integration of climate and land cover. Ecography, 27, 285–298.

Pereira, H.M., Belnap, J., Brummit, N., Collen, B., Ding, H., Gonzalez-Espinosa, M., Gregory, R.D., Honrado, J., Jongman, R.H.G., Juillard, R., McRae, L., Proenca, V., Rodrigues, P., Opige, M., Rodriguez, J.P., Schmeller, D.S., van Swaay, C. & Vieira, C. (2010). Global biodiversity monitoring. Frontiers in Ecology and the Environment, 8, 458–459.

Perry, M. & Hollis, D. (2005). The generation of monthly gridded datasets for a range of climatic variables over the UK. International Journal of Climatology, 25, 1041–1054.

Plummer, M., Best, N., Cowles, K. & Vines, K. (2006). CODA: Convergence Diagnosis and Output Analysis for MCMC. R News, 6, 7–11.

Pollard, E. (1988). Temperature, Rainfall and Butterfly Numbers. The Journal of Applied Ecology, 25, 819–828.

Powney, G.D. & Isaac, N.J.B. (2015). Beyond maps : a review of the applications of biological records. Biological Journal of the Linnean Society.

R Core Development Team. (2014). R: A language and environment for statistical computing. Version 3.1.1. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/.

Raxworthy, C.J., Martinez-meyer, E., Horning, N., Nussbaum, R.A., Schneider, G.E., Ortega-huerta, M.A. & Peterson, A.T. (2003). Predicting distributions of known and unknown reptile species in Madagascar. 33, 837–841.

Rondinini, C., Wilson, K. a., Boitani, L., Grantham, H. & Possingham, H.P. (2006). Tradeoffs of different types of species occurrence data for use in systematic conservation planning. Ecology Letters, 9, 1136–1145.

Rota, C.T., Fletcher, R.J., Evans, J.M. & Hutto, R.L. (2011). Does accounting for imperfect detection improve species distribution models? Ecography, 34, 659–670.

Roy, D.B., Rothery, P., Moss, D., Pollard, E. & Thomas, J. a. (2001). Butterfly numbers and weather: Predicting historical trends in abundance and the future effects of climate change. Journal of Animal Ecology, 70, 201–217.

Schmeller, D.S., Henry, P.Y., Julliard, R., Gruber, B., Clobert, J., Dziock, F., Lengyel, S., Nowicki, P., DÉri, E., Budrys, E., Kull, T., Tali, K., Bauch, B., Settele, J., Van Swaay, C., Kobler, A., Babij, V., Papastergiadou, E. & Henle, K. (2009). Advantages of Volunteer-Based Biodiversity Monitoring in Europe. Conservation Biology, 23, 307–316.

Seo, C., Thorne, J.H., Hannah, L. & Thuiller, W. (2009). Scale effects in species distribution models: implications for conservation planning under climate change. Biology letters, 5, 39–43.

Slade, E.M., Merckx, T., Riutta, T., Bebber, D.P., Redhead, D., Riordan, P. & MacDonald, D.W. (2013). Life-history traits and landscape characteristics predict macro-moth responses to forest fragmentation. Ecology, 94, 1519–1530.

Sousa-Silva, R., Alves, P., Honrado, J. & Lomba, A. (2014). Improving the assessment and reporting on rare and endangered species through species distribution models. Global Ecology and Conservation, 2, 226–237.

Van Strien, A.J., Van Swaay, C. a M. & Termaat, T. (2013). Opportunistic citizen science data of animal species produce reliable estimates of distribution trends if analysed with occupancy models. Journal of Applied Ecology, 50, 1450–1458.

Sturtz, S., Ligges, U. & Gelman, A. (2005). R2WinBUGS: A Package for Running WinBUGS from R. Journal of Statistical Software, 12, 1–16.

Townsend Peterson, A., Soberon, J., Pearson, R., Anderson, R.P., Martinez-Meyer, E., Nakamura, M. & Araujo, M.B. (2011). Ecological Niches and Geographical Distributions. Princeton University Press, Oxford.

Waring, P. & Townsend, M. (2009). Field Guide to the Moths of Great Britain and Ireland, 2nd. ed.n. British Wildlife Publishing, Gillingham, UK.

Warren, M.S., Hill, J.K., Thomas, J. a, Asher, J., Fox, R., Huntley, B., Roy, D.B., Telfer, M.G., Jeffcoate, S., Harding, P., Jeffcoate, G., Willis, S.G., Greatorex-Davies, J.N., Moss, D. & Thomas, C.D. (2001). Rapid responses of British butterflies to opposing forces of climate and habitat change. Nature, 414, 65–69.

Watts, K. (2006). British forest landscapes - the legacy of fragmentation. Quarterly Journal of Forestry, 273–279.

Whittaker, R.., Araujo, M.B., Jepson, P., Ladle, R.J., Watson, J.E.M. & Willis, K.J. (2005). Conservation biogeography: asessment and prospect. Diversity and Distributions, 11, 3–23.

Yen, J.D.L., Thomson, J.R. & Mac Nally, R. (2013). Is there an ecological basis for species abundance distributions? Oecologia, 171, 517–525.

Zillio, T. & He, F. (2010). Modeling spatial aggregation of finite populations. Ecology, 91, 3698–706.

Chapter 4
Measuring β-diversity with species abundance data

4.1 Abstract

In 2003, 24 presence-absence β-diversity metrics were reviewed and a number of trade-offs and redundancies identified. I present a parallel investigation into the performance of abundance-based metrics of β-diversity. I test 29 metrics for 18 desirable properties: metrics should be independent of α-diversity and cumulative along a gradient of species turnover. Similarity should be probabilistic when assemblages are independently and identically distributed. Metrics should have a minimum of zero and increase monotonically with the degree species turnover, decoupling of species ranks and evenness differences. However, complete species turnover should always generate greater values of β than extreme ranks shifts or evenness differences. Metrics should have a fixed upper limit, symmetry ($\beta_{A,B}=\beta_{B,A}$), double-zero asymmetry for double-absences and double-presences and not decrease in a series of nested assemblages. Additionally, metrics should be independent of species replication the units of abundance and differences in total abundance between sampling units. When samples are used to infer β-diversity, metrics should be independent of sample sizes and independent of unequal sample sizes. I also test for five "personality properties". Thirteen metrics were outperformed or equalled across all conceptual and sampling properties. Differences in sensitivity to species' abundance lead to a performance trade-off between sample size bias and the ability to detect turnover among rare species. In general, abundance-based metrics are substantially less biased in the face of undersampling, although the presence-absence metric, β_{sim}, performed well overall. Only $\beta_{Baselga\ R\ turn}$, $\beta_{Baselga\ B\text{-}C\ turn}$ and β_{sim} measured purely species turnover and were independent of nestedness. Among the other metrics, sensitivity to nestedness varied >4-fold. These results indicate large amounts of redundancy among existing β-diversity metrics, while the estimation of unseen shared and unshared species is lacking and should be addressed in the design of new abundance-based metrics.

4.2 Introduction

Metrics of *β*-diversity are widely used in ecological studies, but there is uncertainty about the degree of redundancy among the metrics available and the facets of *β*-diversity being measured. Whittaker (1960, 1972) broadly defined *β*-diversity as the spatial variation (turnover) in species composition and abundance between sampling units, while *α*-diversity is the local diversity within a single sampling unit and γ-diversity measures larger-scale diversity.

The number of studies investigating *β*-diversity has increased considerably in recent years (Koleff *et al.* 2003a; Anderson *et al.* 2011). *β*-diversity has been linked to the shape of the species area-curve (Harte *et al.* 1999), variance in species occupancy (McGlinn & Hurlbert 2012) and species' spatial aggregation (Morlon *et al.* 2008). The distance-decay relationship (the increase in *β*-diversity with geographical distance) is a critical component of three of the six unified theories of biodiversity reviewed by McGill (2010). Measures of *β*-diversity in relation to environmental and spatial gradients have been used to unpick community assembly (Chase 2003) and drivers of global scale biodiversity patterns (Qian & Ricklefs 2007). Empirical measures of *β*-diversity can be used to delineate biotic regions (Holt *et al.* 2013) and to inform the optimal configuration of reserves (Wiersma & Urban 2005). *β*-diversity has been used to evaluate the landscape-scale implications of farm management (Gabriel *et al.* 2006) and to assess the effects of environmental change on biotic homogenisation (Baiser *et al.* 2012). Because *γ*-diversity is entirely determined by the *α* and *β* components of diversity, empirical estimates of *β*-diversity link biodiversity at local and regional scales (Smith 2010). Turnover in abundance also has important implications for ecosystem functioning and monitoring responses to disturbance (Balata *et al.* 2007).

A key distinction is between *β*-diversity metrics that use presence-absence data and metrics that use species abundances (Anderson *et al.* 2011). Abundance data are clearly more information-rich than presence-absence data and this can change how we interpret spatial variation in assemblage structure (Cassey *et al.* 2008). For presence-absence metrics, the only visible differences between sites are in species identities. Abundance-based measures detect more nuanced variation: we may observe all the same species at two sites, but those species may have different abundance ranks (the commonest species here may be rare there, and vice versa). Even when the ranks are the same, evenness of abundances can vary (the common species can be more or less dominant). Consequently, I distinguish sensitivity to (i) species turnover, (ii) species richness differences (iii) rank abundance shifts and (iv) evenness differences as distinct components of *β*-diversity. Abundance-based indices may also be expected to be more robust to incomplete sampling (Beck *et al.* 2013b): stochastic differences in rare species are an artefact of undersampling, but abundance-based metrics are less influenced by turnover of rare species than their presence-absence counterparts. Whilst abundance information makes inferences about *β*-diversity more powerful, it also introduces a source of subjectivity: we need to decide how to weight turnover in common and rare species.

Koleff *et al.* (2003a) compared the performance of 24 presence-absence metrics of *β*-diversity and identified a number of trade-offs and redundancies among the presence-absence metrics available. Overall, they recommended β_{sim} (Lennon et al. 2001) as the best performing index. We are lacking an equivalent investigation into the performance and "personality" of the many abundance-based metrics available.

I test 16 conceptual properties that are important for an abundance-based *β*-diversity metric, whatever the application. Where applicable I note the relationship between these properties and those previously described in the literature.

4.2.1 Desirable properties

I make a distinction between conceptual and statistical properties. Conceptual properties (C1-C16) are intrinsic to the design of the metric (e.g. the use of abundance information and whether the metric has a fixed upper limit). Sampling properties (S1-S2) explore responses to undersampling: true differences between assemblages are confounded by imperfect detection, especially of rare species. I consider both conceptual and sampling properties as desirable when choosing a metric.

C1) *Independence of α-diversity. β*-diversity should be independent of *α*-diversity within assemblage pairs, so that the *α*- and *β*- components of diversity can be partitioned (Jost 2007a; Chase *et al.* 2011) and *β*-diversity can be meaningfully compared between regions differing in *α*-diversity. If *α*- and *β*-diversity are independent, then pairs of assemblages with the same proportion of species turnover should have the same value of *β*-diversity, regardless of whether *α*-diversity within those assemblages is high or low. Legendre & De Cáceres (2013:

property 10) test this property algebraically for 16 dissimilarity metrics. In P1 I consider an alternative where assemblage pairs have unequal species richness.

C2) *β is cumulative along a gradient of species turnover.* When assemblages are positioned along an environmental gradient, species turnover will be directional. Koleff *et al*. (2003a) call this property additivity. Species are gradually replaced as conditions change so turnover between neighbouring pairs of assemblages is lower than between pairs that are farther apart. When samples A, B and C are positioned in sequence along such a gradient, summed β-diversity between consecutive pairs of samples ($\beta_{A,B}$ + $\beta_{B,C}$) should equal the total β-diversity between the end points of the gradient ($\beta_{A,C}$). Metrics with disproportionate sensitivity to small amounts of turnover will lead to overestimates of cumulative β.

C3) *Similarity is probabilistic when assemblages are independently and identically distributed.* When assemblages are independently drawn from within a larger, well-mixed metacommunity, then similarity (that is: 1-β for metrics with an upper limit of 1) among multiple pairs of assemblages should be probabilistic. The expected similarity of assemblages A and C (1-$\beta_{A,C}$) is given by the product of similarities between A and B and B and C, (1-$\beta_{A,B}$)*(1-$\beta_{B,C}$). Metrics that lack an upper limit cannot be converted to their similarity complement and so cannot be probabilistic.

C4) *Minimum of zero.* Legendre & De Cáceres (2013: property 1) state that when comparing an assemblage to itself β should always be zero, and when comparing two different assemblages β should be equal to or greater than zero.

C5) *Fixed upper limit.* Legendre & De Cáceres (2013: property 9) note that bounded metrics are easier to compare than unbounded ones. For example, the maximum value of $\beta_{Euclidean}$ and $\beta_{Manhattan}$ depends on the combined abundances of an assemblage pair, making it difficult to interpret the values of β when assemblage pairs have different numbers of individuals.

C6) *Monotonic increase with species turnover.* β should be a strictly increasing monotonic function of the proportion of species in the first assemblage that are replaced by new species in the second assemblage: otherwise it is not reflecting species turnover. A pair of assemblages in which 20% of assemblage A species are replaced by new species in assemblage B should have lower β-diversity than an assemblage pair with 40% turnover. The property is closely related to the property described by Jost *et al.* (2011) as monotonicity.

C7) *Monotonic increase with the decoupling of species ranks*. An abundance-based β-diversity metric should be sensitive to the degree to which species ranks are decoupled between assemblage pairs (reflecting differences in the dominant and rare species). Therefore, β-diversity should decrease monotonically with increased correlation between species ranks.

C8) *Monotonic increase with differences in evenness.* Even if two sites have the same species, with the same rank order of abundances, they may still differ in evenness: the commonest species may dominate more in some sites than others. A good abundance-based β-diversity metric should increase monotonically as differences in evenness between sites grow larger. Properties C7 and C8 are two aspects of a property described as monotonicity to changes in abundance by Legendre & De Cáceres (2013: property 3).

C9) *β is lower for complete decoupling of species ranks than for complete species turnover.* Consider a pair of assemblages in which all species are unshared and a second pair of assemblages in which all species are shared, but the rank abundances are reversed, such that the dominant species in assemblage A becomes the rarest in assemblage B and vice versa. The first pair of assemblages must be considered more different than the second pair.

C10) *β is lower for evenness differences than for complete species turnover.* As an alternative scenario for abundance differences, consider a pair of assemblages in which all species are shared: in the first assemblage the abundances are perfectly even and in the second assemblage all species are singletons except the dominant species (e.g. extreme unevenness). Compare this to an assemblage pair where all species are shared. As above, the loss or gain of a species should always be deemed a more extreme difference than a shift in its abundance. Sites with no species in common should have the largest values of β (Legendre & De Cáceres 2013: property 5). Properties C9 and C10 describe two alternative scenarios in which this property should hold.

C11) *Symmetry*. Legendre & De Cáceres (2013: property 2) and Koleff *et al.* (2003a) note that the order in which two assemblages, A and B, are considered should not change the value of β for that pair (e.g. $\beta_{A,B} = \beta_{B,A}$).

C12) *Double-zero asymmetry*. Legendre & De Cáceres (2013: property 4) argue that the absence of a species from both assemblages does not indicate resemblence between the two assemblages in the way that shared presences do:

double absences contain no information about the distance in ecological niche space. Consequently, the addition of zero abundances to both assemblages should not change the value of *β* while the addition of shared presences should lower the value of *β*.

C13) *β does not decrease in a series of nested assemblages*. Metrics vary in how they respond to nestedness. However, *β* should never decrease when species richness differences increase, as the addition of unique species should not increase similarity (Legendre & De Cáceres 2013: property 6).

C14) *Independence of species replication.* When all species in both the assemblages being compared are duplicated, the value of *β* should remain constant. This becomes important when identical subsets of an assemblage are pooled (Jost *et al.* 2011; Legendre & De Cáceres 2013: property 7).

C15) *Independence of units of abundance.* When comparing *β* among regions differing in productivity or the units used to measure abundance, metrics that are sensitive to the total abundance in an assemblage pair will be inappropriate. Legendre & De Cáceres (2013: property 8) call this property invariance to measurement units.

C16) *Independent of differences in abundance.* This property was described as invariance to the total abundance in each assemblage by Legendre & de Cáceres (2013: property 11) and density-invariance by Jost *et al.* (2011). It is designed to identify metrics that are mathematically dependent on differences in abundance between sampling units. C15 and C16 differ from undersampling in that there is no stochasticity.

S1) *Unbiased by undersampling*. In all previous simulations I have assumed the simulated assemblages represent the “true” composition. However, *β*-diversity is usually estimated from samples, which generates differences in richness and abundances as a sampling artefact (Chao *et al.* 2005, 2006). A good *β*-diversity metric should remain constant as the sample size decreases.

S2) *Unbiased by unequal sampling effort.* Differences in sample size can also inflate *β*-diversity due to imperfect detection of rare species. A good *β*-diversity metric should remain constant with increasing difference in sample sizes.

4.2.2 Personality properties

In addition to the desirable properties identified above, β-diversity metrics may differ in other respects that are worthy of note. I term this the “personality” of the metrics and their importance will depend on the ecological question concerned.

P1) *Sensitivity to nestedness.* For presence-absence metrics, Koleff *et al.* (2003a) distinguish ‘narrow-sense’ metrics, which measure purely species turnover, from ‘broad-sense’ metrics, which measure both species turnover and differences in species richness. We may want a β-diversity metric to reflect differences in richness, as these will mean that one site will have species that are absent in another. On the other hand, we may want the value of β to measure purely species turnover, especially if we are comparing β-diversity between regions with different species richness. This differs from the test in C1 (independence of differences in α-diversity): in C1, each pair of assemblages I compare has an equal number of species. Here, species richness differs between the two assemblages.

P2) *Relative sensitivity to nestedness and turnover components of β.* I test two metrics ($\beta_{\text{Bray-Curtis}}$ and β_{Ruzicka}) that can be additively partitioned into independent nestedness and turnover components (Baselga 2013; Podani *et al.* 2013; Legendre 2014). For metrics that cannot be deconstructed, it is useful to compare the value of β for complete turnover to that for extreme nestedness to estimate the relative sensitivity to these components.

P3) and P4) *Relative weighting of species turnover and abundance differences.* I have identified two ways in which species abundances can vary between assemblages: decoupling of species ranks and differences in evenness. The relative weighting of these components and species turnover is a useful property to quantify. The ideal weighting is somewhat subjective (provided that β-diversity is less for extreme differences in abundance than for turnover of a species, see C9 and C10, above).

P5) *Relative sensitivity to turnover of rare versus common species* There is scope for variation in how common versus rare species contribute to β. One reason for investigating this is the occupancy-abundance relationship (ONR). Positive ONRs are nearly ubiquitous (Brown 1984) and reflect that rare species are generally more range restricted and so more likely to be turned over than are locally abundant (and more widespread) species.

Here, I manipulate the composition and structure of hypothetical assemblages and apply 29 β-diversity metrics to the resulting assemblage pairs. Each metric is evaluated against 18 desirable properties (C1-C16 and S1-S2) to generate a score card, which I use to identify the best performing abundance-based β-diversity metrics. I then explore how personality properties may affect the choice of metric for different ecological applications.

4.3 Methods

4.3.1 β-diversity metrics

In total, I evaluated 24 abundance-based metrics and five presence-absence metrics (see Supplementary Information in section 4.7.1). All metrics are expressed so that higher values of β indicate more differentiation (1-β for similarity metrics). For comparability, metrics were rescaled relative to the maximum value obtained in each set of simulations, before calculating scores.

4.3.2 Hypothetical species assemblages

Abundance differences in the hypothetical assemblages were modelled using the log series distribution (Fisher *et al.* 1943) using the function *fisher.ecosystem* in R package ‘untb’ (Hankin 2007). The conclusions would be qualitatively identical using other commonly used models of the species abundance distribution (McGill 2010b). A hypothetical species assemblage with 100 species and 10000 individuals was used as the starting assemblage for all simulations.

4.3.4 Evaluation of properties

For β-diversity metrics that have been previously implemented in R, the functions *vegdist* and *d* and *adipart* in R package ‘vegan’ v.2.0-5 (Oksanen *et al.* 2013) were used to calculate β-diversity. Formulae for the remaining metrics can be found in the supplementary material in section 4.7.1. Each of the properties was assessed by exploring how measured β-diversity co-varied with a test-specific parameter, describing some aspect of assemblage structure. I manipulated the starting assemblage according to the specific rules for each test. Each simulation described below was run 10000 times at each unique combination of the test specific parameter and proportion species turnover, t = 0, 0.2, 0.4, 0.6, 0.8 and 1.0 , to obtain median β for that combination. All simulations were carried out in R v.3.0.3 (R Core Development Team 2014). Formulae for evaluating β-diversity metrics for each of the properties can be found in the supplementary material in Section 4.7.2.

C1) *Independence of* α*-diversity*. Fisher's α of assemblages was manipulated using the function *fisher.ecosystem* in R package 'untb' (Hankin 2007). The expected number of individuals was fixed at N = 10000 while manipulating the number of expected species, S, to generate a series of assemblages with S = 300, 250, 200, 150, 100, 80, 60, 40, 20 and 10. Fisher's α was estimated for each assemblage. For each α-diversity:turnover combination, I calculated error as the difference between the median β-diversity at each level of α and the median β-diversity when α was highest (S = 300): dependence on α-diversity was measured as the root mean squared error (RMSE).

C2) *β is cumulative along a gradient of species turnover*. In each simulation, three assemblages, A, B and C, were generated according to the following rules: A proportion of species, t, in assemblage A were randomly selected to be turned over in assemblage B (t = 0, 0.1, 0.2, 0.3, 0.4 and 0.5). Of the species in assemblage B, the same proportion were turned over in assemblage C, with the condition that species shared between assemblages A and B were g times more likely to be turned over in assemblage C than species unique to assemblage B, where g is a test specific parameter which I manipulate to simulate different strengths of directional species turnover (g = 1, 5, 10, 50, 100, 500 or 1000). At each turnover:gradient combination, I calculated error as the difference between observed β-diversity for assemblages A and C ($\beta_{A,C}$) and the value predicted if the metric was cumulative ($\beta_{A,B}$ + $\beta_{B,C}$): departure from cumulative β was evaluated as the RMSE.

C3) *Similarity is probabilistic when assemblages are distributed independently and identically in space*. In each simulation, three assemblages, A, B and C, were generated according to the following rules: A proportion, p (p = 0 to 1 in increments of 0.2) of the species in assemblage 1 were randomly selected to be conserved in assemblage 2. This process was repeated with the species in assemblages 1 and 2 (with the same value of p) to obtain the third assemblage. Species lost from assemblage A can reappear in assemblage C, as we would expect in independent samples drawn from a well-mixed species pool, but entirely novel species can also appear in assemblage C. In each simulation, error was calculated as the difference between observed similarity for assemblages A and C ($1-\beta_{A,C}$) and the similarity predicted if the metric is probabilistic $(1 - \beta_{A,B})(1 - \beta_{B,C})$: departure from probabilistic similarity was evaluated as the (RMSE).

C4) *Minimum of zero.* The starting assemblage was manipulated to generate assemblage pairs with increasing differences in species turnover, t, decoupling of species ranks, r, and evenness differences, ΔE. Methods for these simulations can be found in C7 and C8. Two behaviours were tested: 1) β is zero for identical assemblages and 2) β is greater than or equal to zero when assemblages are different, either because of species turnover, decoupling of species ranks or evenness differences. The metric was scored as TRUE if both qualities were met.

C5) *Fixed upper bound.* This property was evaluated as TRUE/FALSE by applying equation 8 and then equation 3 in Legendre & De Cáceres (2013: property 9) to calculate the upper limit of a metric, using a pair of assemblages with no shared species.

C6) *Monotonic increase with species turnover.* A series of assemblages with increasing species turnover was generated by randomly selecting a proportion of species (t = 0 to 1 in increments of 0.2) in the starting assemblage and assigning them a new identity in the new assemblage. Metrics were scored as TRUE if each consecutive increase in species turnover generated an increase in median β.

C7) *Monotonic increase with decoupling of species ranks*. A series of assemblages with increased decoupling of species ranks was generated by determining species ranks in the new assemblage partially by the ranks in the starting assemblage and partially at random (r = +1.0 (a perfect positive correlation between ranks) to -1.0 (a perfect negative correlation) in increments of 0.1). Metrics were scored as TRUE if each incremental decrease in r, generated an increase in median β at a given level of species turnover.

C8) *Monotonic increase with differences in evenness*. In the starting assemblage for this test all except the dominant species have just one individual (extreme unevenness). A series of assemblages with increasing evenness differences were generated by redistributing individuals from the dominant species among the other 99 species: the probability of being allocated to each species was determined by raising the abundances in a Fisher log series distributed assemblage to a power, b = 0.2, 0.4, 0.6, 0.8, 1.0, 1.2, 1.4, 1.6, 1.8 2.0, 4.0, 6.0 and 8.0. These values were chosen to generate assemblages with both more and less evenness relative to a

Fisher log series distribution. Metrics were scored as TRUE if each incremental increase in ΔE led to an increase in median β.

C9) *β under extreme decoupling of species ranks < β when species turnover is complete* and C10) *β under extreme evenness differences < β when species turnover is complete.* The turnover of a species should be weighted greater than a change in abundance. Metrics were scored as TRUE for these two properties if median β is lower for extreme decoupling of species ranks (r = -1) and extreme evenness differences (ΔE = 0.97) than for complete species turnover (t =1). The relative weighting of abundance differences and species turnover also has a personality component (see P3 and P4).

C11) *Symmetry.* Symmetry was tested by reversing the order in which assemblages A and B were given to a metric. This was tested for assemblage pairs with multiple levels of species turnover, t, decoupling of species ranks, r, and evenness differences, ΔE. A metric was scored as TRUE if $\beta_{A,B} = \beta_{B,A}$ in all simulations.

C12) *Double-zero asymmetry.* I generated a series of eleven assemblage pairs, the first with no double zeros and then consecutively adding up to 10 double zeros to the assemblage pair. This was repeated, but adding double presences of equal abundance. Abundances in each simulation were chosen at random from within the starting assemblage. Two behaviours were tested: 1) β does not change with the addition of double zeros and 2) β decreases with the addition of double-presences. Metrics were scored as TRUE if both conditions were met.

C13) *β does not decrease in a series of nested assemblages.* A series of nested assemblages were generated by randomly selecting a number of species to be lost from the starting assemblage (S = 0 to 90 in increments of 10). Metrics were scored as TRUE if each incremental increase in species loss led to an increase in median β.

C14) *Independence of species replication*. A series of ten assemblage pairs with all species replicated x times at six levels of species turnover, t, was used to simulate the effect of pooling identical subsets of unshared species. At each combination of x (in 1 to 10) and t, error was calculated as the difference between median β in one identical subset and when x identical subsets were pooled. Metrics were scored as the RMSE.

C15) *Independent of the units of abundance.* Following the method in Legendre & De Cáceres (2013), I test this property by generating a series of assemblage pairs in which the abundances in both assemblages are multiplied by a constant factor, (*cc* = 1 to 10). Error was calculated as the difference between median β in the starting assemblage pair (*cc* = 1) and between median β at each combination of *cc* and species turnover, *t*. Metrics were scored as the RMSE.

C16) *Independence of differences in abundance.* I test this property by generating a series of assemblage pairs in which the abundances in *one* assemblage are multiplied by a constant factor, (*c* = 1 to 10). At each *c*:turnover combination, error was calculated as the difference between median β at each value of *c* and median β in the starting assemblage pair, (*c* = 1). Metrics were scored as the RMSE.

The following two properties test the behaviour of metrics when samples are used to infer β-diversity.

S1) *Independence of sample size*. For a series assemblage pairs with different levels of turnover, *t*, both assemblages were randomly sampled, without replacement, to generate a series of assemblage pairs with equal sample sizes of N = 10000 (fully censused), 9000, 8000, 7000, 6000, 5000, 4000, 3000, 2000, 1000, 500, 200, 100, 50, 20, and 10. For each sample size:turnover combination, error was calculated as the difference between median β-diversity at sample size N and median β-diversity in a fully censused assemblage: dependence on sample size was measured as the RMSE.

S2) *Independence of unequal sample sizes*. For a series of assemblage pairs with different levels of turnover, *t*, one assemblage in each pair was randomly sampled, without replacement, while the other was fully sampled to generate sample size differences of ΔN = 0, 1000, 2000, 3000, 4000, 5000, 6000, 7000, 8000, 9000, 9500, 9800, 9900, 9950, 9980, 9990). As above, for each ΔN:turnover combination, error was calculated as the difference between the median β-diversity at sample size difference ΔN and median β-diversity when both assemblages were fully censused (ΔN = 0): dependence on unequal sample size was measured as the RMSE.

P1) *Sensitivity to nestedness*. To generate ten assemblages with differences in species richness, ΔS, I randomly selected S species (see C13) to be lost from the starting assemblage. For each species loss:turnover combination, I calculated error as the difference between the median β-diversity for S and median β-diversity when species richness was equal (S = 0): sensitivity to nestedness was measured as the RMSE.

P2) *Relative sensitivity to nestedness and turnover.* This property was measured as the ratio of β under extreme nestedness but no turnover (ΔS = 90, t = 0), and the value for complete species turnover but no species loss ($t = 1, \Delta S=0$).

P3) and P4) *Relative sensitivity to abundance differences and species turnover*. I calculated β under extreme decoupling of species ranks (r = -1), and extreme differences in evenness (ΔE = 0.97), using simulated assemblages from C7 and C8. These values were expressed as a proportion of the value of median β under complete species turnover, t=1.

P5) *Relative sensitivity to turnover in rare versus common species* I turned over a single species in the starting assemblage, from the dominant (1450 individuals) to the rarest species (1 individual) and recorded the value of β for each. Relative sensitivity to rare and common species was evaluated as the ratio between β when the rarest species was turned over to β when the dominant species was turned over.

In order to investigate redundancy and complementarity among the 29 metrics, a principal component analysis was performed using all quantitatively measured properties, using the function *prcomp* in R version 3.0.3 (R Development Core Team, 2014). I also investigate which of the metrics are Pareto-dominated, that is, those metrics that are outperformed or equalled across all desirable properties.

4.4 Results

I have scored the performance of 29 metrics for 16 conceptual and two sampling properties (Table 4.1). In addition, a further five personality tests have identified more subjective variation in metrics' behaviour (Table 4.2). The results of all simulations are presented in Figs S4.1 – S4.13 in section 4.7.3.

4.4.1 Conceptual and sampling properties

All 29 metrics satisfied properties C4, C6 (minimum of zero and positiveness, monotonic increase with species turnover: Fig. S4.4) and C11 (symmetry). I use the remaining properties to discriminate between the performances of metrics. Thirteen metrics were Pareto-dominated (Table 4.1). I focus on the metrics that

Table 4. 1 Scorecard for 29 β-diversity metrics against the 16 conceptual and two sampling properties described in the text.

Metrics are ordered by number of TRUES and, when equal, by the mean of quantitative scores. Note this weights qualitative properties greater than quantitative properties, such that metrics with one or two fails drop down the scorecard. Metrics have an ideal score of TRUE (T) for qualitative properties and 0 for quantitative properties. C4, C6 and C11 were TRUE for all metrics and scores are not shown.

	Conceptual properties													**Sampling properties**		**Performance summary**		
Metric	**C1**	**C2**	**C3**	**C5**	**C7**	**C8**	**C9**	**C10**	**C12**	**C13**	**C14**	**C15**	**C16**	**S1**	**S2**	**#T**	**# F**	**Mean of quantitative scores**
Morisita	0.0757	0.0197	0.0047	T	T	T	T	T	T	T	0.0030	0.0038	0.0027	0.0159	0.0036	8	0	0.0161
Horn	0.0294	0.0331	0.0024	T	T	T	T	T	T	T	0.0009	0.0016	0.0007	0.1359	0.0357	8	0	0.0300
Morisita-Horn	0.0763	0.0200	0.0048	T	T	T	T	T	T	T	0.0030	0.0037	0.0026	0.1356	0.0899	8	0	0.0420
Jost Simpson	0.0826	0.0642	0.0037	T	T	T	T	T	T	T	0.0030	0.0043	0.0026	0.1157	0.0694	8	0	0.0432
Renkonen*	0.0294	0.0331	0.0024	T	T	T	T	T	T	T	0.0009	0.0016	0.0007	0.1690	0.1433	8	0	0.0476
Kulczynski*	0.0294	0.0331	0.0024	T	T	T	T	T	T	T	0.0009	0.0016	0.2292	0.1690	0.2235	8	0	0.0861
Bray-Curtis*	0.0294	0.0331	0.0024	T	T	T	T	T	T	T	0.0009	0.0016	0.3916	0.1690	0.4151	8	0	0.1304
Canberra	0.0000	0.1584	0.0170	T	T	T	T	T	T	T	0.0000	0.0000	0.3433	0.2260	0.3699	8	0	0.1393
Ružička	0.0312	0.1166	0.0153	T	T	T	T	T	T	T	0.0010	0.0015	0.3966	0.1881	0.3902	8	0	0.1426
†Baselga B-C turn	0.0294	0.0331	0.0024	T	T	T	T	T	T	F	0.0009	0.0016	0.0007	0.1690	0.0031	7	1	0.0300
NESS	0.0062	0.0351	0.0014	T	T	T	T	T	F	T	0.0137	0.0010	0.0009	0.1431	0.0945	7	1	0.0370
†Baselga R turn	0.0312	0.1166	0.0153	T	T	T	T	T	T	F	0.0010	0.0015	0.0006	0.1881	0.0032	7	1	0.0447
†Podani B-C turn*	0.0294	0.0331	0.0024	T	T	T	T	T	T	F	0.0009	0.0016	0.3916	0.1690	0.4156	7	1	0.1305
†Podani R turn*	0.0312	0.1166	0.0153	T	T	T	T	T	T	F	0.0010	0.0015	0.4556	0.1881	0.4736	7	1	0.1604
sim	0.0000	0.0547	0.0000	T	F	F	T	T	T	T	0.0000	0.0000	0.0000	0.1485	0.0026	6	2	0.0257
Classic Sørensen*	0.0000	0.0547	0.0000	T	F	F	T	T	T	T	0.0000	0.0000	0.0000	0.1618	0.2299	6	2	0.0558
Classic Jaccard*	0.0000	0.1584	0.0170	T	F	F	T	T	T	T	0.0000	0.0000	0.0000	0.1854	0.2404	6	2	0.0752
Jost Shannon	0.0302	0.0482	0.0079	T	T	T	T	T	F	F	0.0009	0.0017	0.2529	0.1272	0.3459	6	2	0.1019
Chao Sørensen	0.0300	0.0330	0.0034	T	F	F	T	T	F	T	0.0019	0.0023	0.0015	0.0481	0.0849	5	3	0.0256
Chao Jaccard	0.0300	0.1160	0.0155	T	F	F	T	T	F	T	0.0014	0.0017	0.0014	0.0645	0.1038	5	3	0.0418
Lande Shannon*	0.0294	0.0331	F	F	T	T	T	T	F	T	0.0009	0.0016	0.2322	0.1359	0.1462	5	3	0.0828
CYd	0.1280	0.1400	F	F	T	F	T	T	T	T	0.0003	0.1703	0.1324	0.2091	0.2528	5	3	0.1476
Lande Simpson	0.2586	0.0200	F	F	T	T	T	F	F	T	0.4663	0.0037	0.2905	0.0614	0.0446	4	4	0.1636

Table 4.1 (continued)

	Conceptual properties													Sampling properties		Performance summary		
Metric	**C1**	**C2**	**C3**	**C5**	**C7**	**C8**	**C9**	**C10**	**C12**	**C13**	**C14**	**C15**	**C16**	**S1**	**S2**	**#T**	**#F**	**Mean of quantitative scores**
Binomial	0.4092	0.0547	F	F	F	T	T	T	F	F	0.3233	0.0000	0.1157	0.2704	0.1911	3	5	0.1949
Gower*	0.0000	0.0577	0.1350	T	F	F	F	F	F	T	0.0000	0.0000	0.5054	0.4137	0.4602	3	5	0.1965
Manhattan*	0.0294	0.0331	F	F	F	T	T	T	F	F	0.3244	0.3244	0.2669	0.4458	0.2542	3	5	0.2397
alt. Gower*	0.1802	0.1022	F	F	F	T	F	F	T	T	0.0012	0.3258	0.3457	0.4232	0.3334	3	5	0.2445
Av. Euclidean*	0.2178	0.1786	F	F	F	T	F	F	T	T	0.0022	0.3479	0.3646	0.4762	0.2888	3	5	0.2680
Euclidean*	0.2625	0.1393	F	F	F	T	T	F	F	T	0.3168	0.3775	0.3586	0.5203	0.2670	3	5	0.3203

*Pareto-dominated

†Partitioned turnover component of β

performed best against the conceptual and sampling properties and consider their contrasting strengths and weaknesses.

Nine metrics passed all qualitatively scored tests (β_{Morisita}, β_{Horn}, $\beta_{\text{Morisita-Horn}}$, $\beta_{\text{Jost Simpson}}$ β_{Renkonen}, $\beta_{\text{Kulczynski}}$, $\beta_{\text{Bray-Curtis}}$, β_{Canberra} and $\beta_{\text{Ružička,}}$: C5-C13, Table 4.1). The presence-absence metrics β_{sim}, $\beta_{\text{Classic Jaccard}}$, and $\beta_{\text{Classic Sørensen}}$ failed only C7 and C8 (monotonic increase with decoupling of species ranks and evenness differences: Figs S4.5 and S4.6), as such measures, by definition, are insensitive to differences in abundance. All abundance-based metrics became less sensitive to abundance differences as the species turnover between assemblages became more extreme (Figs S4.5 and S4.6).

Across all quantitative tests, β_{Morisita} obtained the best mean score. The presence-absence metric, β_{sim} performed best or joint best for six of the eight quantitative conceptual and sampling properties, with the exception of C2 (β is cumulative) and S1 (independence of sample size). β_{Morisita} was the most robust metric to undersampling, performing best when both assemblages were undersampled (S1) and second best under unequal sample sizes (S2). β_{sim} was best for S2, but performed poorly for S1 (Figs S4.2 and S4.12; Table 4.1). β_{Canberra} scored equally highly with β_{sim}, $\beta_{\text{Classic Sørensen}}$ and $\beta_{\text{Classic Jaccard}}$ for C1 (independence of α-diversity: Fig. S4.1), C14 (independence of species replication: Fig. S4.7) and C15 (independence of measurement units: Fig. S4.8), but performed poorly on C2 (β is cumulative: Fig. S4.2), C3 (similarity is probabilistic: Fig. S4.3), C16 (independence of differences in abundance: Fig. S4.9) and for both sampling properties (S4.1 and S4.2). β_{Binomial} was joint best for C15 (independence of measurement units: Fig. S4.8), but performed poorly for all other quantitative properties. β_{Horn} and β_{Renkonen} performed relatively well across all quantitative properties, but were never best for any property.

In sampling simulations S1 and S2 (Table 4.1; Figs S4.12 and S4.13) most presence-absence metrics were positively biased by undersampling, with the exception of $\beta_{\text{Chao Sørensen}}$ and $\beta_{\text{Chao Jaccard}}$ which have a correction for undersampling.

Table 4.2 Summary of scores for personality and sampling properties among 29 β-diversity metrics

Properties P1–P5 are described in the text

	Personality properties				
Metric	**P1**	**P2**	**P3**	**P4**	**P5**
Morisita	0.2862	0.8538	0.9940	0.9798	0.0000
Horn	0.1989	0.6046	0.9012	0.9195	0.0007
Morisita-Horn	0.2861	0.8541	0.9940	0.9798	0.0000
Renkonen	0.3305	0.9150	0.9544	0.9801	0.0007
Jost Simpson	0.2631	0.7453	0.9880	0.9604	0.0000
Kulczynski	0.1619	0.4575	0.9544	0.9801	0.0007
Bray-Curtis	0.2678	0.8433	0.9544	0.9801	0.0007
Canberra	0.2759	0.9000	0.7979	0.9802	1.0000
Ružička	0.2825	0.9150	0.9767	0.9900	0.0008
Baselga B-C turn†	0.0198	0.0000	0.9544	0.9801	0.0007
NESS	0.2424	0.7749	0.9634	0.9289	0.0000
Baselga R turn†	0.0219	0.0000	0.9767	0.9900	0.0008
Podani B-C turn†	0.2672	0.0000	0.9543	0.9801	0.0007
Podani R turn†	0.3154	0.0000	0.9767	0.9900	0.0008
sim	0.0000	0.0000	0.0000	0.0000	1.0000
Classic Sørensen	0.2574	0.8182	0.0000	0.0000	1.0000
Classic Jaccard	0.2759	0.9000	0.0000	0.0000	1.0000
Jost Shannon	0.1675	0.1807	0.8676	0.8915	0.0007
Chao Sørensen	0.2665	0.8406	0.0000	0.0000	0.0000
Chao Jaccard	0.2819	0.9134	0.0000	0.0000	0.0000
Lande Shannon	0.1996	1.4297	0.9012	0.9195	0.0007
CYd	0.2582	0.9001	0.6221	0.6243	0.1682
Lande Simpson	0.1121	5.0896	0.9940	48.5149	0.0000
Binomial	0.1823	0.4500	0.3264	0.4599	1.0000
Gower	0.2759	0.9000	1.0000	1.0000	1.0000
Manhattan	0.1860	0.4575	0.9544	0.9801	0.0007
alt. Gower	0.2154	0.9150	1.9088	1.9602	0.0007
Av. Euclidean	0.2430	0.9766	1.4099	9.8504	0.0007
Euclidean	0.2303	0.6905	0.9970	6.9653	0.0007

† partitioned turnover component of β

4.4.2 Personality properties

With the exception of β_{sim} and the partitioned turnover components of $\beta_{\text{Bray-Curtis}}$ and $\beta_{\text{Ružička}}$ all metrics were at least somewhat sensitive to nestedness (P1), although there were four-fold differences in the degree of sensitivity to species richness differences (P2, Table 4.2).

The relative weighting of abundance differences and turnover varied substantially among abundance-based metrics (Table 4.2). With the exception of β_{Gower} $\beta_{\text{alt. Gower}}$, $\beta_{\text{Av. Euclidean}}$, $\beta_{\text{Lande Simpson}}$ and $\beta_{\text{Euclidean}}$, metrics were more sensitive to species turnover than differences in abundance (P3: decoupling of species ranks, P4: differences in evenness, Figs S4.5 and S4.6).

The relative sensitivity to turnover in rare versus common species (P5) varied substantially among metrics from equal weighting of rare and common species (all presence-absence metrics) to metrics that had a negligible response to turnover in rare species ($\beta_{Morisita}$: Fig. S4.11).

A principal component analysis revealed substantial redundancy among the 29 metrics investigated (Fig. 4.1).

4.5 Discussion

The results identify a number of trade-offs in performance, consider redundancy and complementarity among existing metrics and suggest areas to be addressed in the design of new metrics.

In choosing a metric, I suggest that the desirable properties will provide a useful primary filter in choosing a metric. I focus on the best-performing metrics in Table 4.1, but other metrics may still be useful if the relative weighting of the desirable properties is changed, or if personality properties or additional properties, untested here, become important. The personality properties highlight two additional sources of variation which may further filter the appropriate metrics for some applications: *i*) sensitivity to rare species and *ii*) sensitivity to nestedness. My results indicate the first of these is traded-off with performance for sampling properties (Fig. S4.16).

The most extreme example of this trade-off is β_{Morisita}, which is the most independent of sample size (Fig. S4.10), at the expense of being almost completely insensitive to turnover in rare species (Fig. S4.13). β-diversity metrics fall along a continuum in terms of sensitivity to rare species. $\beta_{\text{Classic Sørensen}}$ is conceptually linked to species richness metrics of α-diversity such that rare and dominant species are weighted equally. β_{Horn} relates to Shannon entropy: species are weighted by their relative abundance. β_{Morisita} is linked to the Gini-Simpson index of α-diversity (Jost 2007a): rare species contribute little to the final value of these metrics. Consequently, β_{Morisita} performs well, even with the very partial samples that ecologists usually work with, because the missing rare species in small samples have a negligible effect on the value of β. This may be important: the emphasis β_{Morisita} places on common species is suitable when shifts in dominance are of interest (e.g. when linking diversity to ecosystem function), but will be less appropriate when patterns of turnover in rare species of particular interest (e.g. complementarity of reserve networks: Wiersma & Urban (2005)). Unfortunately,

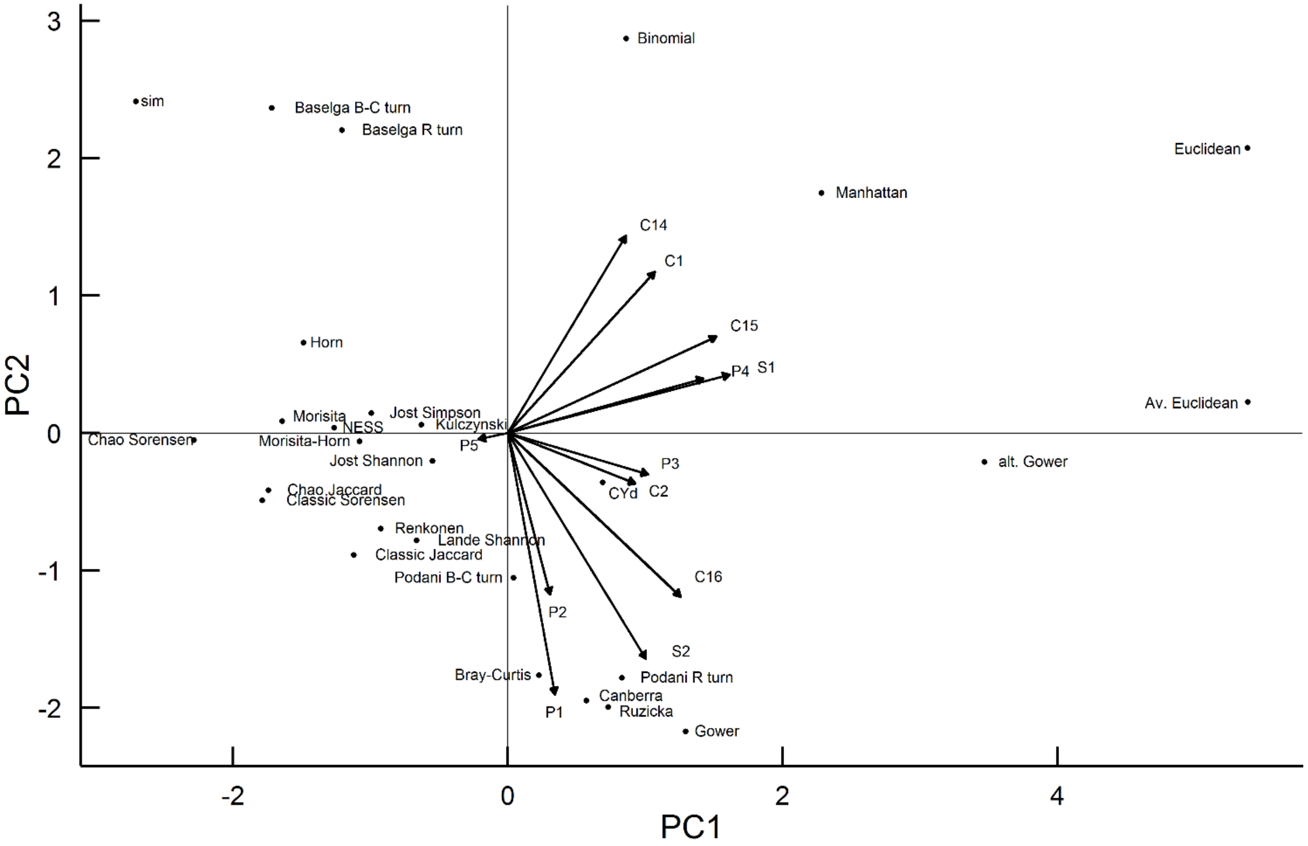

Fig. 4.1 Biplot of the first two principal components axes of the scores of 29 β-diversity metrics based on quantitative scores for properties C1-C2, C14-C16, S1-S2 and P1-P5.

Four partitioned turnover components are also shown, using the partitioning methods proposed by Baselga (2013) and Podani *et al.* (2013). Together, PC1 and PC2 explain 52% of variation in scores.

those metrics that *are* sensitive to turnover in rare species are, consequently, less robust in the face of undersampling.

In general, the results suggest that when insensitivity to sample size (S1 and S2), sensitivity to turnover of individuals (C7 and C8) and/or cumulative β (C2) are priorities, β_{Morisita} should be favoured. When turnover in rare species is important and undersampling is not severe, the presence-absence metric, β_{sim}, is favoured due to superior performance in terms of independence of α-diversity (C1) probabilistic similarity (C3), independence of species replication (C14), measurement units (C15) and differences in abundance (C16). However, β_{Morisita} is almost completely independent of sample size (S1), while β_{sim}, $\beta_{\text{Classic Sørensen}}$ and $\beta_{\text{Classic Jaccard}}$ are eleventh, twelfth and eighteenth. This is consistent with predictions that presence-absence metrics are more sensitive to sample sizes.

An example of where these results have implications for existing studies of β-diversity is in the spatial scaling of β-diversity. Studies using presence-absence metrics have shown that β-diversity decreases with the spatial grain of samples (McGlinn & Hurlbert 2012; Barton *et al.* 2013). One reason for this is statistical: the probability of a rare species being turned over increases at finer grains (Keil *et al.* 2012b) both because rare species are range restricted and because fine-grain samples have (almost by definition) much smaller sample sizes of individuals than do coarse-grain samples. By contrast common species are usually more widespread than rare species and much less likely to be turned over at fine grains. The trade-off I've noted between robustness to undersampling and sensitivity to rare species thus becomes relevant here: those metrics which weight rare species turnover highly (including all presence/absence measures) will likely find β shifting with scale. It follows that abundance-based metrics, particularly those disproportionately influenced by dominant species, will likely be less scale-dependent than presence-absence metrics (Fig. S4.15).

A second consequence of this trade-off is that metrics that are insensitive to turnover in rare species, will also return very low values of β under a positive occupancy-abundance relationship (Fig. S4.14), a pattern that is near ubiquitous. Specialist applications focussing on rare species may need to use metrics that are less robust to undersampling but, consequently, will require larger sample sizes to observe the rarer species: no abundance-based metric is able to account for unseen shared species (i.e. abundance-based equivalents of $\beta_{\textit{Chao Sørensen}}$ and $\beta_{\textit{Chao Jaccard}}$).

Another potential filter of metrics is sensitivity to nestedness (P1). There are circumstances when the partitioning of the nestedness and turnover components will be a priority when choosing a metric. Firstly, metrics measuring purely species turnover address methodological issues associated with species richness gradients (e.g. latitudinal gradients: Koleff, Lennon & Gaston 2003b). Moreover, patterns of nestedness and turnover are likely to emerge as a result of different processes: distinguishing these patterns, may contribute to a more mechanistic understanding of spatial patterns in β-diversity (e.g. Baselga 2010). These simulations include two abundance-based metrics, $\beta_{\text{Bray-Curtis}}$ and $\beta_{\text{Ružička}}$ that can be additively partitioned into independent nestedness and turnover components. I find the partitioning method described by Baselga (2013) generates turnover components that are independent of nestedness, while the method proposed by Podani *et al.* (2013) does not.

A principal component analysis indicated a large amount of redundancy among metrics. Yet the results highlight one property which is lacking among existing abundance-based β-diversity metrics. Three pieces of information are absent in samples of species assemblages; *i*) how many species are missing in the sample, but present at the site *ii*) their abundances and *iii*) whether they are shared or unshared between undersampled assemblage pairs. Abundance-based β-diversity metrics that estimate this information and adjust the value of β accordingly are one avenue for improving performance when there is undersampling. Recent developments in biodiversity sampling theory (Green & Plotkin 2007; Morlon *et al.* 2008; McGill 2011) and hierarchical Bayesian techniques that model the observation process (Kéry & Royle 2008) provide a useful starting point for developing such metrics.

The issues I have raised highlight that β-diversity is a multi-faceted concept. Any study measuring β-diversity should be explicit about its goals (which properties should be emphasised) and assumptions (e.g. about sampling) when filtering the available metrics.

4.6 References

Anderson, M.J., Crist, T.O., Chase, J.M., Vellend, M., Inouye, B.D., Freestone, A.L., Sanders, N.J., Cornell, H. V., Comita, L.S., Davies, K.F., Harrison, S.P., Kraft, N.J.B., Stegen, J.C. & Swenson, N.G. (2011). Navigating the multiple meanings of beta diversity: a roadmap for the practicing ecologist. *Ecology Letters*, **14**, 19–28.

Baiser, B., Olden, J.D., Record, S., Lockwood, J.L. & McKinney, M.L. (2012). Pattern and process of biotic homogenization in the New Pangaea. *Proceedings of the Royal Society of London - Series B: Biological Sciences*, **279**, 4772–7.

Balata, D., Piazzi, L. & Benedetti-Cecchi, L. (2007). Sediment disturbance and loss of beta diversity on subtidal rocky reefs. *Ecology*, **88**, 2455–61.

Barton, P.S., Cunningham, S.A., Manning, A.D., Gibb, H., Lindenmayer, D.B. & Didham, R.K. (2013). The spatial scaling of beta diversity. *Global Ecology and Biogeography*, **22**, 639–647.

Baselga, A. (2010). Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography*, **19**, 134–143.

Baselga, A. (2013). Separating the two components of abundance-based dissimilarity: balanced changes in abundance vs. abundance gradients. *Methods in Ecology and Evolution*, **4**, 552–557.

Beck, J., Holloway, J.D. & Schwanghart, W. (2013). Undersampling and the measurement of beta diversity. *Methods in Ecology and Evolution*, **4**, 370–382.

Brown, J.H. (1984). On the Relationship between Abundance and Distribution of Species. *American Naturalist*, **124**, 255–279.

Cassey, P., Lockwood, J.L., Olden, J.D. & Blackburn, T.M. (2008). The varying role of population abundance in structuring indices of biotic homogenization. *Journal of Biogeography*, **35**, 884–892.

Chao, A., Chazdon, R.L., Colwell, R.K. & Shen, T.-J. (2005). A new statistical approach for assessing similarity of species composition with incidence and abundance data. *Ecology Letters*, **8**, 148–159.

Chao, A., Chazdon, R.L., Colwell, R.K. & Shen, T.-J. (2006). Abundance-based similarity indices and their estimation when there are unseen species in samples. *Biometrics*, **62**, 361–71.

Chase, J.M. (2003). Community assembly: when should history matter? *Oecologia*, **136**, 489–498.

Chase, J.M., Kraft, N.J.B., Smith, K.G., Vellend, M. & Inouye, B.D. (2011). Using null models to disentangle variation in community dissimilarity from variation in α-diversity. *Ecosphere*, **2**, Article 24.

Fisher, R.A., Corbet, A.S. & Williams, C.B. (1943). The relation between the number of species and the number of individuals in a random sample of an animal population. *Journal of Animal Ecology*, **12**, 42–58.

Gabriel, D., Roschewitz, I., Tscharntke, T. & Thies, C. (2006). Beta diversity at different spatial scales: Plant communities in organic and conventional agriculture. *Ecological Applications*, **16**, 2011–2021.

Green, J.L. & Plotkin, J.B. (2007). A statistical theory for sampling species abundances. *Ecology Letters*, **10**, 1037–45.

Hankin, R.K.S. (2007). Introducing untb, an R Package For Simulating Ecological Drift Under the Unified Neutral Theory of Biodiversity. *Journal of Statistical Software*, **22**, 1–15.

Harte, J., McCarthy, S., Taylor, K., Kinzig, A. & Fischer, M.L. (1999). Estimating species-area relationships from plot to landscape scale using species spatial-turnover data. *Oikos*, **86**, 45–54.

Holt, B.G., Lessard, J.-P., Borregaard, M.K., Fritz, S.A., Araújo, M.B., Dimitrov, D., Fabre, P.-H., Graham, C.H., Graves, G.R., Jønsson, K.A., Nogués-Bravo, D., Wang, Z., Whittaker, R.J., Fjeldså, J. & Rahbek, C. (2013). An update of Wallace's zoogeographic regions of the world. *Science*, **339**, 74–8.

Jost, L. (2007). Partitioning diversity into independent alpha and beta components. *Ecology*, **88**, 2427–2439.

Jost, L., Chao, A. & Chazdon, R. (2011). Compositional similarity and β (beta) diversity. *Biological Diversity: frontiers in measurement and assessment* (eds A.E. Magurran & B.J. McGill), pp. 66–84. Oxford University Press, Oxford.

Keil, P., Schweiger, O., Kühn, I., Kunin, W.E., Kuussaari, M., Settele, J., Henle, K., Brotons, L., Pe'er, G., Lengyel, S., Moustakas, A., Steinicke, H. & Storch, D. (2012). Patterns of beta diversity in Europe: the role of climate, land cover and distance across scales. *Journal of Biogeography*, **39**, 1473–1486.

Kéry, M. & Royle, J.A. (2008). Hierarchical Bayes estimation of species richness and occupancy in spatially replicated surveys. *Journal of Applied Ecology*, **45**, 589–598.

Koleff, P., Gaston, K.J. & Lennon, J.J. (2003a). Measuring beta diversity for presence-absence data. *Journal of Animal Ecology*, **72**, 367–382.

Koleff, P., Lennon, J.J. & Gaston, K.J. (2003b). Are there latitudinal gradients in species turnover? *Global Ecology and Biogeography*, **12**, 483–498.

Legendre, P. (2014). Interpreting the replacement and richness difference components of beta diversity. *Global Ecology and Biogeography*, **23**, 1324–1334.

Legendre, P. & De Cáceres, M. (2013). Beta diversity as the variance of community data: dissimilarity coefficients and partitioning. *Ecology Letters*, **16**, 951–63.

McGill, B.J. (2011). Linking biodiversity patterns by autocorrelated random sampling. *American Journal of Botany*, **98**, 481–502.

McGill, B.J. (2010). Towards a unification of unified theories of biodiversity. *Ecology Letters*, **13**, 627–42.

McGlinn, D.J. & Hurlbert, A.H. (2012). Scale dependence in species turnover reflects variance in species occupancy. *Ecology*, **93**, 294–302.

Morlon, H., Chuyong, G., Condit, R., Hubbell, S., Kenfack, D., Thomas, D., Valencia, R. & Green, J.L. (2008). A general framework for the distance-decay of similarity in ecological communities. *Ecology Letters*, **11**, 904–17.

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P.M., Stevens, H.H. & Wagner, H. (2013). vegan: Community Ecology Package. R Package version 2.0-10. http://cran.r-project.org/package=vegan.

Podani, J., Ricotta, C. & Schmera, D. (2013). A general framework for analyzing beta diversity, nestedness and related community-level phenomena based on abundance data. *Ecological Complexity*, **15**, 52–61.

Qian, H. & Ricklefs, R.E. (2007). A latitudinal gradient in large-scale beta diversity for vascular plants in North America. *Ecology Letters*, **10**, 737–44.

R Core Development Team. (2014). R: A language and environment for statistical computing. Version 3.1.1. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/.

Smith, A.B. (2010). Caution with curves: Caveats for using the species–area relationship in conservation. *Biological Conservation*, **143**, 555–564.

Whittaker, R.H. (1972). Evolution and Measurement of Species Diversity. *Taxon*, **21**, 213–251.

Whittaker, R.H. (1960). Vegetation of the Siskiyou Mountains , Oregon and California. *Ecological Monographs*, **30**, 280–338.

Wiersma, Y.F. & Urban, D.L. (2005). Beta Diversity and Nature Reserve System Design in the Yukon, Canada. *Conservation Biology*, **19**, 1262–1272.

4.7 Supplementary Material

4.7.1 *β*-diversity metrics

Table S4.1 Formulae for the 33 *β*-diversity metrics.

Data indicates whether metrics use presence-absence (p-a) or abundance (abd) data

Index	Formula	Range	Data	Reference
sim	$\beta = \frac{\min(b,c)}{\min(b,c) + a}$	0 – 1	p-a	(Lennon *et al.* 2001) based on (Simpson 1949), as expressed by (Koleff *et al.* 2003a)
Classic Sørensen	$\beta = 1 - \frac{2a}{2a + b + c}$	0 – 1	p-a	(Sørensen 1948) as expressed by (Koleff *et*

Index	Formula	Range	Data	Reference
				al. 2003a)
Classic Jaccard	$\beta = 1 - \frac{a}{a+b+c}$	0 – 1	p-a	(Jaccard 1912) as expressed by (Koleff *et al.* 2003a)
Chao Sørensen	$\beta = 1 - \frac{2\hat{U}\hat{V}}{\hat{U}+\hat{V}}$	0 - 1	abd	(Chao *et al.* 2005)
Chao Jaccard	$\beta = 1 - \frac{\hat{U}\hat{V}}{\hat{U}+\hat{V}-\hat{U}\hat{V}}$	0 – 1	abd	(Chao *et al.* 2005)
Ružička	$\beta = \frac{2\left(\sum_{i=1}^{s}\lvert x_{ij}-x_{ik}\rvert \,/\, \sum_{i=1}^{s}\lvert x_{ij}+x_{ik}\rvert\right)}{1+\left(\sum_{i=1}^{s}\lvert x_{ij}-x_{ik}\rvert \,/\, \sum_{i=1}^{s}\lvert x_{ij}+x_{ik}\rvert\right)}$	0 – 1	abd	(Ružička 1958)
Baselga Ružička turn	$\beta = \frac{2(\min \mathrm{B}, \mathrm{C})}{A + 2\min(B,C)}$	0 – 1	abd	(Legendre 2014)
Baselga Ružička nest	$\beta = \left(\frac{\lvert B-C\rvert}{A+B+C}\right)\left(\frac{A}{A+2\min(B,C)}\right)$	0 - 1	abd	(Legendre 2014)
Podani Ružička turn	$\beta = \frac{2\min(\mathrm{B},\mathrm{C})}{A+B+C}$	0 – 1	abd	(Podani *et al.* 2013)
Podani Ružička nest	$\beta = \left(\frac{\lvert B-C\rvert}{A+B+C}\right)$	0 – 1	abd	(Podani *et al.* 2013)
Bray-Curtis	$\beta = \frac{\sum_{i=1}^{s}\lvert x_{ij}-x_{ik}\rvert}{\sum_{i=1}^{s}\lvert x_{ij}+x_{ik}\rvert}$	0 – 1	abd	(Bray & Curtis 1957)
Baselga B-C turn	$\beta = \frac{\min(B,C)}{A+\min(B,C)}$	0 – 1	abd	(Baselga 2013)
Baselga B-C nest	$\beta = \left(\frac{\lvert B-C\rvert}{2A+B+C}\right)\left(\frac{A}{A+\min(B,C)}\right)$	0 – 1	abd	(Baselga 2013)
Podani B-C turn	$\beta = \frac{2\min(\mathrm{B},\mathrm{C})}{2A+B+C}$	0 – 1	abd	(Legendre 2014)
Podani B-C nest	$\beta = \left(\frac{\lvert B-C\rvert}{2A+B+C}\right)$	0 – 1	abd	(Legendre 2014)
Canberra	$\beta = \frac{1}{S}\left[\sum_{i=1}^{S}\left(\frac{\lvert x_{ij}-x_{ik}\rvert}{x_{ij}+x_{ik}}\right)\right]$	0 – 1	abd	(Lance & Williams 1967)

Index	Formula	Range	Data	Reference
Morisita	$\beta = 1 - \frac{2 \sum x_{ij} x_{ik}}{(\lambda_j + \lambda_k) N_j N_k}$	0 – 1	abd	(Morisita 1959)
Morisita-Horn	$\beta = 1 - \frac{2 \sum x_{ij} x_{ik}}{[(\sum x_{ij}^2 / N_j^2) + (\sum x_{ik}^2 / N_{ik}^2)] N_j N_k}$	0 – 1	abd	(Horn 1966)
Horn	$\beta = 1 - \frac{\sum[(x_{ij} + x_{ik}) \log(x_{ij} x_{ik})] - \sum(x_{ij} \log x_{ij}) - \sum(x_{ik} \log x_{ik})}{[(N_j + N_k) \log(N_j N_k)] - (N_j \log N_j) - (N_k \log N_k)}$	0 – 1	abd	(Horn 1966)
Kulczynski	$\beta = 1 - 0.5 \left(\frac{\sum \min(x_{ij}, x_{ik})}{N_j} + \frac{\sum \min(x_{ij}, x_{ik})}{N_k} \right)$	0 – 1	abd	(Kulczynski 1927)
Renkonen	$\beta = 1 - \sum_{i=1} \min(p_{ij}, p_{ik})$	0 – 1	abd	(Renkonen 1938)
NESS$_{(m = 50)}$	$\beta = 1 - \frac{2 \sum_{i=1}^{S} \mu_{ij}(m)\, \mu_{ik}(m)}{\sum_{i=1}^{S} [\mu_{ij}(m)]^2 + \sum_{i=1}^{S} [\mu_{ik}(m)]^2}$	0 – 1	abd	(Grassle & Smith 1976)
Gower	$\beta = \frac{1}{S} \sum_{i=1}^{S} \frac{\lvert x_{ij} - x_{ik} \rvert}{\max(x_i) - \min(x_i)}$	0 – 1	abd	(Gower 1971)
Jost Shannon	$\beta = \frac{{}^1D_\gamma}{{}^1D_{\bar{\alpha}}} - 1$	0 – 1	abd	(Jost 2006, 2007b), rescaled from 0 - 1
Jost Simpson	$\beta = \frac{{}^2D_\gamma}{{}^2D_\alpha} - 1$	0 – 1	abd	(Jost 2006, 2007b), rescaled from 0 – 1
Euclidean distance	$\beta = \sqrt{\sum_{i=1}^{S} (x_{ij} - x_{ik})^2}$	0 – 1	abd	(Clifford & Stephenson 1975)
Average Euclidean distance	$\beta = \sqrt{\frac{\sum_{i=1}^{S} (x_{ij} - x_{ik})^2}{S}}$	0 – no upper limit	abd	see (Krebs 1998)
Manhattan	$\beta = \sum_{i=1}^{S} \lvert x_{ij} - x_{ik} \rvert$	0 – no upper limit	abd	see (Krebs 1998)
Alternate Gower	$\beta = \frac{\sum_{i=1}^{S} \lvert x_{ij} - x_{ik} \rvert}{\sum_{i=1}^{S} w_i}$	0 – no upper limit	abd	(Anderson *et al.* 2006)
CYd	$\beta = \frac{1}{S} \sum_{i=1}^{S} \frac{n_i \log {}^1\!/_2 - x_{ij} \log x_{ik} + x_{ik} \log x_{ij}}{n_i}$	0 – no upper limit	abd	(Cao *et al.* 1997)
Binomial	$\beta = \frac{\sum_{i=1}^{S} x_{ij} \log(x_{ij}/n_i) + x_{ik} \log(x_{ik}/n_i) - n_i \log {}^1\!/_2}{n_i}$	0 – no upper limit	abd	(Anderson & Millar 2004)

Index	Formula	Range	Data	Reference
Lande Shannon	$\beta = H_\gamma - \overline{H}_\alpha$	0 - no upper limit	abd	(Lande 1996)
Lande Simpson	$\beta = \lambda_\gamma - \overline{\lambda}_\alpha$	0 - no upper limit	abd	(Lande 1996)

Table S4.2 Notation used in formulae for the 33 *β*-diversity metrics

Symbol	Definition
β	Beta-diversity
a	Matching component: The number of species shared between the focal and contrasted assemblages
b	Matching component: The number of species unique to the contrasted assemblage and absent from the focal assemblage
c	Matching component: The number of species unique to the focal assemblage and absent from the contrasted assemblage
x_{ij}	The number of individuals of species *i* in assemblage *j*
x_{ik}	The number of individuals of species *i* in assemblage *k*
x_i	$= x_{ij} + x_{ik}$ = total number of individuals of species *i* in assemblages *j* and *k* combined
S	The total number of species in focal and contrasted assemblages
N_j	Total number of individuals in assemblage *j*
N_k	Total number of individuals in assemblage *k*
p_{ij}	Relative abundance of species *i* in assemblage *j*
p_{ik}	Relative abundance of species *i* in assemblage *k*
$H_{\overline{\alpha}}$	$\frac{1}{2}\left(\sum_{i=1}^{S} p_{ij} \log p_{ij} + \sum_{i=1}^{S} p_{ik} \log p_{ik}\right)$ = mean of Shannon entropy (Shannon 1948) in assemblages *j* and *k*
H_γ	$\sum_{i=1}^{S} p_{ij} + p_{ik} \log p_{ij} + p_{ik}$ = Shannon entropy (Shannon 1948) for assemblages *j* and *k* pooled

Symbol	Definition
$\lambda_{\overline{\alpha}}$	$= \frac{1}{2}\left[\frac{\sum\ [x_{ij}\,(x_{ij}-1)]}{N_j(N_j-1)}\right] + \left[\frac{\sum\ [x_{ik}\,(x_{ik}-1)]}{N_k(N_k-1)}\right]$ = mean of Simpson's index of diversity (Simpson 1949) for assemblages *j* and *k*
λ_{γ}	$= \left[\frac{\sum\ [x_i\,(x_i-1)]}{x_i(x_i-1)}\right]$ = Simpson's index of diversity (Simpson 1949) for assemblages *j* and *k* pooled
$\mu_{ij}\,(m)$	$= 1-(1-p_{ij})^m$, where *m* is the size of a random sample drawn from a population
$\mu_{ik}(m)$	$= 1-(1-p_{ik})^m$, where *m* is the size of a random sample drawn from a population
w_i	a weight applied to species *i* in order to exclude joint absences. If $x_{ij} + x_{ik} = 0$, then $w_i = 0$, if $x_{ij} + x_{ik} > 0$, then $w_i = 1$
${}^1D_{\alpha}$	$= \exp[-w_1 \sum_{i=1}^{S} p_{i1} \log p_{i1} - w_2 \sum_{i=1}^{S} p_{i2} \log p_{i2}]$
${}^1D_{\gamma}$	$= \exp\left[-\sum_{i=1}^{S} w_j p_{ij} - \sum_{i=1}^{S} w_k p_{ik}\right]$, where w_j and w_k are weights reflecting the relative sizes of assemblages *j* and *k*
${}^2D_{\alpha}$	$= \left(\frac{1}{N}\sum_{i=1}^{S} p_{i1}^2 + \frac{1}{N}\sum_{i=1}^{S} p_{i2}^2\right)^{\frac{1}{1-2}}$
${}^2D_{\gamma}$	$= \left\{\sum_{i=1}^{S}\left[\frac{1}{N}\,(p_{i1}+p_{i2})^{\frac{1}{1-2}}\right]^2\right\}^{\frac{1}{1-2}}$
D_{jk}	Shared species, present in assemblage *j* and assemblage *k*
I [expr]	Indicator function, *I* = 1 if expression is true, *I* = 0 if expression is false
f_{1+}	$= \sum_{i=1}^{D_{jk}} I\left[x_{ij} = 1, x_{ik} \geq 1\right]$ = observed number of shared species that are singletons in assemblage *j*
f_{+1}	$= \sum_{i=1}^{D_{jk}} I\left[x_{ik} = 1, x_{ij} \geq 1\right]$ = observed number of shared species that are singletons in assemblage *k*
f_{2+}	$= \sum_{i=1}^{D_{jk}} I\left[x_{ij} = 2, x_{ik} \geq 1\right]$ = observed number of shared species that are doubletons in assemblage *j*
f_{+2}	$= \sum_{i=1}^{D_{jk}} I\left[x_{ik} = 2, x_{ij} \geq 1\right]$ = observed number of shared species that are doubletons in assemblage *k*
$\widehat{U}$	$= \sum_{i=1}^{D_{jk}} \frac{x_{ij}}{N_j} + \frac{N_k-1}{N_k}\frac{f_{+1}}{2f_{+2}}\sum_{i=1}^{D_{jk}} \frac{x_{ij}}{N_j} I(x_{ik} = 1)$
$\widehat{V}$	$= \sum_{i=1}^{D_{jk}} \frac{x_{ik}}{N_k} + \frac{N_j-1}{N_j}\frac{f_{1+}}{2f_{2+}}\sum_{i=1}^{D_{jk}} \frac{x_{ik}}{N_k} I\left(x_{ij} = 1\right)$

4.7.2 Evaluation of metrics against desirable and personality properties

Table S4.3 Summary of the 18 desirable properties abundance-based *β*-diversity metrics, comprising 16 conceptual (C1-16) and two sampling properties (S1-S2).

Properties are described in the methods section. The scores were standardised by the range of observed values for metric *i*, $\boldsymbol{\beta_{i,range}}$ in each test.

Property	Score for metric *i*
C1. Independent of *α*-diversity	$\mathrm{C1}_i = \sqrt{\frac{1}{n_t n_\alpha}\sum_{t=1}^{n_t}\sum_{\alpha=1}^{n_\alpha}\left(\frac{\beta_{i,t,\alpha,} - \beta_{i,t,\alpha max}}{\beta_{i,range}}\right)^2}$, where $\beta_{i,t,\alpha}$ and $\beta_{i,t,\alpha max}$ are median *β*-diversity for metric *i* at turnover *t* and *α*-diversity *α* and α_{max}, respectively, $\beta_{i,range}$ is the range of observed *β*-diversity for metric *i* in this test, n_t is the number of turnover levels, here 6, n_α is the number of levels of *α*-diversity, here 10.
C2. *β* is cumulative along a gradient of species turnover	$\mathrm{C2}_\mathrm{i} = \sqrt{\frac{1}{n_t n_g n_j}\sum_{t=1}^{n_t}\sum_{g=1}^{n_g}\sum_{j=1}^{n_j}\left(\frac{\left(\beta_{i,t,g,j}^{A,C} - (\beta_{i,t,g,j}^{A,B} + \beta_{i,t,g,j}^{B,C})\right)}{\beta_{i,range}}\right)^2}$, where $\beta_{i,t,g,j}^{A,C}$, is *β*-diversity for metric *i* between assemblages A and C at turnover *t*, under a gradient of strength *g* in simulation *j*, $\beta_{i,t,g,j}^{A,B} + \beta_{i,t,g,j}^{B,C}$ is *β*-diversity expected under additivity, $\beta_{i,range}$ is the range of *β*-diversity for metric *i* in this test, n_t is the number of turnover levels, here 6, n_g is the number of gradient strengths, here 7, and n_j is the number of simulations at each unique combination of *t* and *g*, here 10000.
C3. Similarity is probabilistic when assemblages are independently and identically distributed	$\mathrm{C3}_i = \sqrt{\frac{1}{n_t n_j}\sum_{t=1}^{n_t}\sum_{j=1}^{n_j}\left(\frac{\left(1-\beta_{i,t,j}^{A,C}\right) - \left(1-\beta_{i,t,j}^{A,B}\right)\left(1-\beta_{i,t,j}^{B,C}\right)}{\beta_{i,range}}\right)^2}$, where $\beta_{i,t,j}^{A,C}$ is the value of *β*-diversity for metric *i* between assemblages A and C at turnover *t* in simulation *j* and $\beta_{i,j,t}^{A,B}\beta_{i,j,t}^{B,C}$ is *β*-diversity expected under probabilistic similarity, $\beta_{i,range}$ is the range of observed *β*-diversity for metric *i* in this test, n_t is the number of turnover levels and n_j is the number of simulations at each level of *t*, here 10000.

Property	**Score for metric *i***
C4. Minimum of zero and positive	C4$_{i}$ = TRUE / FALSE for $\beta_i^{A,A} = 0$ and $\beta_i^{A,B} \geq 0$ where $\beta_i^{A,A}$ and $\beta_i^{A,B}$ are median β-diversity for metric *i* in 10000 simulations for two identical assemblages and two different assemblages where there is either species turnover, decoupling of species ranks or evenness differences.
C5. Monotonic: β increases in a series of assemblages with increasing species turnover	C5$_{i}$ = TRUE / FALSE for if $t_{A,B} < t_{A,C}$ then $\beta_{i,t}^{A,B} < \beta_{i,t}^{A,C}$, where $t_{A,B}$ and $t_{A,C}$ are the proportion of species turned over between assemblages *A* and *B* and between *A* and *C,* respectively and $\beta_{i,t}^{A,B}$ and $\beta_{i,t}^{A,C}$ are median β-diversity in 10000 simulations for metric *i* at increasing levels of turnover, t.
C6. Monotonic: β increases in a series of assemblages with increasing decoupling of species ranks	C6$_{i}$ = TRUE / FALSE for if $r_{A,B} < r_{A,C}$ then $\beta_{i,r}^{A,B} > \beta_{i,r}^{A,C}$, where $r_{\text{A,B}}$ and $r_{A,C}$ are the partial correlation between species ranks in assemblages *A* and B and *A* and *C*, respectively and $\beta_{i,r}^{A,B}$and ,$\beta_{i,r}^{A,C}$ are median β-diversity in 10000 simulations for metric *i* with incrementally decreasing correlation between species ranks, r.
C7. Monotonic: β increases in a series of assemblages with increasing evenness differences	C7$_{i}$ = TRUE / FALSE for if $\Delta E_{A,B} < \Delta E_{A,\,C}$ then $\beta_i^{A,B} < \beta_i^{A,C}$, where $\Delta E_{\text{A, B}}$ and $\Delta E_{A,\,C}$ are the difference in evenness between assemblages *A* and *B* and *A* and *C*, respectively and $\beta_i^{A,B}$ and $\beta_i^{A,C}$ are median β-diversity in 10000 simulations for metric *i* with incrementally increasing levels of evenness differences, ΔE.
C8. β when extreme decoupling of species ranks < β when species turnover is complete	C8$_{i}$ = TRUE / FALSE for $\beta_{i,\,tmax,\,rmax} > \beta_{i,\,tmin,\,rmin}$, where $\beta_{i,\,tmax,\,rmax}$ and $\beta_{tmin,\,rmin}$ are the median values of β-diversity for metric *i* under complete species turnover and no decoupling of species and under extreme decoupling of species ranks and no species turnover, respectively.
C9. β under extreme differences in evenness < β when species turnover is complete	C9$_{i}$ = TRUE / FALSE for $\beta_{i,tmax,\,\Delta Emin} > \beta_{i,\,tmin,\,\Delta Emax}$, where $\beta_{i,tmax,\,\Delta Emin}$ and $\beta_{i,\,tmin,\,\Delta Emax}$ are the median values of β-diversity under complete species turnover and no evenness difference and under no species turnover and extreme evenness difference, respectively.

Property	**Score for metric *i***
C10. Fixed upper bound	$C10_i$ = TRUE/FALSE for $\frac{1}{2}\sum\beta^2_{i,t_{max}}$ = 1, where β_i is the value of β-diversity for metric *i* when there is complete species turnover between assemblages.
C11. Symmetry	$C11_i$ = TRUE/FALSE for $\beta_{i,A,B} = \beta_{i,B,A}$, where $\beta_{i,A,B}$ and $\beta_{i,B,A}$ are the values of β-diversity for metric *i* for assemblages A and B and B and A, respectively
C12. Double-zero asymmetry	$C12_i$ = TRUE / FALSE for *ab* and *pr* in 1:10, $\beta_{i,\mathrm{ab}} = \beta_{i,,ab=0}$ and $\beta_{i,\mathrm{pr}} < \beta_{i,,pr=0}$ where $\beta_{i,\mathrm{a}}$ and $\beta_{i,,a=0}$ are the values of β-diversity for metric *i* when *ab* double absences and no double absences, respectively, have been added to the assemblage pair. $\beta_{i,\mathrm{pr}}$ and $\beta_{i,,pr=0}$ are the values of β-diversity for metric *i* when *pr* double presences and no double presences, respectively, have been added to the assemblage pair.
C13. β does not decrease in a series of nested assemblages	$C13_i$ = TRUE / FALSE for $S_{1,2} < S_{1,3}$ then $\beta^{1,2}_{i,t} \leq \beta^{1,3}_{i,t}$, where *S* is difference in species richness between assemblages *1* and *2* and *1* and *3,* respectively and $\beta^{1,2}_i$ and $\beta^{1,3}_i$ are median β-diversity of assemblages *1* and *2* and *1* and *3,* respectively, for metric *i* at turnover, *t* in 10000 simulations.
C14. Independent of species replication	$C14_i = \sqrt{\frac{1}{n_t n_x}\sum_{t=1}^{n_t}\sum_{x=1}^{n_x}\left(\frac{\beta_{i,t,x} - \beta_{i,t,}}{\beta_{i,range}}\right)^2}$, where $\beta_{i,t}$ is median β-diversity in 10000 simulations for metric *i* at turnover *t* and $\beta_{i,t,x}$ is median β-diversity when *x* identical subsets are pooled (species replication), $\beta_{i,range}$ is the range of observed β-diversity for metric *i* in this test, n_t = the number of turnover levels, here 6, and n_x is the number of levels of species replication, *x* , here 10.
C15. Independent of measurement units	$C15_i = \sqrt{\frac{1}{n_t n_{cc}}\sum_{t=1}^{n_t}\sum_{cc=1}^{n_{cc}}\left(\frac{\beta_{i,t,cc} - \beta_{i,t}}{\beta_{i,range}}\right)^2}$, where $\beta_{i,t}$ is median β-diversity in 10000 simulations for metric *i* at turnover *t* and $\beta_{i,t,cc}$ is median β-diversity when abundances in both assemblages are multiplied by a constant factor cc. $\beta_{i,range}$ is the range of observed β-diversity for metric *i* in this test, n_t is the number of turnover levels, here 6 and n_c is the number of levels of the constant factor, *cc* , here 10.

Property	**Score for metric *i***
C16. Independent of differences in abundance	$\mathrm{C16_i} = \sqrt{\frac{1}{n_t n_c}\sum_{t=1}^{n_t}\sum_{c=1}^{n_c}\left(\frac{\beta_{i,t,c} - \beta_{i,t}}{\beta_{i,range}}\right)^2}$, where $\beta_{i,t}$ is median *β*-diversity in 10000 simulations for metric *i* at turnover *t* and $\beta_{i,t,c}$ is median *β*-diversity when abundances in one assemblage are multiplied by a constant factor *c*. $\beta_{i,range}$ is the range of observed *β*-diversity for metric *i* in this test, n_t is the number of turnover levels, here 6 and n_c is the number of levels of the constant factor, *c* , here 10.
S1. Independent of sample size	$S1_\mathrm{i} = \sqrt{\frac{1}{n_t n_N}\sum_{t=1}^{n_t}\sum_{N=1}^{n_N}\left(\frac{\beta_{i,t,N} - \beta_{i,t,Nmax}}{\beta_{i,range}}\right)^2}$, where $\beta_{i,t,N}$ and $\beta_{i,t,Nmax}$ are median *β*-diversity in 10000 simulations for metric *i* at turnover *t* and sample sizes *N* and $N_{\max}$, respectively, $\beta_{i,range}$ is the range of observed *β*-diversity for metric *i* in this test, n_t = the number of turnover levels, here 6 and n_N is the number of sample size levels, here 16.
S2. Independent of unequal sample sizes	$S2_i = \sqrt{\frac{1}{n_t n_{\Delta N}}\sum_{t=1}^{n_t}\sum_{\Delta N=1}^{n_{\Delta N}}\left(\frac{\beta_{i,t,\Delta N} - \beta_{\ i,t,\Delta Nmin}}{\beta_{i,range}}\right)^2}$, where $\beta_{i,t,\Delta N}$ and $\beta_{i.t,\Delta Nmin}$ are median *β*-diversity in 10000 simulations for metric *i* at turnover *t* and sample size difference ΔN and ΔN_{min}, respectively, $\beta_{i,range}$ is the range of observed *β*-diversity for metric *i* in this test, n_t = the number of turnover levels, here 6 and $n_{\Delta N}$ is the number of levels of sample size difference, here 16.

Table S4.4 Summary of the five personality properties (P1-5) against which *β*-diversity metrics were evaluated.

Score is the method used to evaluate *β*-diversity metric *i* for each property.

Personality	**Score**
P1. Sensitivity to differences in *α*-diversity	$P1_i = \sqrt{\frac{1}{n_{\Delta\alpha} n_t}\sum_{t=1}^{n_t}\sum_{\Delta\alpha=1}^{n_{\Delta\alpha}}\left(\frac{\beta_{\ i,t,\Delta\alpha,} - \beta_{i,t,\Delta\alpha min,}}{\beta_{i,range}}\right)^2}$, where $\beta_{i,t,\Delta\alpha}$ and $\beta_{i,t,\Delta\alpha min}$ are the median values of *β*-diversity for metric *i* at turnover *t* and sample size difference $\Delta\alpha$ and $\Delta\alpha_{min}$, respectively, $\beta_{i,range}$ is the range of *β*-diversity for metric *i* in this simulation and *n* is the number of unique combinations of $\Delta\alpha$ and *t*.

Personality	**Score**
P2. Relative sensitivity to nestedness and turnover components of β	$P2_i = \frac{\beta_{i,tmax,\ smin}}{\beta_{i,tmin,\ smax}}$, where $\beta_{i,tmax,smin}$ and $\beta_{i,tmin,smax}$ are the median values of β-diversity under complete species turnover and no species nestedness and for extreme species loss and no species turnover, respectively.
P3. Relative sensitivity to decoupling of species ranks and species turnover components of β	$P3_i = \frac{\beta_{i,tmax,rmax}}{\beta_{i,tmin,rmin}}$, where $\beta_{i,tmax,rmax}$ and $\beta_{i,tmin,rmin}$ are the median values of β-diversity for metric *i* under complete species turnover and no decoupling of species ranks and under extreme decoupling of species ranks and no species turnover, respectively.
P4. Relative sensitivity to evenness differences and species turnover components of β	$P4_i = \frac{\beta_{i,tmax,\Delta Emin}}{\beta_{i,tmin,\Delta E=max}}$, where $\beta_{i,tmax,\Delta Emin}$ and $\beta_{i,tmin,\ \Delta Emax}$ are the median values of β-diversity for metric *i* under complete species turnover and no evenness differences and under extreme evenness difference and no species turnover, respectively
P5. Relative sensitivity to turnover in rare versus common species	$P5_i = \frac{\beta_{i,n_{min}}}{\beta_{i,n_{max}}}$, where $\beta_{i,n_{min}}$ and $\beta_{i,n_{max}}$are the values of β for metric *i* when the rarest and commonest species, respectively, are turned over.

4.7.3 Supplementary Results

Figures S4.1 – 13 are the results of simulations testing the 33 metrics in Table S4.1 against the 16 conceptual and two sampling and in Table S4.3 and five personality traits in Table S4.4. On each of the *x* axes is a test-specific parameter describing some aspect of assemblage structure. The scores for each metric are shown above the plots and were calculated using the methods in Tables S4.3 and S4.4.

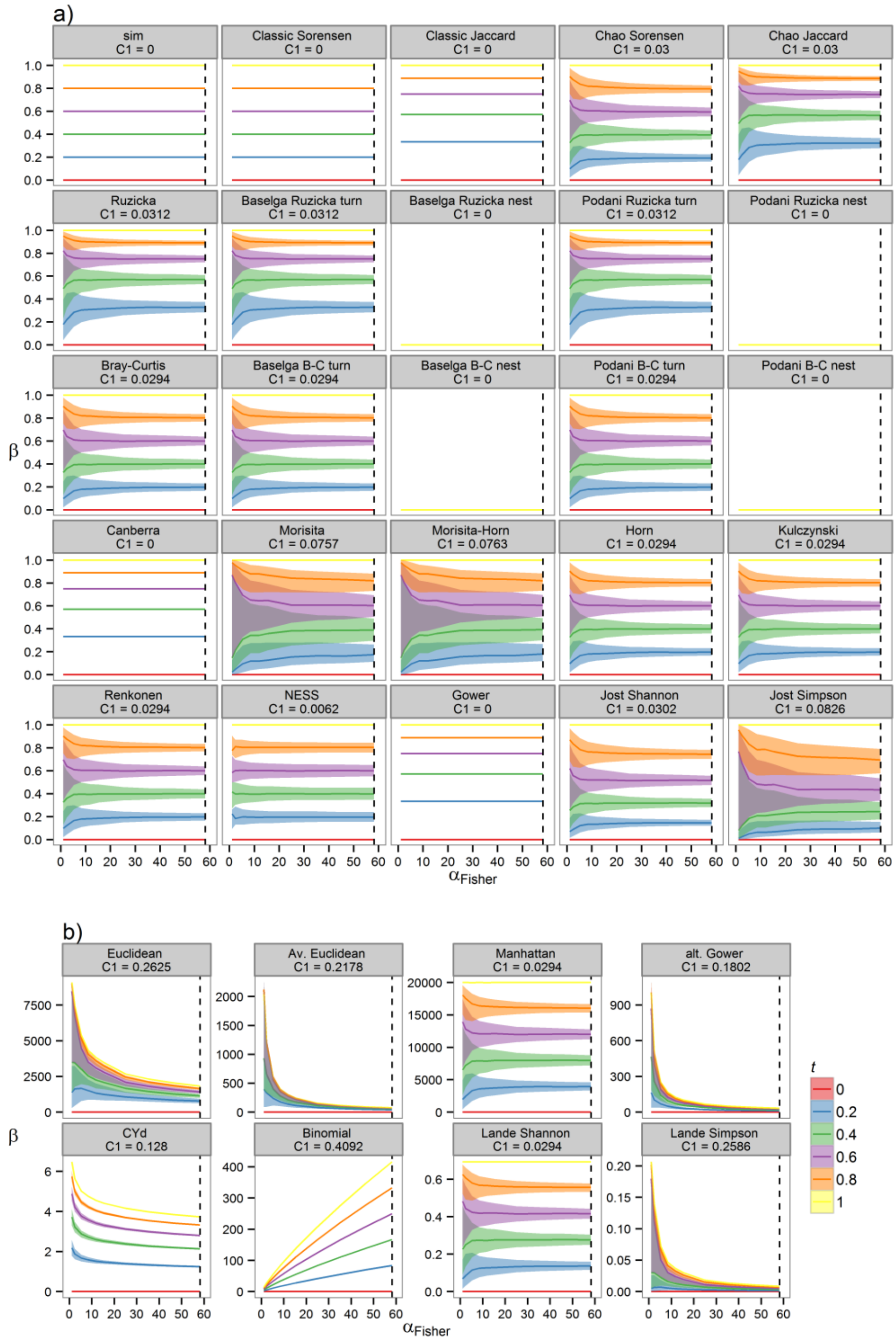

Fig. S4.1 Effect of *α*-diversity of assemblages on *β*

Effect of α (e.g. both low α or both high α) on the value of β for a) 25 metrics with a fixed upper limit and b) 8 metrics with no maxima. Solid lines and shaded areas are the median and interquartile range, respectively, of β for 10000 simulations at each unique combination of species turnover, t, and Fisher's α-diversity, αFisher. Metrics scored for desirable property C1, independence of α-diversity. Vertical dashed black lines intersect the reference values of median β at high αFisher.

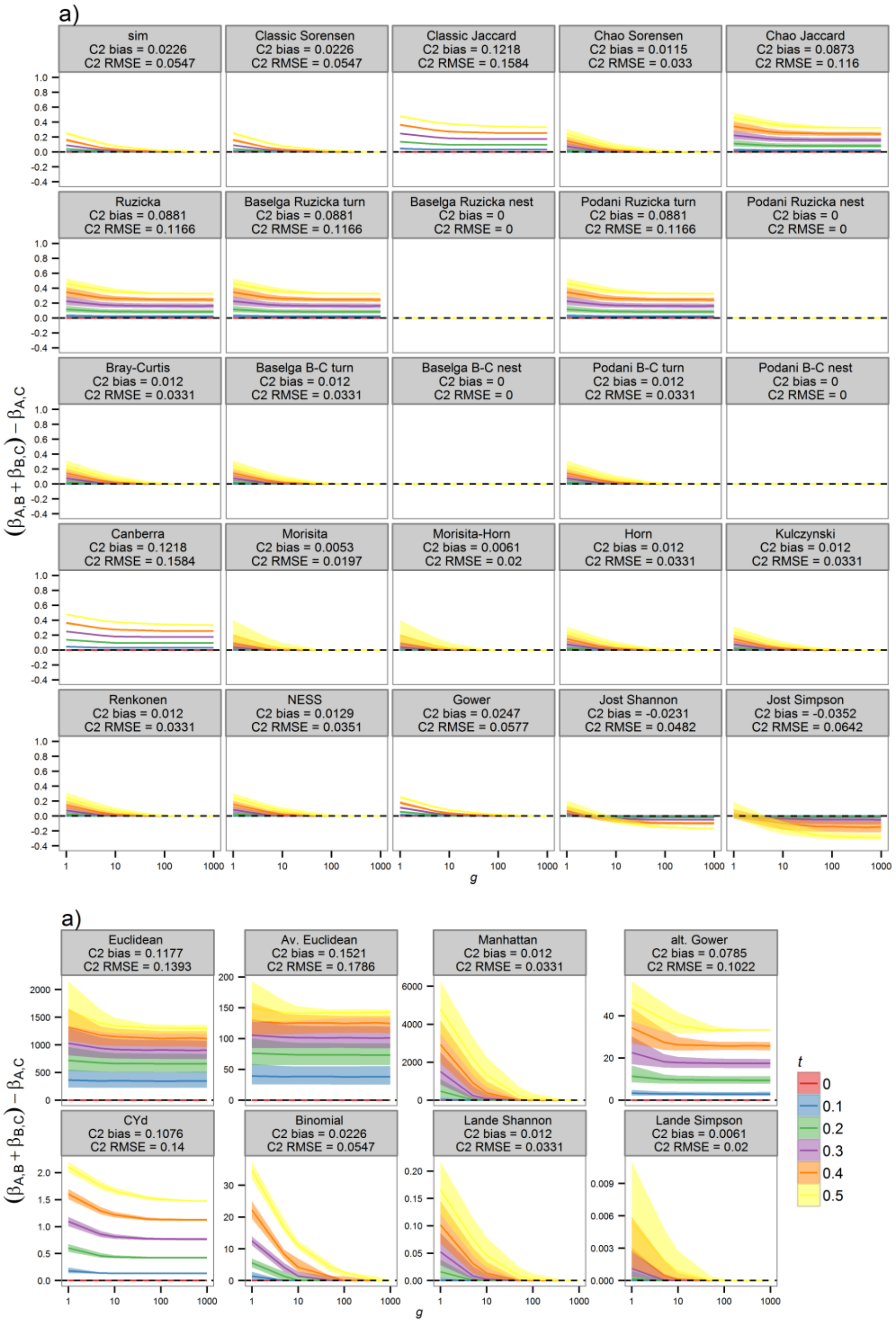

Fig. S4.2 Cumulative *β*-diversity

Values of *β*-diversity under different strengths of directional species turnover along a simulated environmental gradient, *g* for a) 25 metrics with a defined upper limit b) 8 metrics with no maxima. Solid lines and shaded areas are the median and interquartile range, respectively, of the differences between observed $\beta_{A,C}$ and that predicted if *β* were cumulative along a gradient of turnover ($\beta_{A,B}$+$\beta_{B,C}$), based on 10000 simulations at each unique combination of species turnover, *t*, and environmental gradient, *g*. Metrics are scored for property C2, *β* is cumulative along a gradient of species turnover. Horizontal dashed black lines at 0 represent perfect cumulative behaviour. Scores for bias are also presented in order to evaluate whether the metrics are systematically sub- or supra-additive.

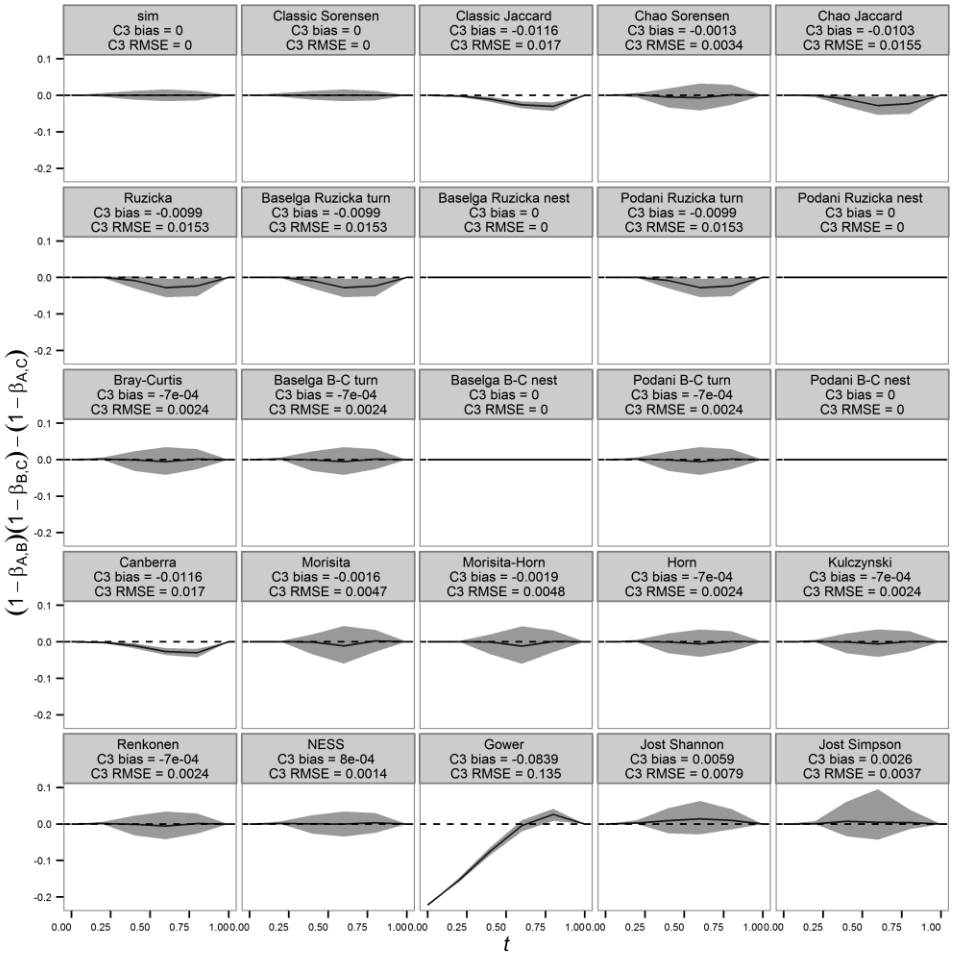

Fig. S4.3 Probabilistic *β*-diversity

β-diversity in simulated assemblages that are independent draws form a well-mixed metacommunity for 25 metrics with fixed upper limits. Metrics without upper limits do not have a similarity complement. Solid lines and shaded areas are the median and interquartile range, respectively, of the differences between observed similarity, $(1-\beta_{A,C})$ and that predicted if similarity were probabilistic, $(1-\beta_{A,B})(1-\beta_{B,C})$ based on 10000 simulations at each level of species turnover, *t*. Metrics are scored for desirable property C3, similarity is probabilistic when assemblages are independently and identically distributed. Horizontal dashed black lines at 0 represent perfect probabilistic behaviour. The scores for bias are also presented to evaluate whether the metrics are systematically sub- or supra-probabilistic.

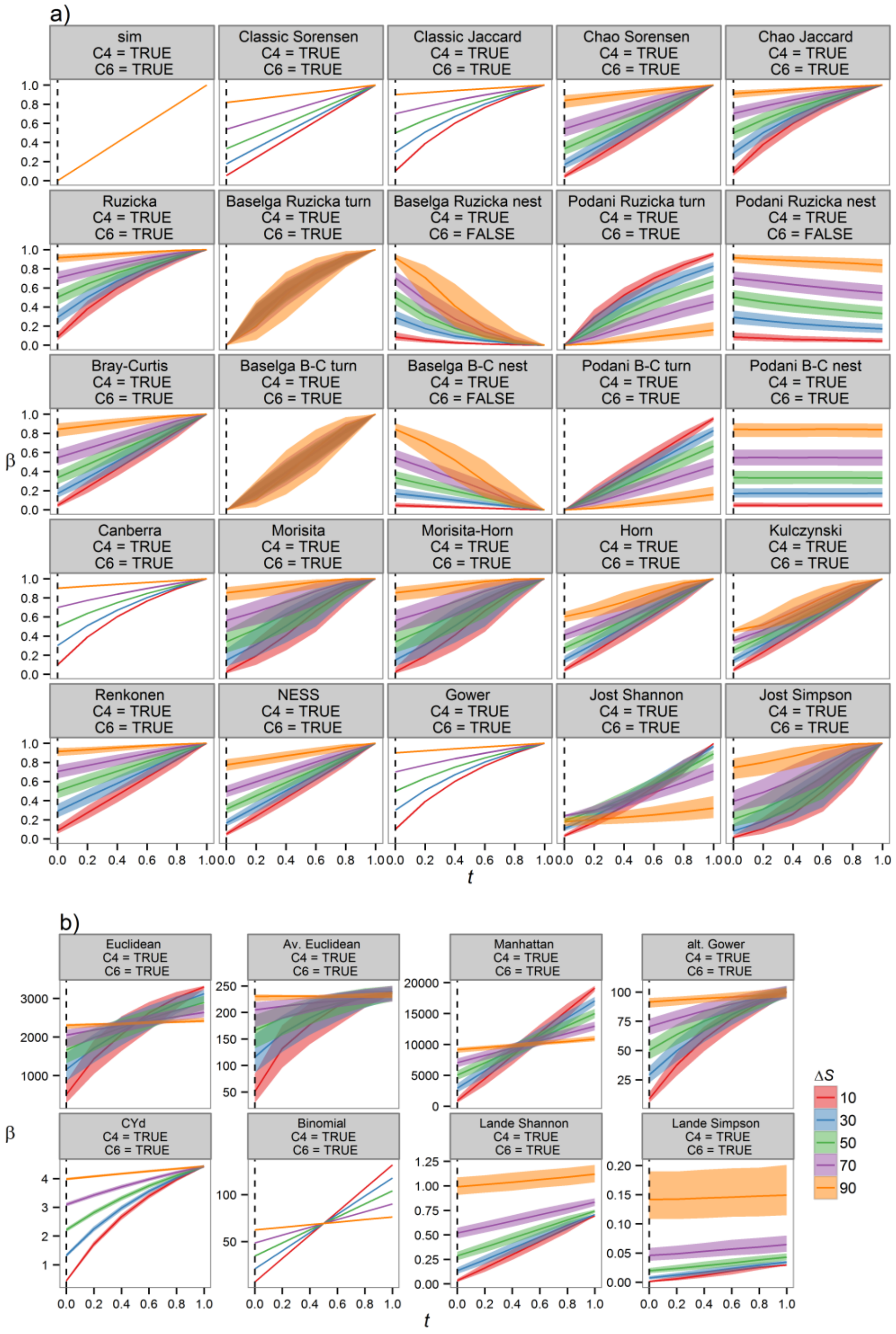

Fig. S4.4 Effect of species turnover on *β*-diversity

Simulations for a) 25 metrics with a fixed upper limit b) 8 metrics without maxima Solid lines and shaded areas are the median and interquartile range, respectively, of *β* based on 10000 simulations at each combination of species turnover, *t* and species loss, *ΔS*. Metrics are scored as TRUE or FALSE for desirable property C4, minimum of zero and positive and C6, monotonic increase with species turnover. Vertical dashed black lines intersect the reference values of median *β* at *t* = 0 (no species turnover).

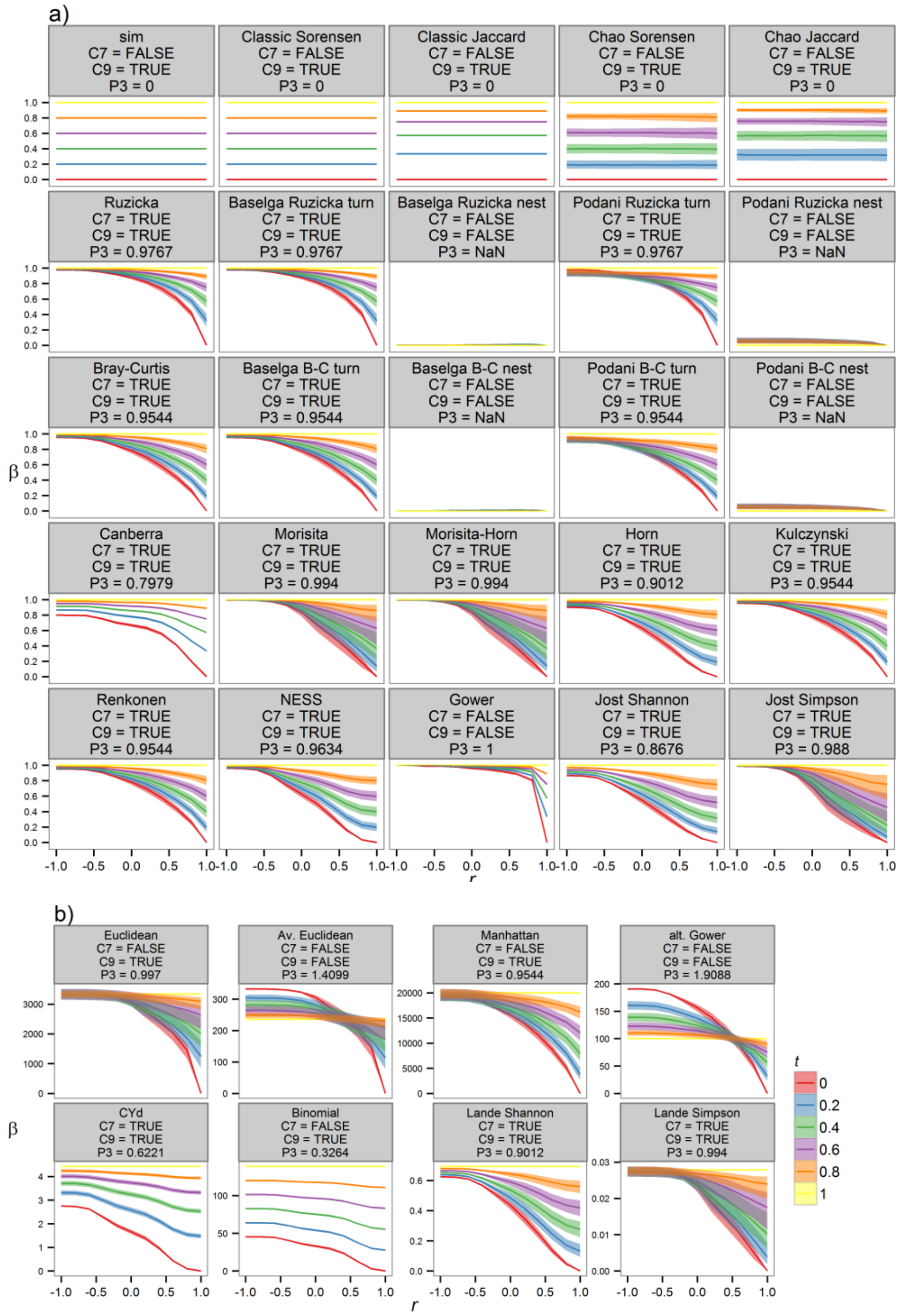

Fig. S4.5 Effect of decoupling of species ranks on *β*-diversity

Simulations of decoupling of ranks in species assemblages for a) 25 metrics with defined maxima and minima b) 8 metrics with no defined maxima. Solid lines and shaded areas are the median and interquartile range, respectively, of β based on 10000 simulations at each unique combination of species turnover, t, and partial correlation between ranks, r. Metrics are scored for desirable properties C7, monotonic increase with decoupling of species ranks and C9, extreme decoupling of species ranks (partial correlation = -1) is less than β for complete species turnover. Metrics are also scored for P3, relative sensitivity to decoupling of species ranks and species turnover. Vertical dashed black lines intersect the reference values of median β at r = 1 (perfect correlation between ranks).

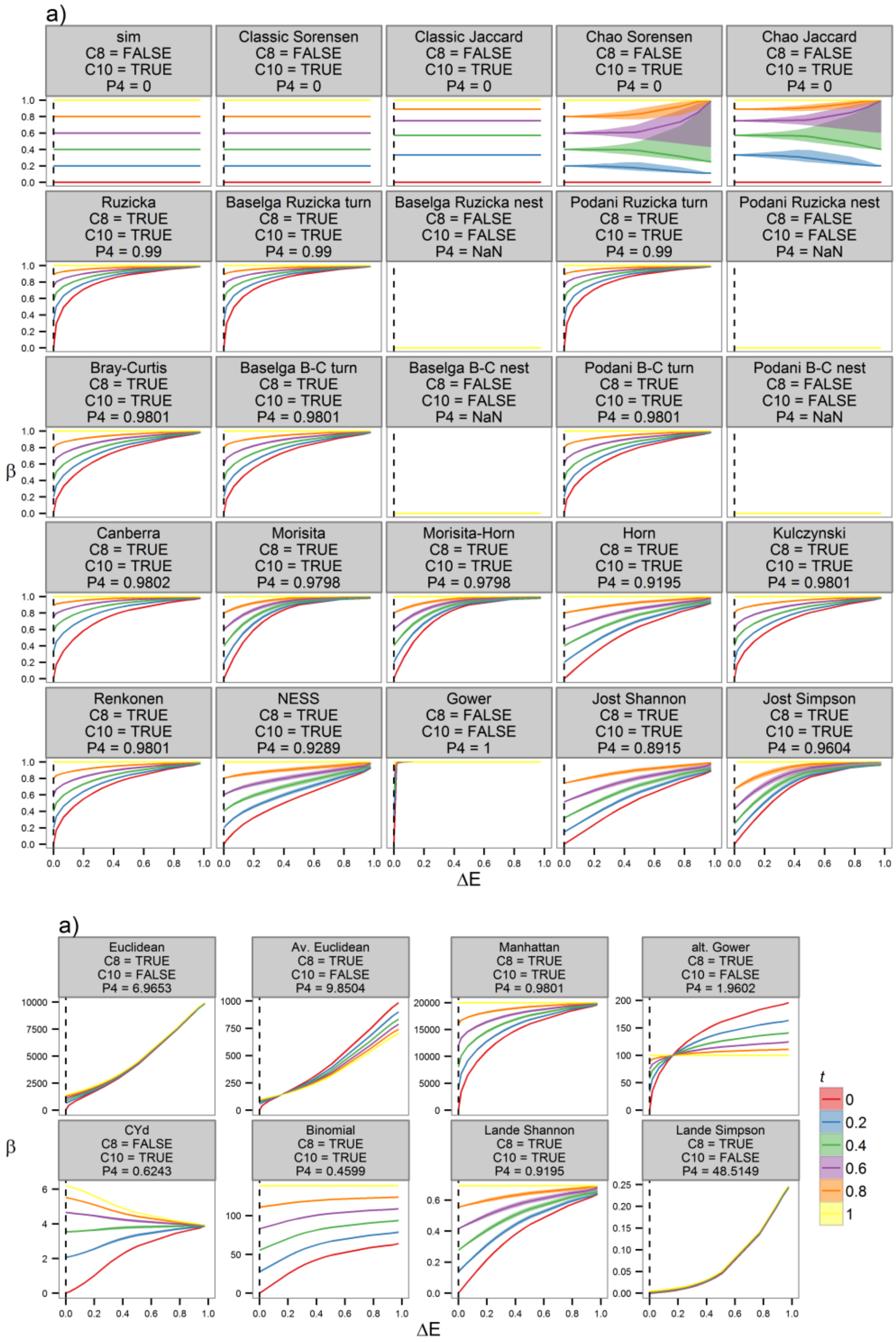

Fig. S4.6 Effect of evenness differences on *β*-diversity

Simulations of evenness differences in species assemblages for a) 25 metrics with fixed upper limits b) 8 metrics with no maxima. Solid lines and shaded areas are the median and interquartile range, respectively, of *β* based on 10000 simulations at each unique combination of species turnover, *t*, and difference in evenness, Δ*E*. Metrics are scored for desirable properties C8, monotonic increase with evenness differences, and C10, median *β* under extreme evenness differences (Δ*E* ~ 1) is less than median *β* when species turnover is complete, (*t*=1). Metrics are also scored for P4, relative sensitivity to evenness differences and species turnover components of *β*. Vertical dashed black lines intersect the reference values of median *β* at Δ*E*=0 (no evenness differences).

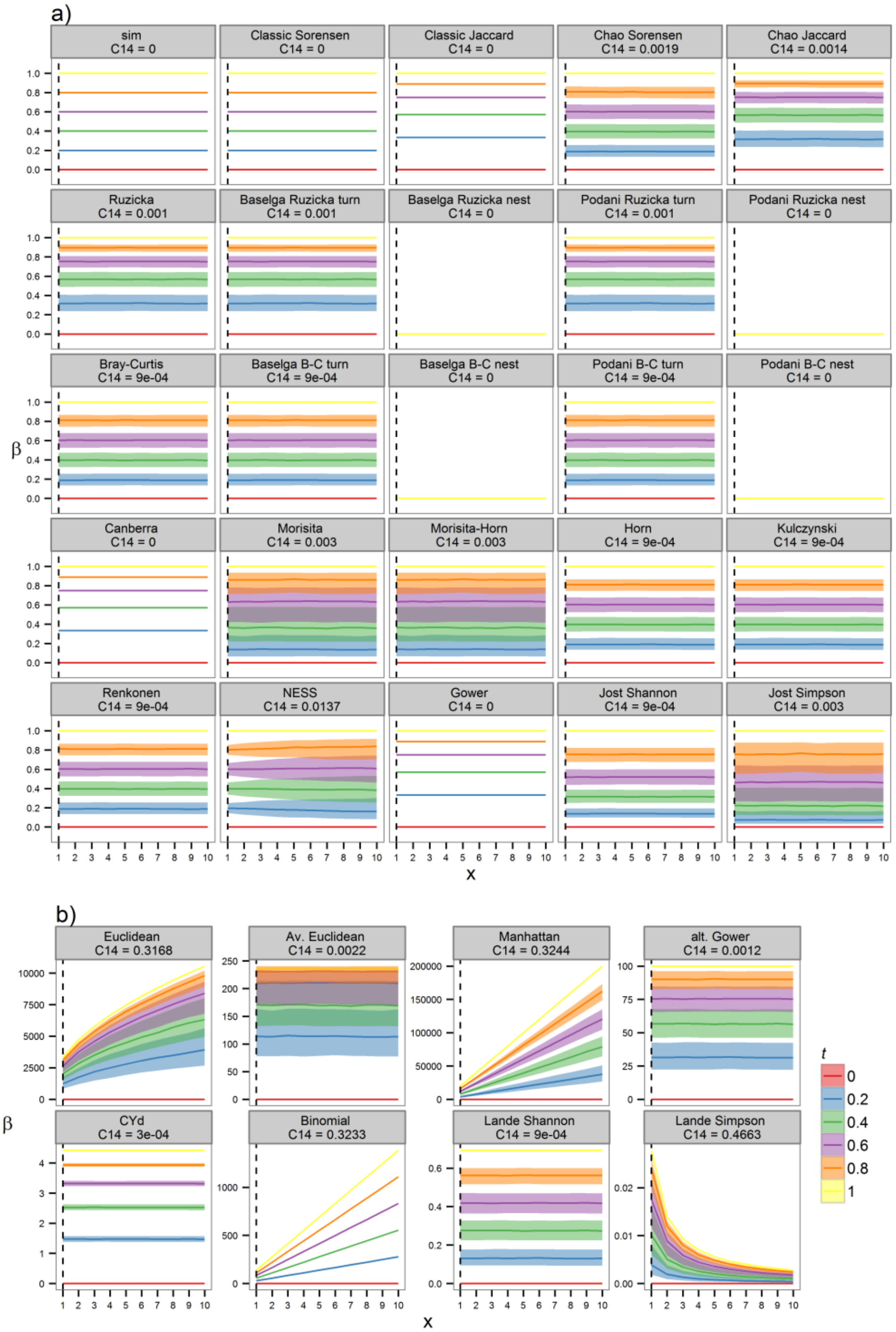

Fig. S4.7 Effect of species replication on *β*-diversity

Simulations of species replication in species assemblages (pooling x identical subsets of an assemblage pair) for a) 25 metrics with fixed upper limits b) 8 metrics with no maxima. Solid lines and shaded areas are the median and interquartile range, respectively, of β based on 10000 simulations at each unique combination of species turnover, t, and number of species replication events, x. Metrics are scored for desirable property C14, independence of species replication. Vertical dashed black lines intersect the reference values of median β at x=1 (no species replication).

Fig. S4.8 Effect of units used to measure abundance on *β*-diversity

Simulations of assemblage pairs with different units of abundance for a) 25 metrics with fixed upper limits b) 8 metrics with no maxima. Solid lines and shaded areas are the median and interquartile range, respectively, of β based on 10000 simulations at each unique combination of species turnover, t, and a constant factor, cc, by which abundances in both assemblages are multiplied. Metrics are scored for desirable property C15, independence of measurement units. Vertical dashed black lines intersect the reference values of median β at cc=1 (no change in measurement units).

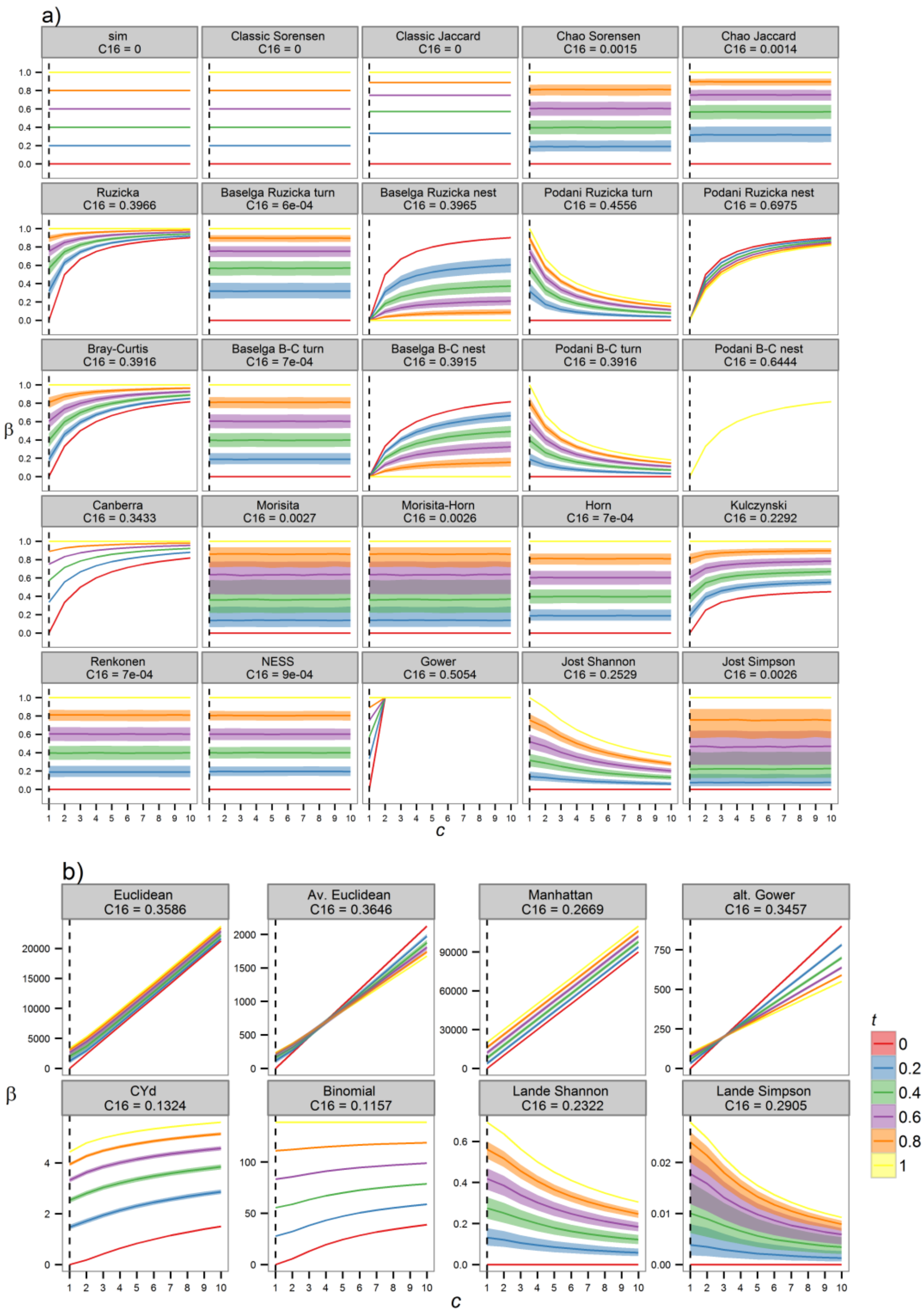

Fig. S4.9 Effect of differences in abundance on *β*-diversity

Simulations of differences in abundance between assemblages for a) 25 metrics with fixed upper limits b) 8 metrics with no maxima. Solid lines and shaded areas are the median and interquartile range, respectively, of *β* based on 10000 simulations at each unique combination of species turnover, *t*, and a constant factor, *c*, by which abundances in one assemblage are multiplied. Metrics are scored for desirable property C16, independence of differences in abundance. Vertical dashed black lines intersect the reference values of median *β* at *c*=1 (no abundance differences).

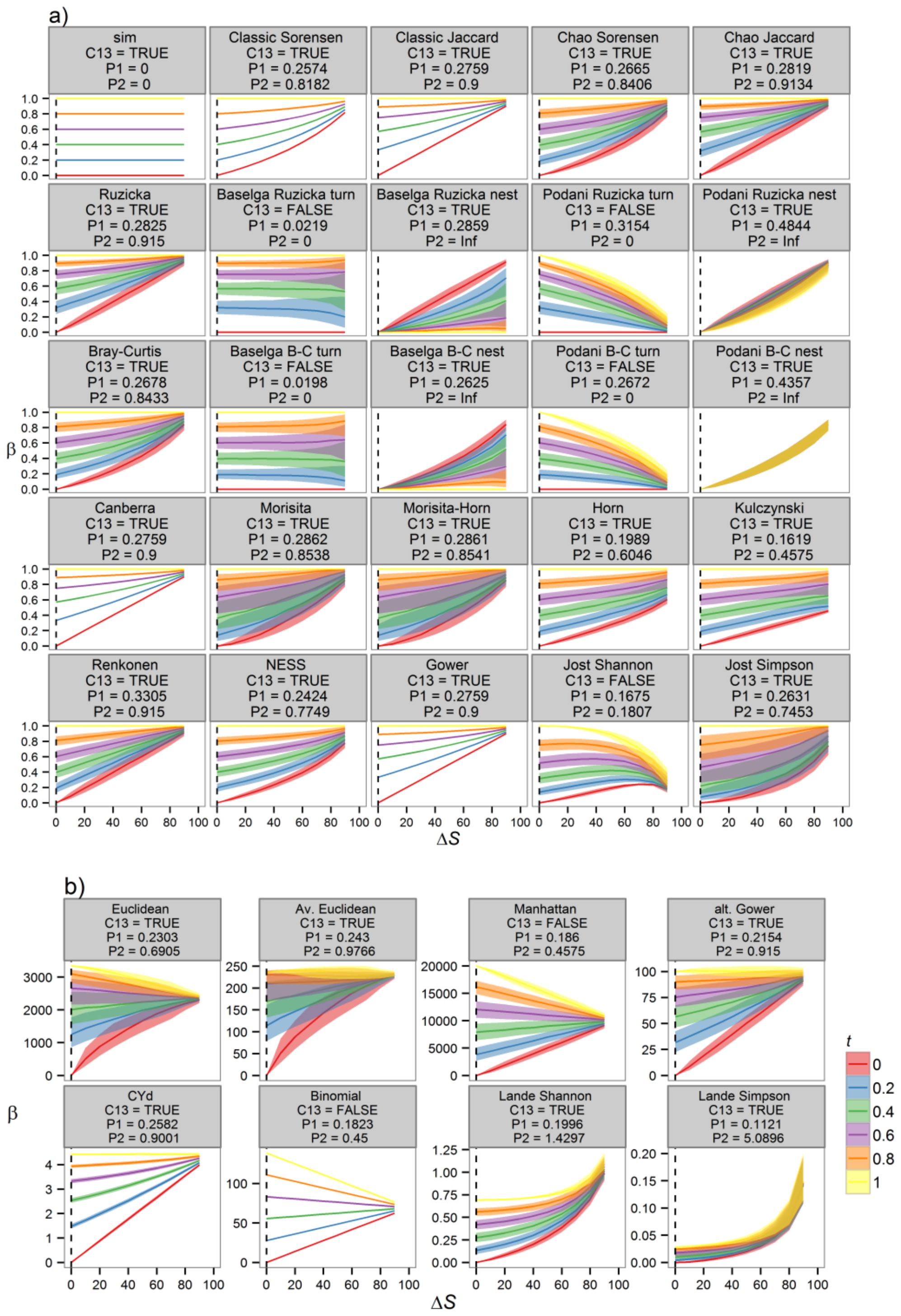

Fig. S4.10 Effect of nestedness on the value of *β*-diversity

Simulations of the effect of nestedness of assemblages pairs for a) 25 metrics with fixed upper limits and b) 8 metrics with no maxima. Solid lines and shaded areas are the median and interquartile range, respectively, of β based on 10000 simulations at each unique combination of species turnover, t, and difference in species richness, ΔS. Metrics are scored for desirable property C13, β does not decrease in a series of nested assemblages and personality traits P1, sensitivity to nestedness, and P2 relative sensitivity to nestedness and turnover. Vertical dashed black lines intersect the reference values of median β at ΔS=0 (no differences in species richness).

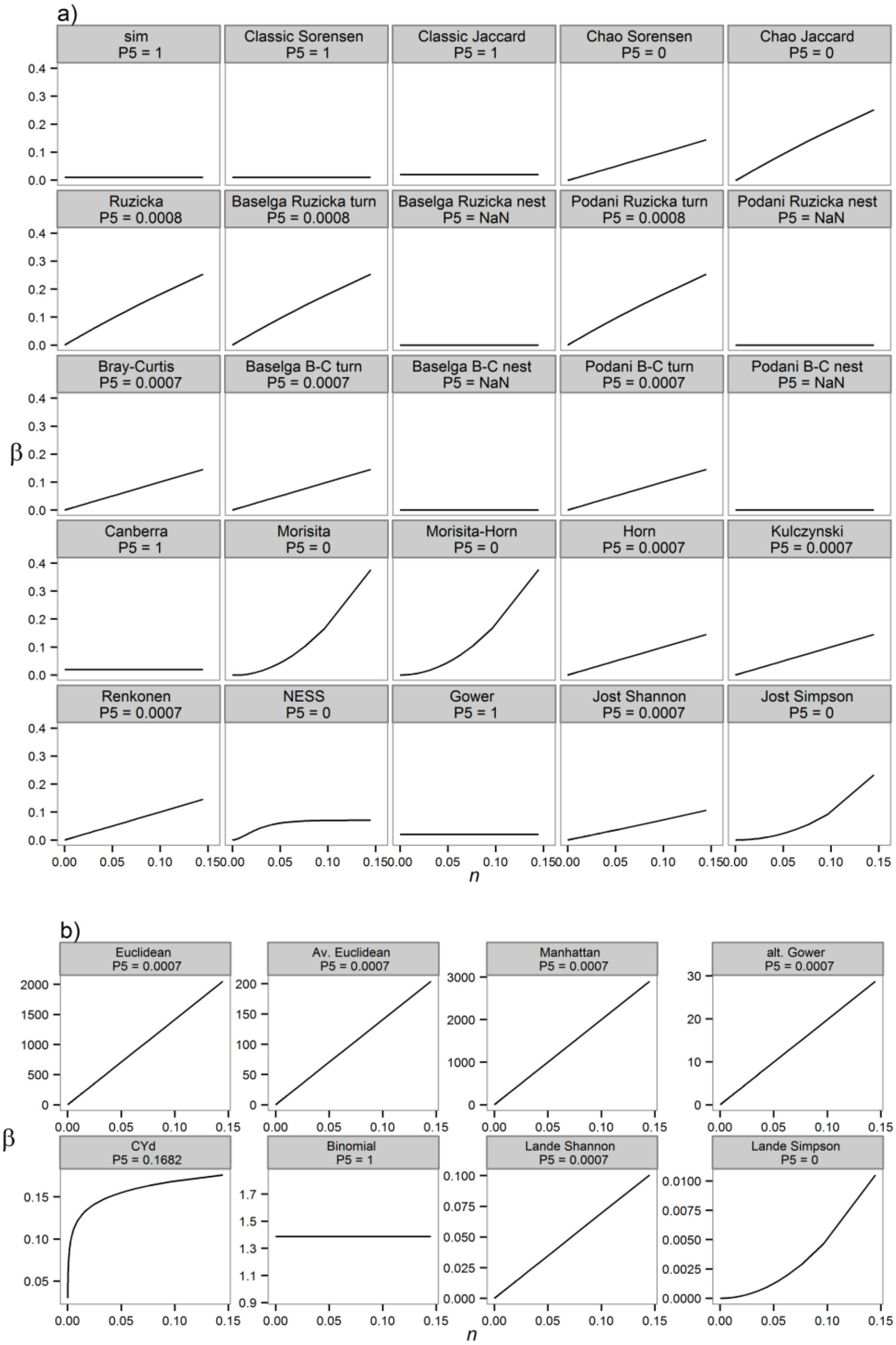

Fig. S4.11 Sensitivity to turnover in rare versus common species

Simulations of species turnover in common and rare species for a) 25 metrics with fixed upper limits b) 8 metrics with no maxima. Solid lines are the value of β when a single species with relative abundance, n, is turned over. Metrics are scored for personality trait P5, relative sensitivity to turnover in rare versus common species. A value of 1 indicates that a metric weights turnover in rare and common species equally, while a value of less than one indicates rare species contribute less to the value of β. A value of zero indicates a metric is almost completely insensitive to turnover in rare species.

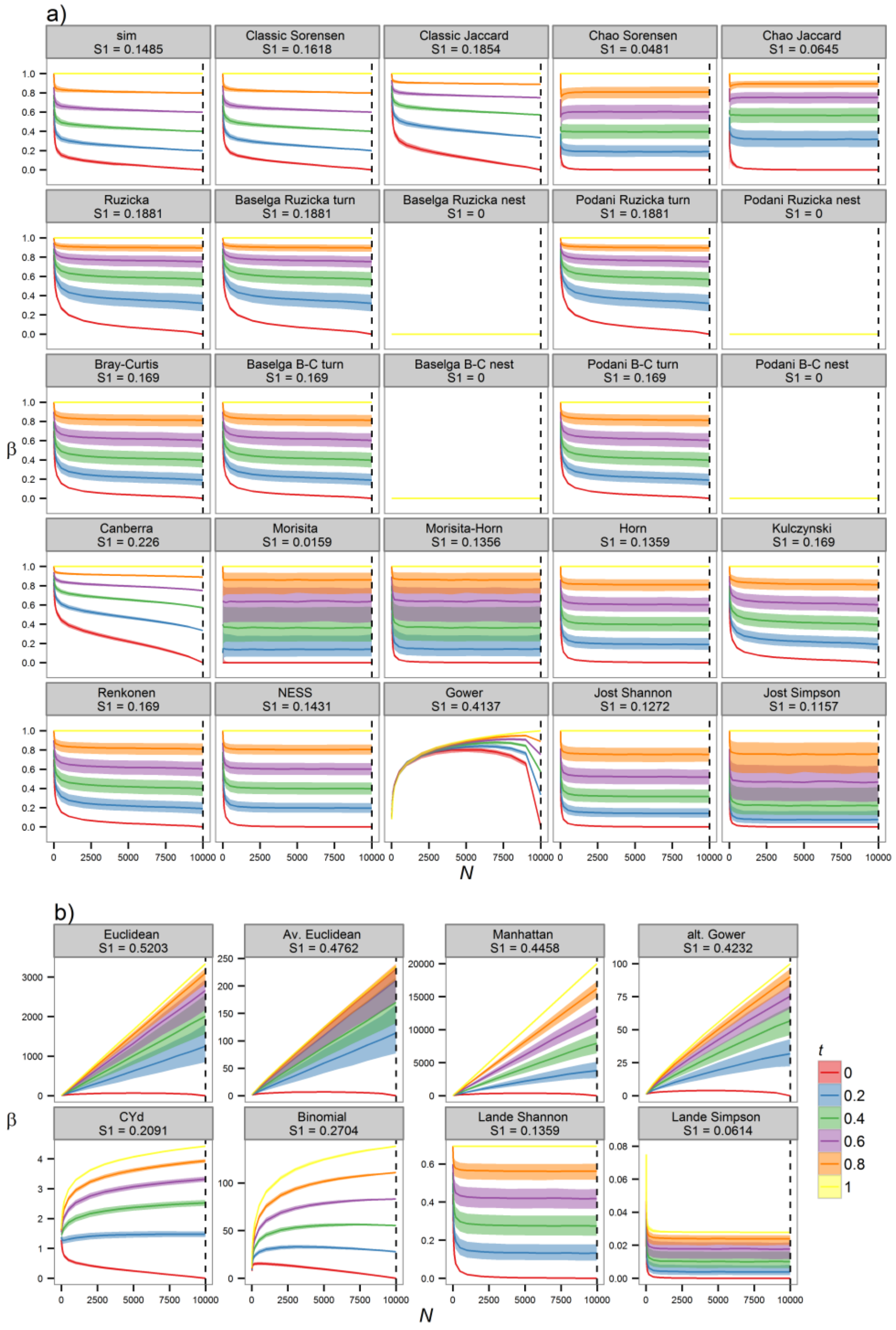

Fig. S4.12 Effect of sample size on *β*-diversity

Simulations of sample size in species assemblages for a) 25 metrics with defined minima and maxima and b) 8 metrics with no defined maxima. Solid lines and shaded areas are the median and interquartile range, respectively, of *β* for 10000 simulations at each unique combination of species turnover, t, and sample size, N. Metrics are scored for desirable property S1, independence of sample size. Vertical dashed black lines intersect the reference values of median β at N=10000 (fully censused assemblages).

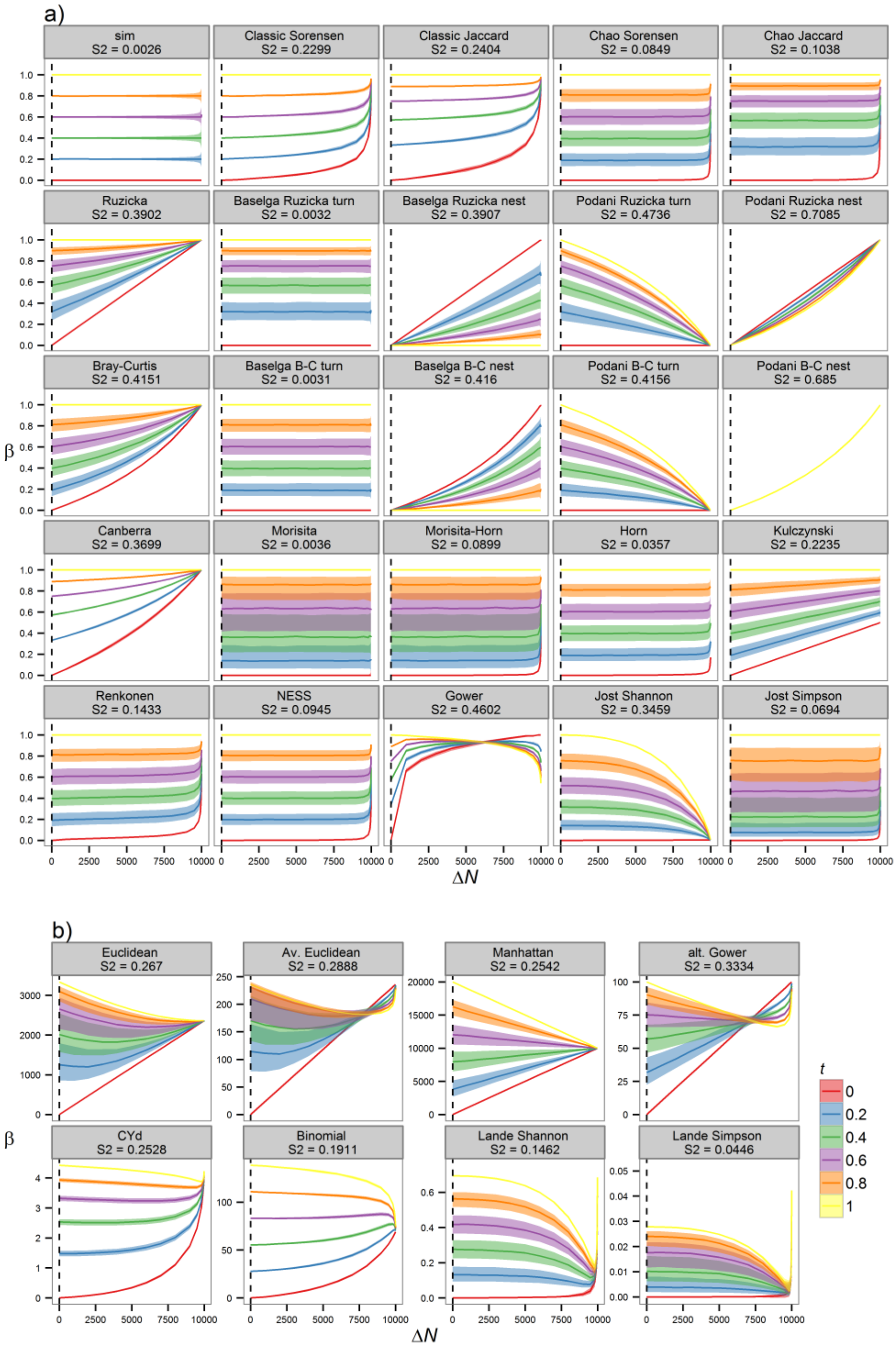

Fig. S4.13 Effect of unequal sample size on *β*-diversity

Simulations of differences in sample size between assemblages for a) 25 metrics with fixed upper limits b) 8 metrics with no maxima. Solid lines and shaded areas are the median and interquartile range, respectively, of *β* for 10000 simulations at each unique combination of species turnover, *t,* and sample size difference, *ΔN*. Metrics are ordered by their scores for desirable property S2, unbiased by unequal sample size. Vertical dashed black lines intersect the reference values of median *β* at *ΔN*=0 (equal sample sizes).

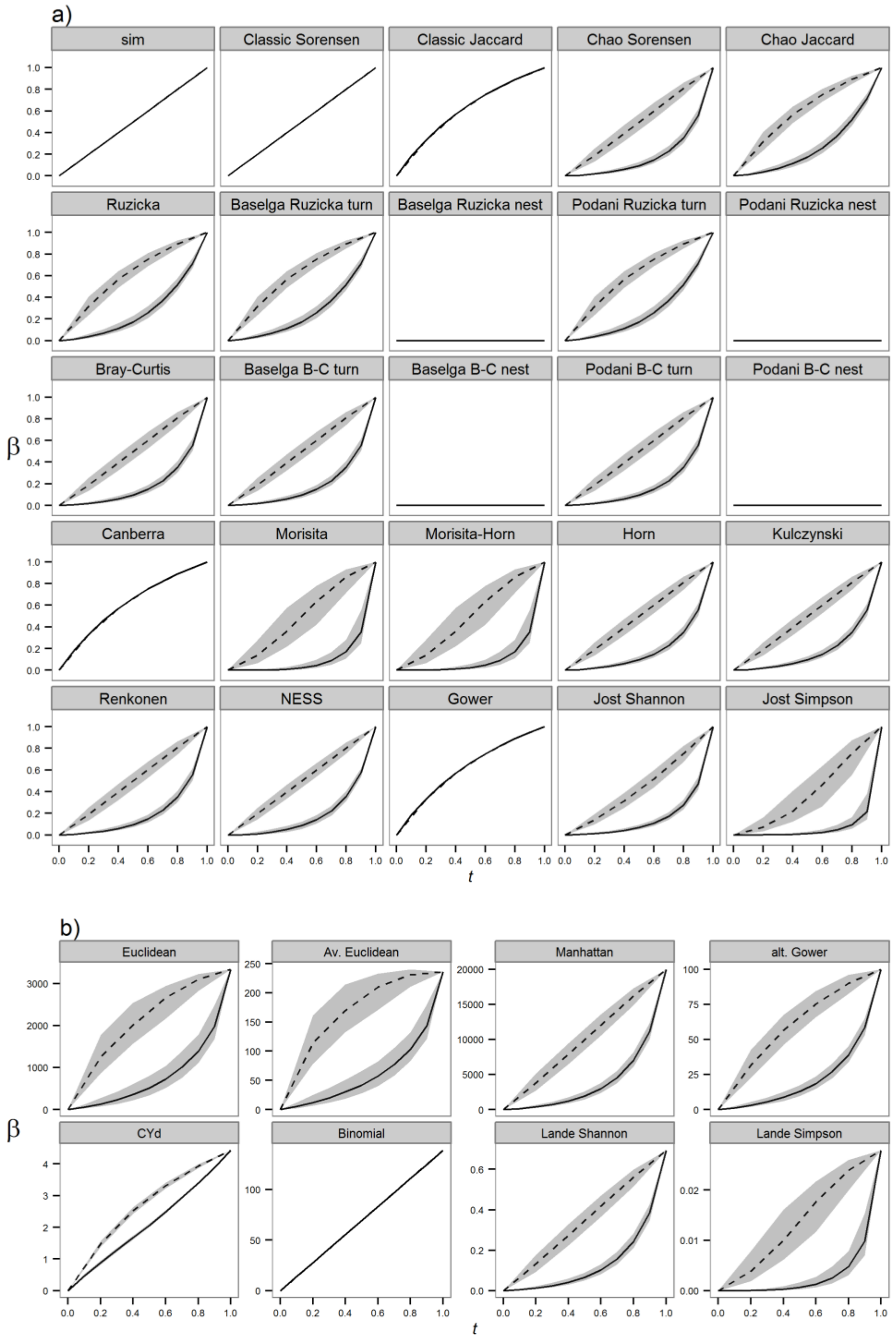

Fig. S4.14 Effect of species turnover on β-diversity under a positive occupancy-abundance relationship (ONR)

Simulations of species turnover assuming a positive relationship between local abundance and occupancy within a study region for a) 25 metrics with fixed upper limits b) 8 metrics with no maxima. Dashed black lines are the median of β under random species turnover. Solid black lines are the median of β when the probability of a species being turned over is inversely proportional to its relative abundance (a positive ONR with exponent 0.65). Shaded areas are the interquartile ranges of β. Median and interquartile range values are based on 10000 simulations at each level of species turnover, t.

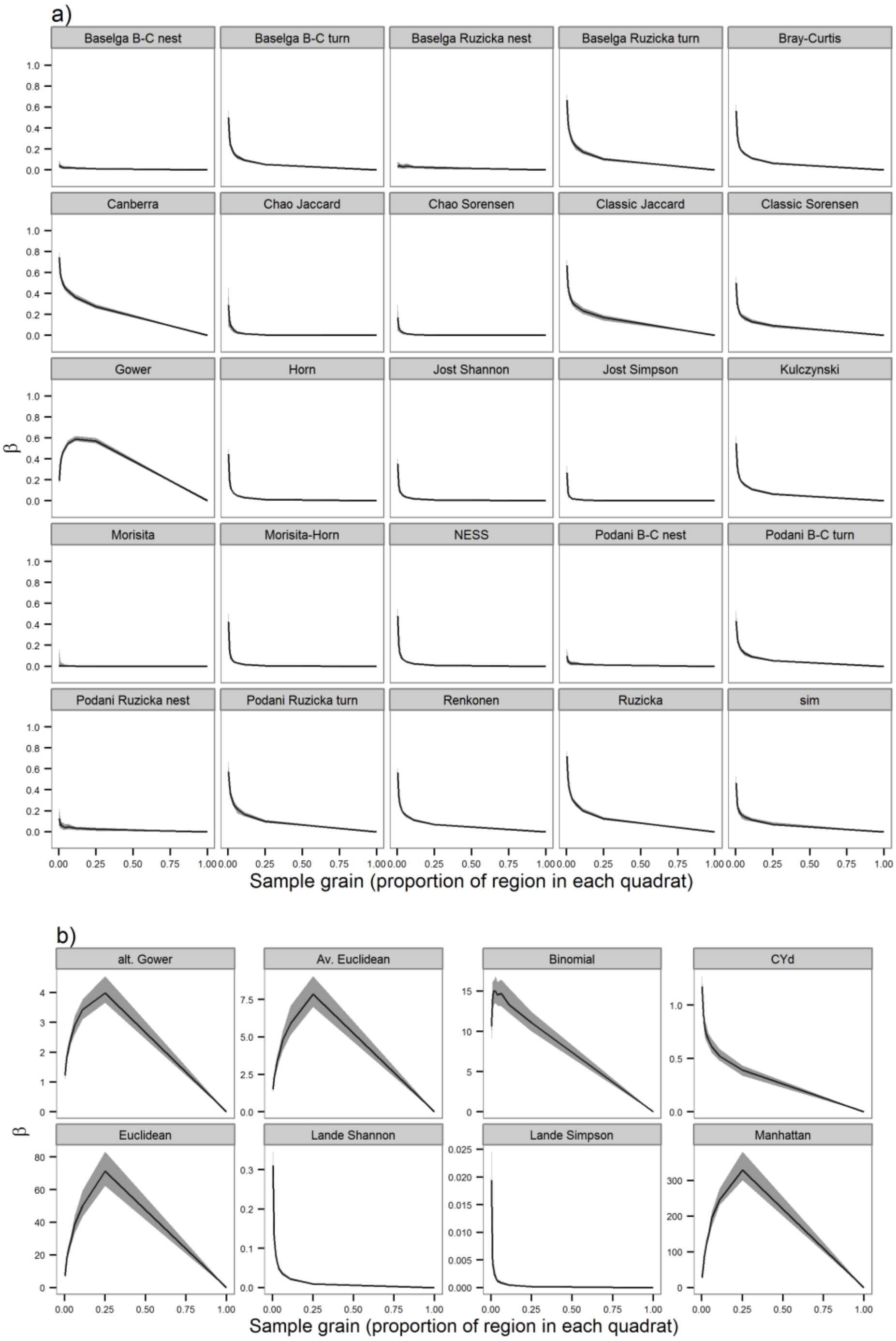

Fig. S4.15 Effect of the spatial grain of sampling on *β*-diversity

Simulations sampling species assemblages different spatial grains for a) 25 β-diversity metrics with fixed upper limits b) 8 metrics with no maxima. Solid lines and shaded areas are the median and interquartile, respectively, of β based on 100 simulations at each spatial grain. Individuals of each species are assumed to be distributed according to an inhomogeneous Poisson point process (the Thomas process). Quadrat pairs are equally sized and their position is sampled at random from within the simulated study region.

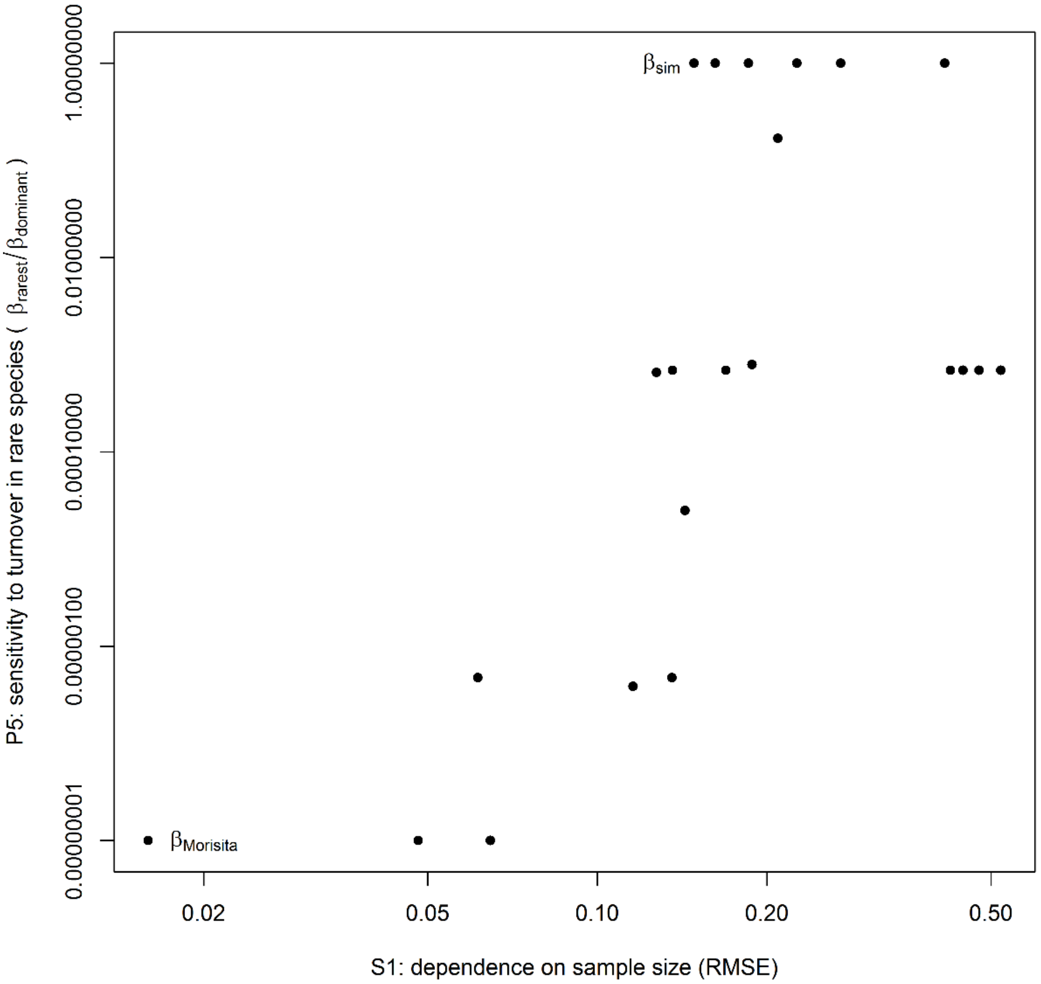

Fig. S4.16 Trade-off between sampling property S1 (independence of sample size) and personality property P5 (relative sensitivity to turnover in rare and common species).

Black dots are the 29 metrics tested against the two properties. $\beta_{\mathrm{Morisita}}$ and β_{sim} represent two extremes of this trade-off.

4.7.4 References for supplementary material

Anderson, M.J., Ellingsen, K.E. & McArdle, B.H. (2006). Multivariate dispersion as a measure of beta diversity. Ecology Letters, 9, 683–93.

Anderson, M.J. & Millar, R.B. (2004). Spatial variation and effects of habitat on temperate reef fish assemblages in northeastern New Zealand. Journal of Experimental Marine Biology and Ecology, 305, 191–221.

Baselga, A. (2013). Separating the two components of abundance-based dissimilarity: balanced changes in abundance vs. abundance gradients. Methods in Ecology and Evolution, 4, 552–557.

Bray, J.R. & Curtis, J.T. (1957). An Ordination of the upland forest communities of southern Wisconsin. Ecological Monographs, 27, 326–349.

Cao, Y., Williams, W.P. & Bark, A.W. (1997). Similarity Measure Bias in River Benthic Auswuchs Community Analysis. Water Environment Research, 69, 95–106.

Chao, A., Chazdon, R.L., Colwell, R.K. & Shen, T.-J. (2005). A new statistical approach for assessing similarity of species composition with incidence and abundance data. Ecology Letters, 8, 148–159.

Clifford, H.T. & Stephenson, W. (1975). An Introduction to Numerical Classification. Academic Press, New York.

Gower, J.C. (1971). A General coefficient of similarity and some of its properties. Biometrics, 27, 857–871.

Grassle, J.F. & Smith, W. (1976). A Similarity Measure Sensitive to the Contribution of Rare Species and Its Use in Investigation of Variation in Marine Benthic Communities. Oecologia, 25, 13–22.

Horn, H.S. (1966). Measurement of overlap in comparative ecological studies. American Naturalist, 100, 419–424.

Jaccard, P. (1912). The distribution of the flora in the alpine zone. New Phytologist, 11, 37–50.

Jost, L. (2006). Entropy and diversity. Oikos, 113, 363–375.

Jost, L. (2007). Partitioning diversity into independent alpha and beta components. Ecology, 88, 2427–2439.

Koleff, P., Gaston, K.J. & Lennon, J.J. (2003). Measuring beta diversity for presence-absence data. Journal of Animal Ecology, 72, 367–382.

Krebs, C. (1998). Ecological Methodology, 2nd ed.n. Harper and Row, New York.

Kulczynski, S. (1927). Die pflanzenassoziationen der Penninen. Bulletin International de l'Academie Polonaise des Sciences et des Lettres, Classe des sciences mathematiques et naturelles, Serie B, Supp 2, 57–203.

Lance, G.N. & Williams, W.T. (1967). Mixed-data classificatory programs I.) Agglomerative Systems. Australian Computer Journal, 1, 15–20.

Lande, R. (1996). Statistics and partitioning of species diversity, and similarity among multiple communities. Oikos, 76, 5–13.

Legendre, P. (2014). Interpreting the replacement and richness difference components of beta diversity. Global Ecology and Biogeography, 23, 1324–1334.

Lennon, J.J., Koleff, P., Greenwood, J.J.D. & Gaston, K.J. (2001). The geographical structure of British bird distributions: diversity, spatial turnover and scale. Journal of Animal Ecology, 70, 966–979.

Morisita, M. (1959). Measuring of interspecific association and similarity between communities. Memoirs of the Faculty of Science, Kyushu University, Series E: Biology, 3, 65–80.

Podani, J., Ricotta, C. & Schmera, D. (2013). A general framework for analyzing beta diversity, nestedness and related community-level phenomena based on abundance data. Ecological Complexity, 15, 52–61.

Renkonen, O. (1938). Statisch-ökologische Untersuchungen über die terrestrische Käferwelt der finnischen Bruchmoore. Annales Zoologici Societatis Zoologicæ-Botanicæ Fennicæ Vanamo, 6, 1–231.

Ružička, M. (1958). Anwendung mathematisch-statistischer Methoden in der Geobotanik (Synthetische Bearbeitung von Aufnahmen). Biologia, Bratislava, 13, 647–661.

Shannon, C.E. (1948). A mathemtical theory of communication. Bell System Technical Journal, 27, 379–423.

Simpson, E.H. (1949). Measurement of Diversity. Nature, 163, 688.

Sørensen, T.A. (1948). A method of establishing groups of equal amplitude in plant sociology based on similarity of species content, and its application to analyses of the vegetation on Danish commons. Kongelige Danske Videnskabernes Selskabs Biologiske Skrifter, 5, 1–34.

Chapter 5

Climate, habitat and distance as correlates of spatial patterns of β-diversity in British macro-moth species

5.1 Abstract

Understanding spatial patterns in β-diversity, and the drivers thereof, can inform reserve selection and improve predictions of the effects of habitat loss and climate change on biodiversity. In this chapter, I use hierarchical partitioning of generalised linear models of β-diversity to quantify the independent and joint contributions of climatic variables, landcover and geographical distance in structuring the community composition of British macro-moths. I compare conclusions based on eight models using community composition derived from two datasets (the standardised Rothamsted Insect Survey and opportunistic records from the National Moth Recording Scheme) and five different β-diversity metrics ($\beta_{\mathrm{Morisita}}$, β_{Horn}, $\beta_{\mathrm{Sørensen}}$, $\beta_{\mathrm{Sør.turn}}$, $\beta_{\mathrm{Sør.nest}}$). The independent contributions of all predictors to β-diversity were low to moderate: Across all eight models the independent contribution of climate explained, on average, the most variation in β-diversity (4.65 ± 4.69 %), followed by geographical distance (4.58 ± 4.15 %). Landcover consistently explained the least variation β-diversity (1.11 ± 1.20 %). Together, geographical distance, climate and landcover were better able to explain spatial patterns in abundance-based β-diversity metrics ($\beta_{\mathrm{Morisita}}$, β_{Horn}) compared with presence-absence metrics ($\beta_{\mathrm{Sørensen}}$) and were better able to explain spatial patterns in the standardised Rothamsted Insect Survey than opportunistic National Moth Recording Scheme. The purely turnover component of $\beta_{\mathrm{Sørensen}}$ was substantially better explained than the purely nestedness component ($\beta_{\mathrm{Sør.nest}}$). Conclusions about the overall explanatory power and relative independent effects of geographical distance, climate and landcover vary among the metrics and datasets that are used to quantify spatial patterns in β-diversity..

5.2 Introduction

β-diversity quantifies spatial variation in the composition of species assemblages (Tuomisto 2010a; b). This aspect of biodiversity captures the complementarity of local communities and thereby connects local (*α*) and regional (*γ*) diversity (Whittaker 1960, 1972; Ricotta *et al.* 2002; McGlinn & Hurlbert 2012). Spatial patterns in *β*-diversity emerge from the distribution and abundance of individual species and the degree to which these distributions overlap in space and time (Plotkin & Muller-Landau 2002). Understanding spatial patterns in *β*-diversity has important implications for managing biodiversity: spatially random reserve selection, habitat loss and climate change will have disproportionate impacts on biodiversity if *β*-diversity is spatially structured rather than spatially random (Legendre *et al.* 2005).

Species distributions are driven by the interplay between niche and neutral processes (Wennekes *et al.* 2012), but the relative contributions of these processes are still unclear. Niche and neutral hypotheses predict different spatial patterns in *β*-diversity. This provides a framework with which to test hypotheses about the processes driving species distributions and community assembly. Specifically, ecologists have employed a number of methods designed to partition the relative contributions of environmental, spatial and habitat heterogeneity by quantifying the strength of these associations with observed patterns in *β*-diversity (Harrison *et al.* 1992; Ferrier *et al.* 2007; Legendre 2008; Keil *et al.* 2012b; Fitzpatrick *et al.* 2013).

The niche hypothesis stresses the deterministic role of the environment in filtering the species that can persist at a given location, due to their unique set of traits and adaptations (Chase & Leibold 2003). Environmental filtering by climate is well described in ecological studies (Parmesan *et al.* 1999; Hill *et al.* 2011). Some of the best examples of this come from UK Lepidoptera: a large body of evidence suggests that their distributions are thermally constrained due to physiological limits on survival, development or reproduction (Bryant *et al.* 1997; Conrad *et al.* 2002; Davies *et al.* 2006; Buckley *et al.* 2011; Fox 2013). Habitat quantity and quality will also determine the distribution and abundance of species through the availability of adult and larval host plants (and other biotic interactions) and the effect of vegetation structure and topology on survival and reproduction (Spalding & Parsons 2004; Summerville & Crist 2004). Environmental filtering predicts spatial patterns in *β*-diversity will result from both species turnover and nestedness (where an assemblage is a perfect subset of those species in the contrasted assemblage).

In contrast, neutral theory (Hubbell 2001; Rosindell *et al.* 2011, 2012) assumes that all species are equivalent in terms of per capita fitness, such that spatial variation can only be generated through stochastic processes (ecological drift) like dispersal limitation and random disturbance events leading to unpredictable extinctions (demographic stochasticity). These processes would be expected to generate spatial patterns of β-diversity that are correlated strongly with geographic distance but not with environmental variables such as climate. Moreover, neutral processes cannot generate gradients in species richness, so we would not expect to see a strong pattern of nestedness within spatial patterns of β-diversity. Unfortunately, stochastic patterns may be partially or even wholly driven by important deterministic processes we don't understand or variables have failed to measure accurately, raising the question of whether it is possible to quantify truly neutral processes.

Spatial patterns in β-diversity can be described as a pairwise matrix of β-diversity between each site in the analysis, derived from a site (rows) by species (columns) matrix of presence (1) or absence (0), or the abundances for each species. A complication is that not all β-diversity metrics measure the same underlying concept (chapter 4). Both the replacement (turnover) of species and the gain or loss of species (nestedness) along environmental and spatial gradients contribute to spatial patterns in β-diversity (Koleff *et al.* 2003a; Baselga 2012), but turnover and nestedness are derived from different processes (Svenning *et al.* 2011; Dobrovolski *et al.* 2012; Ulrich & Almeida-Neto 2012; Calderón-Patrón *et al.* 2013). Moreover, metrics can place different emphasis on variation in common and rare species (chapter 4), such that presence-absence and abundance data may reveal different spatial patterns in β-diversity. A third source of variation in quantifying β-diversity is how robust a metric is in the face of undersampling of communities, which can lead to bias in estimates of β.

In this chapter, I apply a suite of metrics covering these three facets of β-diversity metrics in order to explore how the choice of method affects conclusions about the role of environmental variables and geographical distance. Firstly, I quantify the independent and joint contributions of geographical distance, climate and landcover to spatial variation in β-diversity of British macro-moths, using community composition data for 331 species. Secondly, I ask whether model explanatory power and the relative importance of environmental and spatial predictors remain consistent when β-diversity is measured using presence-absence versus abundance data. Thirdly, I compare model explanatory power and the relative independent contributions of the predictors when β-diversity is estimated from unstructured biological records versus high-quality monitoring data from the same locations. Finally, I explore how partitioning β-diversity into its purely turnover and nestedness components influences the overall explanatory power and relative independent contributions of geographical distance, climate and landcover.

5.3 Methods

To explore the relative contributions of geographical distance, climateand landcover heterogeneity in structuring patterns of macro-moth β-diversity in mainland Britain, pairwise dissimilarity matrices were obtained for macro-moth community composition, mean monthly temperature, percentage landcover and geographical distance. Data manipulation was performed in R 3.0.3 (R Core Development Team 2014).

5.3.1 Community composition data

The focal insect taxon for this study are the British larger moth species (macro-moths) studied by Conrad *et al.* (2006). Two sources of data were used to explore patterns of β-diversity in British macro-moth species. The first data set comprise a subset of 148 light traps in the Rothamsted Insect Survey (RIS) that were operating between 2000 and 2011. In most cases, the abundances of moth species captured in these light traps have been recorded nightly during every year that the trap has been in operation using a standardised protocol. Of these 148 traps, I included only the 76 light traps that had been operating for five or more years between 2000 and 2011 in order to ensure maximum comparability across trap sites.

From these data, I created two matrices of community composition with a row for each site (unique 1km^2 grid reference) and a column for each species. The first matrix (henceforth called RISa) comprised the total abundances of 329 macro-moth species between 2000 and 2011 by summing the annual abundances of species in each light trap across all years. The second matrix (RISp), with the same structure, comprised presences (1) and absences (0) in order to compare patterns of β-diversity measured with abundance data and presence-absence data.

The third community composition matrix was derived from the National Moth Recording Scheme (NMRSp). I extracted all moth records collected in mainland Britain between 2000 and 2011 with a precision of $\leq$ 1km^2. These records were used to generate a matrix of presence (1) and absence (0) with a row for each site (unique 1km^2 grid reference) and a column for each of the 331 macro-moth species with records. A total of 66 grid cells were shared between the NMRS and RIS and were used to compare patterns of β-diversity between the two data sets (Fig. 5.1).

5.3.2 Pairwise β-diversity matrices

Pairwise β-diversity matrices were created for 8 combinations of dataset and metric (e.g. n = 2145 pairwise β-diversities among 66 grid cells). These were $\beta_{\mathrm{Morisita}}$ (Morisita 1959) and β_{Horn} (Horn 1966), applied to the RISa community composition matrix, $\beta_{\mathrm{Sørensen}}$ (Sørensen 1948), $\beta_{\mathrm{Sør.turn}}$ (Baselga 2010) and $\beta_{\mathrm{Sør.nest}}$ (Baselga 2010) applied to the RISp and $\beta_{\mathrm{Sørensen}}$, $\beta_{\mathrm{Sør.turn}}$ and $\beta_{\mathrm{Sør.nest}}$ applied to the NMRSp. These metrics were chosen to reflect two of the key personality traits of β-diversity (chapter 4). $\beta_{\mathrm{Morisita}}$, β_{Horn} and $\beta_{\mathrm{Sørensen}}$ form a continuum in terms of how abundance data is used: $\beta_{\mathrm{Morisita}}$ is influenced predominantly by differences (turnover or loss of individuals) in common species, while β_{Horn} weights species by their relative

Fig. 5.1 Distribution of the 66 1km^2 grid cells sampled by both the Rothamsted Insect Survey (RIS) light trap network and the National Moth Recording Scheme (NMRS) between 2000 and 2011.

Macro-moth community composition at each site was summarised as presence-absence (NMRSp and RISp) and abundance (RISp) in site (rows) by species (columns) matrices and used to generate site by site pairwise matrices of β-diversity.

abundance and $\beta_{\text{Sørensen}}$ weights turnover of all species equally. β-diversity metrics can also be narrow-sense or broad-sense. Narrow-sense metrics measure purely the degree to which species (for presence-absence metrics) or individuals (for abundance-based metrics) are replaced by other species in the contrasted assemblage (turnover). Broad-sense metrics measure both species turnover and the degree to which there is variation in either richness (for presence-absence metrics) or total abundance (for abundance-based metrics) between the two assemblages (nestedness: Koleff *et al.* 2003). $\beta_{\text{Sørensen}}$ can be partitioned into the turnover (also known as β_{sim}) and nestedness components of β-diversity (Baselga 2010, 2013). These components of $\beta_{\text{Sørensen}}$ ($\beta_{\text{Sør.turn}}$ and $\beta_{\text{Sør.nest}}$) are quantified so that the contribution of geographical distance and environment to the turnover and nestedness components of β-diversity can be unpicked.

β_{Morisita} was calculated using the function vegdist in R package vegan (Oksanen *et al.* 2013). A function to calculate β_{Horn} was written in the R language by adapting the formula in Jost *et al.* (2011). $\beta_{\text{Sørensen}}$ (and the and nestedness components) were calculated using the function beta.pair in R package betapart (Baselga *et al.* 2013).

5.3.3 Climate and habitat heterogeneity

Euclidean distances between percentage cover of landcover classes and mean monthly temperature were used as a proxies for habitat and climate heterogeneity, respectively. Landcover data for each of the 66 1km^2 grid cells in the analysis were obtained from the UK Landcover Map 2007 (Morton *et al.* 2011) in the form of a matrix of percentage cover with sites as rows and the 23 broad land-cover classes as columns. A site by site dissimilarity matrix of Euclidean distances was created using the function vegdist in R package vegan (Oksanen *et al.* 2013). Mean monthly temperature data were taken from the Met Office UKCP09 datasets (Perry & Hollis 2005), quantified as the mean for that month of all years between 2000 and 2011 to generate mean temperature matrices with sites as rows and months as columns. A site by site dissimilarity matrix of Euclidean distances was obtained for temperature using the function vegdist in R package vegan (Oksanen *et al.* 2013).

5.3.4 Geographic distance

Pairwise geographic distances between the sites were calculated in kilometres based on the coordinates of the 66 grid cells on the Ordnance Survey National Grid, using the function rdist.earth in R package fields (Nychka *et al.* 2015).

5.3.5 Statistical analysis

The independent contributions of climate, landcover and geographic distance to macro-moth *β*-diversity were quantified using a hierarchical partitioning method (Chevan & Sutherland 1991) implemented using the function hier.part in R package hier.part (Walsh & Mac Nally 2013). Prior to statistical analyses all three dissimilarity matrices were rescaled to a mean of zero and a standard deviation of 1. Hierarchical partitioning was applied to a generalised linear model with *β*-diversity as the response variable and dissimilarity in temperature, landcover and geographic distance as predictors, assuming quasi-binomial error structure to account for over-dispersion. Hierarchical partitioning was based on goodness of fit for the 8 candidate models (2^3 models for 3 explanatory variables), measured as the root mean squared predicted error (RMSPE: sum of squares of the residuals divided by the residual degrees of freedom). Hierarchical partitioning quantifies the independent and joint contributions of each predictor as the mean of increases in goodness of fit (e.g. decrease in RMSPE) across all possible candidate models that include that predictor, where decreases in RMSPE are relative to the null model (intercept only). The association of each predictor with *β*-diversity is partitioned into an independent contribution and joint effects with all other variables to address the issue of multi-collinearity among predictors. Independent and joint contributions of climate, landcover and geographic distance are expressed as the percentage of spatial variation in *β*-diversity associated with each predictor. Joint contributions with other predictors are also quantified for each predictor and represent the component of explanatory power that cannot be disassociated from other predictors (Mac Nally 2002). In the Results section I report the independent and joint effects of the three explanatory variables as percentages of the total variation explained, in both absolute and relative contributions (the former includes the unexplained variation but the latter does not).

The assumption of independence among data points is violated in this analysis, due to spatial autocorrelation in the distributions of species. Therefore, tests for significant effects of predictors were performed by randomising the values of each predictor independently over 1000 replicates and calculating the independent effect for each replicate, using the function hp.rand in R package hier.part (Walsh & Mac Nally 2013). Statistical significance of each predictor was based on the 95% confidence intervals of *Z*-scores ($Z >= 1.65$, Mac Nally 2002). This hierarchical partitioning method was applied eight times, for each of the dataset-metric combinations described above.

5.4 Results

5.4.1 Independent and joint effects of climate, landcover and distance

Based on the Z-scores of randomisation tests of predictors, the independent effects of all three predictors (geographical distance, climate and landcover) were

Table 5.1 Summary of hierarchical partitioning of 8 generalised linear models of pairwise β-diversity of British macro-moths as a function of geographic distance, landcover dissimilarity and climate dissimilarity

A quasi-binomial error structure was assumed. Dependent variables are β-diversity derived from macro-moth community composition in the Rothamsted Insect Survey using abundance data (RISa), presence-absence data (RISp) or the National Moth Recording Scheme using presence-absence data (NMRSp), calculated using one of five metrics of β-diversity. RMSPE is the root mean squared predicted error of each model. Total is the change in RMSPE for the full model relative to the null model. J is the change in RMSPE due to the joint effects of each variable that cannot be uncoupled from other predictors. I is the change in RMSPE due to the independent effects of each predictor. Z-scores are derived from 1000 randomisations of each predictor variable. * denotes observed independent effects are significantly different from 0 at the 5% level. % I are the independent effects of each predictor expressed as a percentage of model explanatory power.

Dependent variable	**RMSPE**	**Predictor**	**Total**	**J**	**I**	**Z-score**	**% I**
RISa β_{Morisita}	7.51	geographical distance	-0.73	-0.28	-0.44	163.18*	39.90
		landcover	-0.17	-0.03	-0.14	47.91*	12.83
		climate	-0.83	-0.31	-0.53	174.31*	47.27
RISa β_{Horn}	5.44	geographical distance	-0.96	-0.34	-0.62	276.80*	42.20
		landcover	-0.22	-0.02	-0.19	99.12*	13.16
		climate	-1.03	-0.38	-0.65	284.40*	44.64
RISp β_{Sor}	5.34	geographical distance	-0.36	-0.12	-0.25	127.85*	46.79
		landcover	-0.11	-0.01	-0.10	50.26*	18.38
		climate	-0.31	-0.13	-0.18	107.24*	34.83
RISp $\beta_{\text{Sør.nest}}$	5.25	geographical distance	0.00	0.00	0.00	0.22	6.20
		landcover	-0.01	0.00	-0.01	8.12*	57.71
		climate	-0.01	0.00	-0.01	4.14*	36.08
RISp $\beta_{\text{Sør.turn}}$	3.13	geographical distance	-0.55	-0.19	-0.36	289.92*	43.89
		landcover	-0.07	0.00	-0.07	49.88*	8.13
		climate	-0.61	-0.21	-0.39	290.68*	47.98
NMRSp $\beta_{\text{Sørensen}}$	11.15	geographical distance	-0.15	-0.05	-0.10	29.13*	56.50
		landcover	-0.01	0.00	-0.01	3.05*	7.63
		climate	-0.11	-0.04	-0.07	16.71*	35.87
NMRSp $\beta_{\text{Sør.nest}}$	10.11	geographical distance	-0.10	-0.04	-0.06	16.84*	37.69
		landcover	-0.05	0.00	-0.04	12.47*	25.73
		climate	-0.10	-0.04	-0.06	19.42*	36.59
NMRSp $\beta_{\text{Sør.turn}}$	9.13	geographical distance	-0.55	-0.18	-0.37	117.89*	56.64
		landcover	-0.02	-0.01	-0.01	2.30*	1.44
		climate	-0.46	-0.18	-0.27	86.96*	41.92

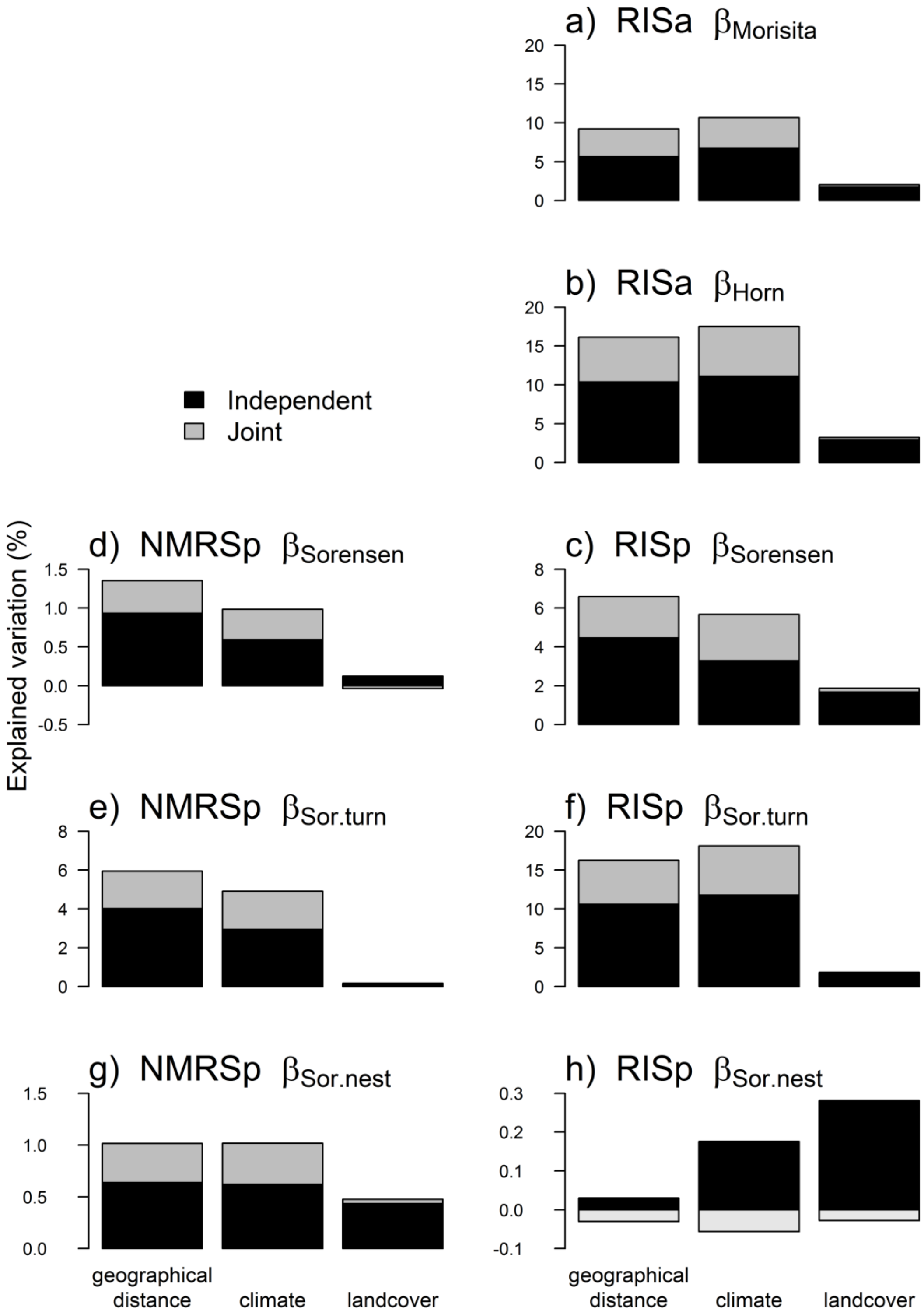

Fig. 5.2 Independent and joint contributions (expressed as percentages of the total explained spatial variation in β-diversity) of geographical distance, climate and landcover to β-diversity

The dependent variable, β-diversity, is derived from eight metric-dataset combinations. Independent and joint effects are estimated from hierarchical partitioning of generalised linear models.

significantly ($P < 0.05$) associated with β-diversity in seven of the eight models. The exception was $\beta_{\text{Sør.nest}}$ applied to the RISp data, for which the independent effect of geographic distance was not significant (Table 5.1). However, the independent contributions of all predictors to β-diversity were generally quite low: the greatest independent contribution of any predictor was the effect of climate (11.770 %) in the model with RISp $\beta_{\text{Sør.turn}}$ as the dependent variable (Fig. 5.2). However, small independent effects are expected when there are correlations between variables, especially climate and geographical distance in this case. Across all eight models the independent contribution of climate explained, on average, the most variation in β-diversity (4.654 ± 4.693 %), followed by geographical distance (4.582 ± 4.152 %). Landcover consistently explained the least variation in β-diversity (1.111 ± 1.019 %), with the exception of the model with $\beta_{\text{Sør.nest}}$ applied to the RISp data as the dependent variable. There was substantial variation in the independent contributions of geographical distance, climate and landcover among the models with different metrics and datasets used to quantify β-diversity (note the different axis scales in Fig. 5.2).

In all models, the joint contributions of predictors were less than the independent contributions. Joint contributions were greatest for geographical distance (2.485 ± 2.310 %) and climate (2.728 ± 2.595) and least for landcover (0.138 ± 0.146 %). Negative joint contributions for RISp $\beta_{\text{Sør.nest}}$ and RISp $\beta_{\text{Sørensen}}$ indicate suppressive, rather than additive joint effects among predictors (Fig. 5.2).

The explanatory power of geographical distance, climate and landcover together varied between the eight metric-dataset combinations used to quantify β. The model with RISa β_{Horn} as the dependent variable was best explained by geographical distance, climate and landcover predictors, which together accounted for 16.940 % of variation in β (Fig. 5.3a). The three predictors were least able to explain variation in NMRSp $\beta_{\text{Sør.nest}}$, accounting for 0.297 % of variation in β (Fig 5.4a).

5.4.2 Presence-absence and abundance-based metrics

In comparisons of presence-absence and abundance-based β-diversity metrics applied to the RIS data, overall model explanatory power (Fig. 5.3a) was substantially greater when the abundance-based metrics β_{Horn} (16.940 %) and β_{Morisita} (12.903 %) were used, compared to the presence-absence metric $\beta_{\text{Sørensen}}$ (6.085 %) and was greatest of all for β_{Horn}. The relative independent contributions of climate, landcover and geographic distance did not change substantially depending on whether presence-absence or abundance data were used to quantify

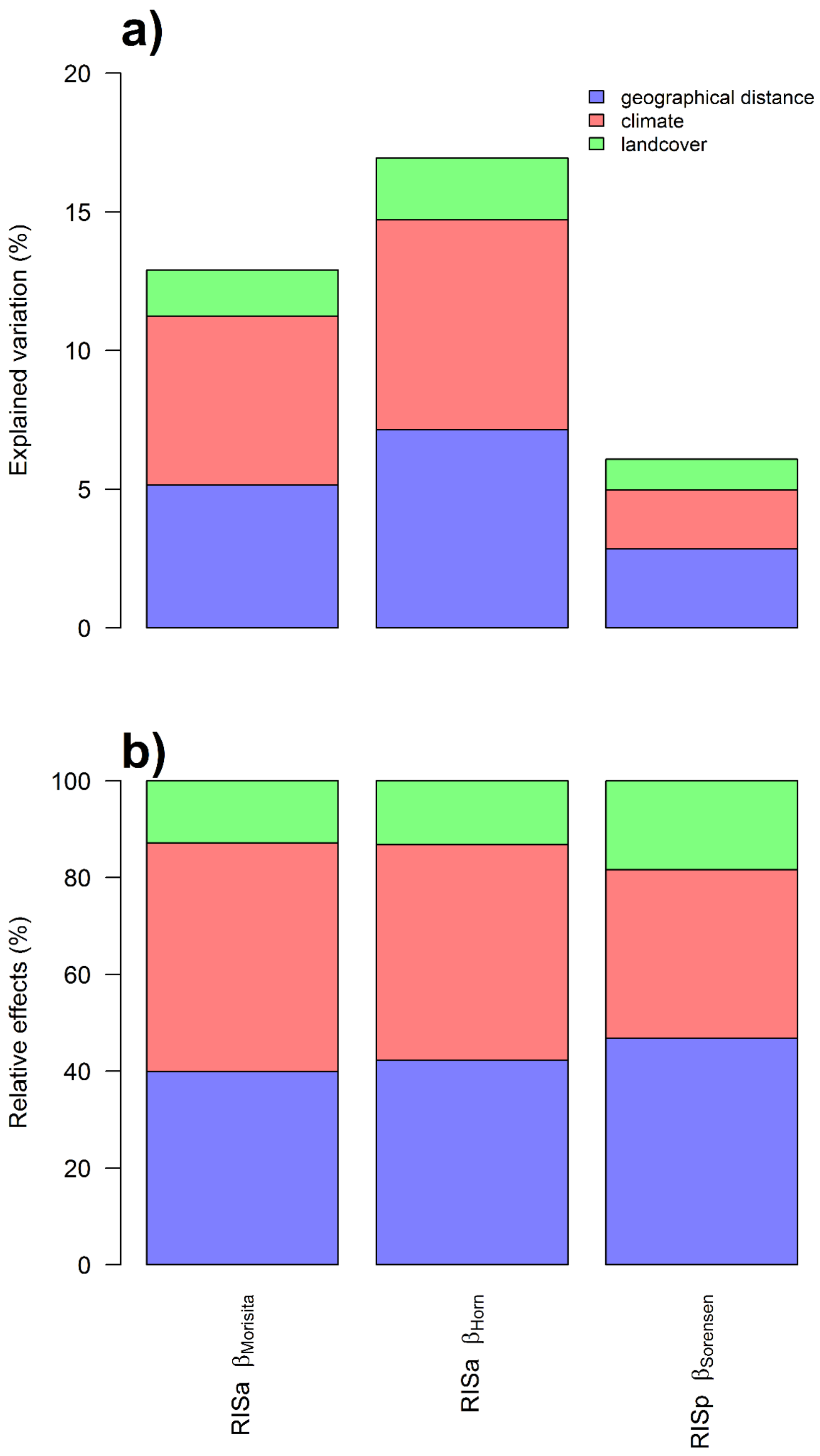

Fig. 5.3 Comparison of independent effects of landcover dissimilarity, climate dissimilarity and geographic distance on the β-diversity of British macro-moths quantified using $\beta_{Morisita}$, β_{Horn} (abundance-based metrics) and $\beta_{Sørensen}$ (presence-absence) applied to Rothamsted Insect Survey

Independent effects are expressed as a) the percentages of total variation and b) the relative percentages of total explained variation. The metrics form a continuum in terms of the contribution of turnover in common versus rare species to the value of β. Independent contributions were estimated using hierarchical partitioning of generalised linear models.

β, but the relative contributions of both landcover and geographical distance increased for β-diversity metrics that place greater emphasis on turnover in rare species (e.g. moving from β_{Morisita} to β_{Horn} to $\beta_{\text{Sørensen}}$: Fig. 5.3b). The relative independent effects of landcover dissimilarity were 12.8, 13.1 and 18.4% for $\beta_{\text{Morisita,}}$ β_{Horn} and $\beta_{\text{Sørensen}}$, respectively, while independent effects of geographic distance were 39.9, 42.2 and 46.8%, respectively. Independent effects of climate dissimilarity were 47.3, 44.6 and 34.8% for $\beta_{\text{Morisita,}}$ β_{Horn} and β_{sim}, respectively (Fig. 3b).

5.4.3 Opportunistic and standardised data

In comparisons between opportunistic NMRSp data and the standardised RISp data to quantify β-diversity, model explanatory power (Fig. 5.4a) was higher for the RISp (6.085 and 9.525 %, for $\beta_{\text{Sørensen}}$ and $\beta_{\text{Sør.turn}}$, respectively) as opposed to the NMRSp (2.140 and 7.596 % for $\beta_{\text{Sørensen}}$ and $\beta_{\text{Sør.turn,}}$ respectively). $\beta_{\text{Sør.nest}}$ was poorly explained in both data sets, but, in contrast to $\beta_{\text{Sørensen}}$ and $\beta_{\text{Sør.turn}}$, explanatory power was higher in the NMRSp (2.000 %) than the RISp (0.297 %). The relative independent effects (Fig. 5.4b) of climate, landcover and geographic distance on $\beta_{\text{Sørensen}}$ were broadly similar between the NMRSp and the RISp. However, when $\beta_{\text{Sørensen}}$ was partitioned into turnover ($\beta_{\text{Sør.turn}}$) and nestedness ($\beta_{\text{Sør.nest}}$) components, there were substantial differences in the independent effects of landcover dissimilarity and geographic distance on the nestedness component: the independent effect of landcover on $\beta_{\text{Sør.nest}}$ increased from 25.726 % in the NMRSp to 57.713 % in the RISp, while the effect of geographic distance decreased from 37.688 % in the NMRSp to 6.202 % in the RISp (Fig. 5.4b).

5.4.4 Turnover and nestedness metrics

In comparisons between turnover and nestedness metrics within the RISp, geographical distance, climate and landcover were able to explain most spatial variation in the purely turnover component of β-diversity ($\beta_{\text{Sør.turn}}$: 9.525 %), followed by combined nestedness and turnover ($\beta_{\text{Sørensen}}$: 6.085 %). The purely nestedness component was poorly explained ($\beta_{\text{Sør.nest}}$: 0.297 %). The relative contributions of climate and landcover were much greater and geographical distance much lower for $\beta_{\text{Sør.nest}}$ compared to $\beta_{\text{Sørensen}}$ and $\beta_{\text{Sør.turn}}$ (Fig. 5.4b).

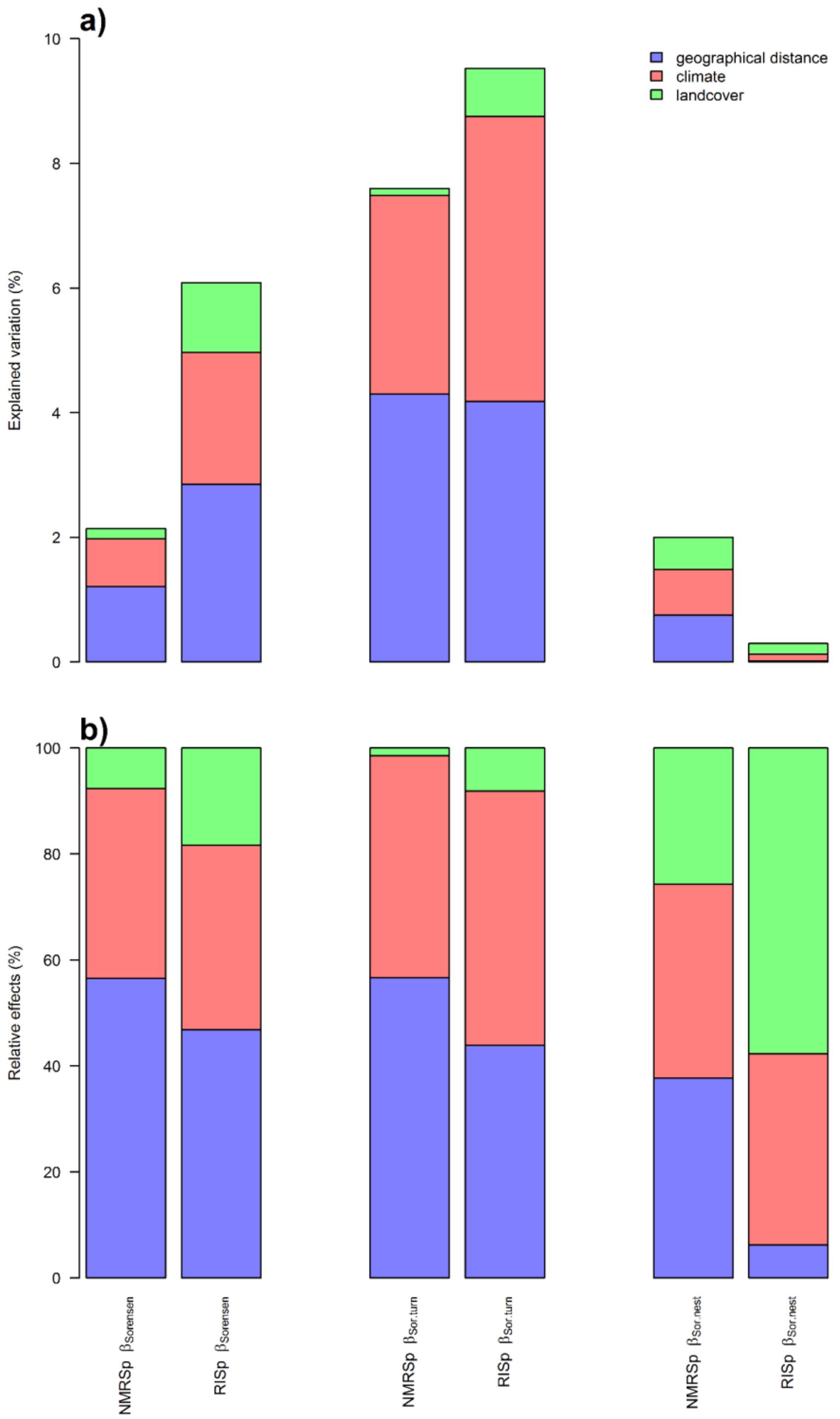

Fig. 5.4 Comparison of independent effects of geographic distance, climate and landcover on the β-diversity of British macro-moths quantified using $\beta_{Sørensen}$, $\beta_{Sør.turn}$ and $\beta_{Sør.nest}$ applied to the National Moth Recording Scheme (NMRSp) and the Rothamsted Insect Survey (RISp)

Independent effects are expressed as a) the percentages of total variation and b) the relative percentages of total explained variation. $\beta_{Sørensen}$ is partitioned into purely turnover ($\beta_{Sør.turn}$) and nestedness ($\beta_{Sør.nest}$) components of β. Independent contributions were estimated using hierarchical partitioning of generalised linear models.

5.5 Discussion

The results have produced two key findings about the independent contributions of climate, landcover and geographic distance to the *β*-diversity of British moths. Firstly, model explanatory power varied substantially depending on the metrics (presence-absence versus abundance) and the datasets (RIS versus NMRS) used to quantify *β*-diversity. Secondly, the perceived relative effects of mean annual temperature, landcover heterogeneity and geographical distance depend on the interpretation of abundance information by metrics (emphasis on rare versus common species), data quality (degree of undersampling) and the component of *β*-diversity being measured (e.g. purely nestedness or purely turnover).

5.5.1 General patterns in the independent effects of climate, landcover and distance

The results indicate that climate and geographical distance are the most important predictors of spatial patterns in the *β*-diversity of British macro-moths while the independent contribution of landcover, as measured, is substantially lower. This broad pattern is consistent across all turnover metrics and data sets used to quantify *β*-diversity. Both niche and neutral processes are known to structure spatial patterns of *β*-diversity at regional scales. Examples include geometrid moths in Borneo (Beck & Vun Khen 2007), mammals in North America (Qian *et al.* 2009) and Bornean dipterocarps (Paoli *et al.* 2006). However, other studies have found that primarily niche (Jiménez-Valverde *et al.* 2010; Püttker *et al.* 2014) or primarily neutral processes (Keil *et al.* 2012b) structure *β*-diversity. The contribution of geographical distance captures the role of dispersal limitation and stochastic demography (neutral processes) in structuring to *β*-diversity, but can also pick up variation that is really associated with unmeasured (and spatially structured) predictors (Warren *et al.* 2014) and with spatially structured sampling error, which is likely to particularly strong in the NMRSp data. I discuss this further in section 5.5.3 in relation to the comparison of results derived from standardised and opportunistic data sets. I also discuss some potentially important environmental predictors of macro-moth community composition that were not included in these models in the sections below on unexplained variation and spatial autocorrelation in *β*-diversity.

Climate and landcover are different aspects of the ecological niche. Keil *et al.* (2012) found the effect of landcover becomes stronger at finer grains, but our landcover data has a relatively fine grain of 1 km^2 and is still only weakly associated with macro-moth β-diversity. In Chapter 2, I noted that light traps have a restricted sampling range and therefore are likely to undersample the community in 1 km^2 grid cells, introducing stochasticity into observed communities that would reduce the amount of variation that is unambiguously associated with landcover. This is an example of the problem of choosing the appropriate spatial grain of environmental predictors and matching this to the spatial grain at which species occurrences and abundances are mapped (Bradter et al). The small contribution of landcover in explaining spatial patterns of β-diversity also suggests that the landcover classes may not be well-resolved enough to capture the variation in habitat quantity and quality that structure macro-moth communities. In the case of woodland, moth assemblages have been shown to vary not only between woodland types (e.g. broadleaved versus conifer, which are separate landcover classes), but also within these woodland types depending on, for example, the age class of coppice management (Broome *et al.* 2011) and the tree diversity and species mix of woodland patches (Fuentes-Montemayor *et al.* 2012). Likewise, there is evidence that spatial variation in agricultural practices such as organic and conventional farming and agri-environment scheme implementation, influence moth communities (Pocock & Jennings 2008; Taylor & Morecroft 2009), yet all of these management types fall under the arable landcover class. In addition, all 23 landcover classes were used to derive a measure of habitat heterogeneity, which may dilute the effects of variation in the landcover classes that are most important in determining spatial patterns in macro-moth β-diversity, that is, the heterogeneity of landcover classes that have little relevance for macro-moths (e.g.) will drastically reduce the explanatory power of landcover heterogeneity in these analyses. One way to derive a subset of these landcover classes that, a priori, would be expected to predict macro-moth turnover would be to refer a resource-based habitat classification, such as those for British butterflies (Shreeve *et al.* 2001) and central European macro-moths (Pavlikova & Konvicka 2012).

Despite the overall pattern, the results do identify substantial variation between metrics and data sets in terms of both explanatory power and the independent effects of climate, landcover and geographical distance. This is consistent with other studies that have found that niche and neutral processes may drive spatial patterns in different facets of β-diversity (Svenning *et al.* 2011; Baselga 2013) and that data quality can influence conclusions about niche versus neutral processes (Jones *et al.* 2008). I explore some of these sources of variation in the following sections.

5.5.2 Comparison of presence-absence and abundance metrics

Within the RIS data, geographical distance, climate and landcover were better able to explain spatial patterns in abundance-based β-diversity metrics (β_{Morisita} and β_{Horn}) than presence-absence metrics ($\beta_{\text{Sørensen}}$). This is not surprising, given that the additional information in abundance data will provide a much more nuanced picture of spatial variation in community structure, reflecting the turnover and/or loss of individuals, where presence-absence metrics would detect no differences. An unexpected finding is that spatial patterns in β_{Horn} were better explained by geographical distance, climate and landcover than patterns in β_{Morisita}. β_{Horn} makes use of abundance information (like β_{Morisita} and unlike $\beta_{\text{Sørensen}}$), but is more sensitive to differences in rare species than β_{Morisita}. Our simulations in chapter 4 indicated that β_{Morisita} would return extremely low values of β under a positive occupancy-abundance relationship (because rare species are more range restricted) and this is a pattern which is seems to be extremely strong within the British macro-moths (Fig. 5.5). This implies that locally rare macro-moths are more likely to be turned over among the grid cells in our analysis than locally common macro-moths. This may explain why for β_{Horn} (which is more sensitive to the rarer species that seem to be driving macro-moth turnover) is better explained than β_{Morisita} (which places much greater emphasis on spatial variation in dominant species) and $\beta_{\text{Sørensen}}$ (which cannot detect spatial variation in relative abundance). These results suggest that there may be an optimum use of abundance information by metrics that is reduced when emphasis is shifted too far towards differences in either rare ($\beta_{\text{Sørensen}}$) or common (β_{Morisita}) species.

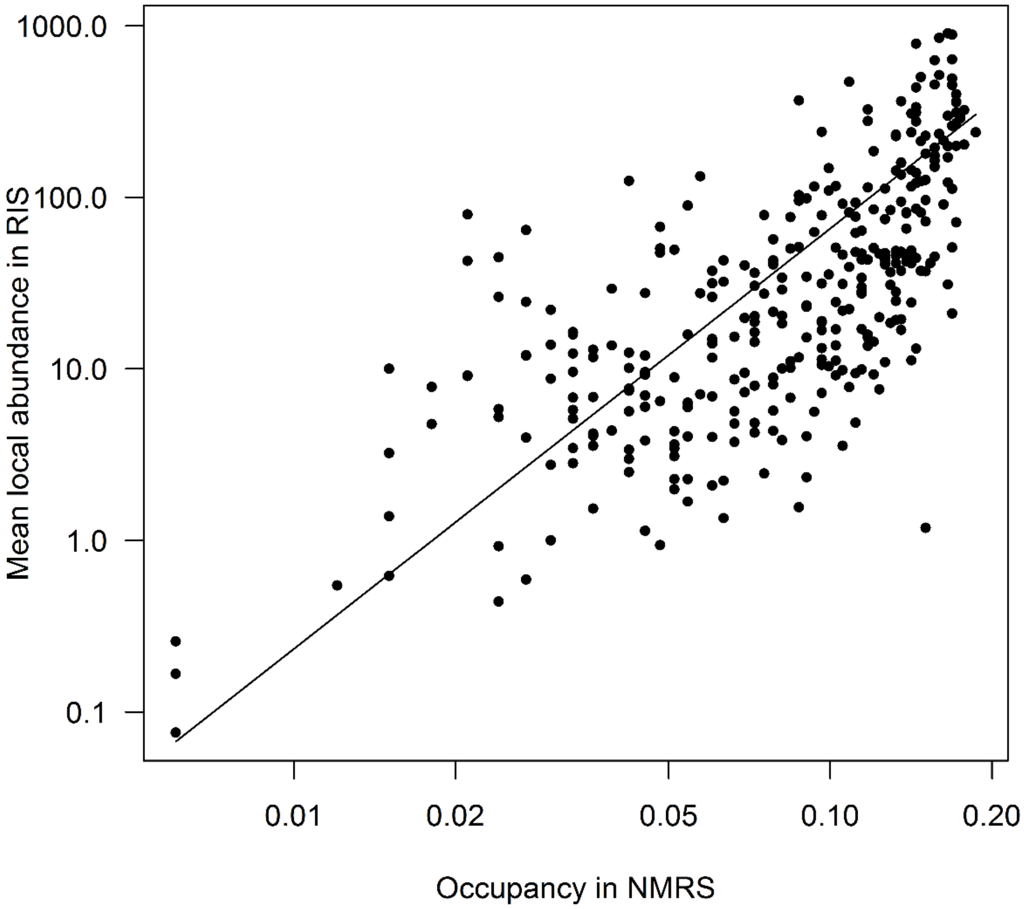

Fig. 5.5 Occupancy-abundance relationship for the 325 British macro-moth species in 66 1km^2 grid cells shared between the National Moth Recording Scheme (NMRS) and the Rothamsted Insect Survey (RIS) between 2000 and 2011

Occupancy is estimated as the proportion of grid cells with one or more records in the NMRS. Mean local abundance is estimated as the mean of total annual counts in the Rothamsted Insect Survey.

The relative contributions of geographical distance, climate and landcover also varied among the presence-absence and abundance-based metrics. The results suggest that β-diversity metrics that are predominantly sensitive to spatial variation in common species (β_{Morisita}) demonstrate relatively weaker associations with landcover and geographical distance and a stronger association with climate. Presence-absence and abundance information have previously led to opposing conclusions about impacts (positive or negative) of invasive species on biotic homogenisation (Cassey *et al.* 2008) and there is evidence that the abundance and the composition of communities can be structured by different processes (Siepielski *et al.* 2010; Siepielski & Mcpeek 2013). Consequently our results suggest that climate may be associated with more subtle spatial variation in the abundances of species, while landcover and geographical distance contribute more to compositional variation (e.g. species turnover and/or the gain or loss of species).

One mechanistic hypothesis for the positive ONR (Fig. 5.5) is that habitat generalists are widespread and abundant because they can exploit resources that are also widespread and locally abundant (Borregaard & Rahbek 2010). If generalist macro-moths are both more widespread and more locally abundant than specialists, then spatial variation amongst common species may be weak: this may explain why β_{Morisita} (which is almost entirely influenced by variation in common species and insensitive to differences in rare species: chapter 4) has weaker associations with landcover (as a proxy for habitat heterogeneity) than metrics that can better detect variation in rare species (β_{Horn} and, to a greater degree, $\beta_{\text{Sørensen}}$).

5.5.3 Comparison of opportunistic and standardised data

Together, geographical distance, climate and landcover explained substantially less variation in the opportunistic NMRSp data than the standardised RISp data. The abundances in the RIS were converted to presence absences for this analysis, so the contribution of abundance information can be ruled out as the cause of greater unexplained variation in NMRSp. A key feature of the NMRSp is spatial variation in recording in the NMRSp due to opportunistic data collection, compared to standardised recording protocols in the RISp. Undersampling has been shown to positively bias β-diversity metrics (see chapter 4; Chao *et al.* 2006; Beck *et al.* 2013), thus some unexplained spatial variation in β-diversity will be due to spatial patterns in recording activity. The impact of under-recording should generate spatial patterns in nestedness, rather than species turnover because, among grid cells with identical communities, the species accumulation curve predicts that undersampled sites will contain a subset of the species in well-sampled sites (Chao *et al.* 2009). This is consistent with the observation that $\beta_{\text{Sør.nest}}$ (measuring purely nestedness) was the only metric to be better explained using NMRSp rather than RISp data. In the absence of β-diversity metrics to account for unseen shared and unshared species in biological records (currently methods are available for presence absence, but not abundance-based metrics), these results suggest that the partitioning of nestedness and turnover components can be informative about the extent to which the data collection process drives spatial patterns in β-diversity.

The relative independent contribution of geographical distance to spatial patterns in β-diversity were always greater in the NMRSp, while landcover and climate contributions were always less. This suggests that the relative contribution of neutral processes may be overestimated when biological records are used to quantify *β*-diversity, presumably because variation in recording activity generates a spatial signature, which is confounded with geographical distance.

5.5.4 Partitioning of the turnover and nestedness components of *β*-diversity

Together, geographical distance, climate and landcover were best able to explain the purely turnover component of *β*-diversity, but poorly explained spatial patterns in nestedness. This suggests spatial variation in macro-moth *β*-diversity is predominantly due to the replacement of species along geographical and environmental gradients, rather than differences in species richness, or that important environmental or spatial drivers of macro-moth nestedness are missing from these models. I discuss some potentially important missing covariates in the section “Unexplained variation” below. One relevant issue is that I did not apply turnover and nestedness components of an abundance-based metric here. The Bray-Curtis metric can also be partitioned into purely turnover and nestedness components which reflect purely turnover of individuals and purely gradients in abundance, respectively (Baselga 2013), and might be expected to paint a more detailed picture of spatial variation in nestedness than the partitioned presence-absence nestedness component applied here.

The weaker relative independent effects of geographical distance on nestedness in the RISp is consistent with the hypothesis that neutral processes (encompassed in geographical distance) should drive spatial patterns in species turnover (due to stochastic extinction-colonisation dynamics and dispersal limitation), but not in species nestedness (Svenning *et al.* 2011).

5.5.5 Unexplained variation

Together geographical distance, climate and landcover explained only a limited amount of variation in the *β*-diversity of British macro-moths (just 16.940 % in the best model), suggesting that important environmental predictors of macro-moth *β*-diversity are missing from these models. Indeed, one assumption of partitioning the contributions of niche and neutral processes is that all important environmental variables driving spatial variation in *β*-diversity are included in the model (Caruso *et al.* 2012). This is rarely the case, especially for a less well-studied taxonomic group like macro-moths for which the climate and habitat associations of individual species are often poorly known (Fox 2013). The perceived role of niche processes in structuring spatial patterns in *β*-diversity is, therefore, likely to be greatly underestimated in these results. Potentially important missing variables for determining spatial patterns in British macro-moth communities include spatial patterns in monthly rainfall (see chapter 3; Pollard 1988, but see Jonason *et al.* 2014), mean minimum temperature and the interaction between wind, rain and temperature to reflect exposure to Atlantic weather systems in westerly and high elevation regions. Other environmental factors that may be important in determining spatial patterns in macro-moth communities include light and chemical pollution (Fox 2013). Finally, historical patterns have been shown to have a substantial effect on regional and local patterns in *β*-diversity (Dexter *et al.* 2012; Dobrovolski *et al.* 2012; Fitzpatrick *et al.* 2013). However, a number of British macro-moths have a boreal distribution, that is, northern Britain is the southern edge of the distribution (Hill *et al.* 2010). Moreover, the effects of these historical processes are likely to be weaker for highly mobile taxa like macro-moths. A priori, we would expect landcover heterogeneity to

5.5.6 Sources of spatial autocorrelation in *β*-diversity

Spatial autocorrelation is a form of non-independence among data points which, in non-spatial models, can bias estimates of variable importance towards more spatially structured predictors as well as invalidating traditional tests of significance (Lennon 2000). The risk of falsely rejecting the null hypothesis (no association between a predictor and spatial patterns of *β*-diversity) was addressed here by using randomisation tests to determine if estimates of independent effects were significantly different from those expected by chance. However, the impact of spatial autocorrelation on the independent contributions of geographical distance, climate and landcover is more difficult to address.

I have assumed (as in previous partitioning studies) that geographical distance among grid cell pairs captures the stochastic colonisation and extinction events and dispersal limitation (e.g. neutral processes), which generates spatial variation in community composition even among grid cells with similar environmental conditions. However, there are additional sources of spatial autocorrelation in *β*-diversity which may invalidate this assumption. Firstly, there may be spatial autocorrelation in *β*-diversity that cannot be explained by geographical distance alone (Andrew *et al.* 2012). In my analyses, two examples of additional sources of spatial autocorrelation that aren't accounted for, but may be important, are the latitudinal gradients in species richness (the RIS and the NMRS) and recording intensity (mainly relevant to the NMRS). *β*-diversity metrics can be sensitive to both regional diversity (e.g. a pair of sites from species rich region may have greater *β*-diversity that an pair of sites from a species poor region: Koleff *et al.* 2003b) and sample size (*β*-diversity estimated from smaller samples is greater than *β*-diversity in well-sampled assemblages: chapter 4; Beck *et al.* 2013). This implies that a pair of environmentally similar grid cells in Scotland may have very different pairwise β-diversities to a matching pair in England, either because of the effect on estimated β-diversity of lower regional diversity and/or lower recording activity in Scotland. A second issue with interpreting the contribution of geographical distance as neutral processes was highlighted by Smith & Lundholm (2010), who noted that the dispersal rates (usually considered a neutral process) can increase the variation in β-diversity that is explained by environmental as well as spatial predictors. This can occur if dispersal limitation interacts with habitat selection to increase the establishment of species in suboptimal grid cells adjacent to high quality grid cells. The emerging pattern is driven by the spatial structure of the environment, but is associated with geographical distance and not environmental predictors. Together, unmeasured environmental variables (see previous section), unexplained spatial autocorrelation and spatial autocorrelation generated by non-neutral process limit the extent to which the relative independent effects of climate plus landcover and geographical distance can be interpreted as the footprint of niche versus neutral processes.

One method to account for account for the unexplained spatial autocorrelation (not captured by geographical distance) would be to include an autocovariate in the models before applying hierarchical partitioning (e.g. Heikkinen *et al.* 2005). Alternatively, a generalised least squares model with a spatially autocorrelated error term would account for unexplained spatial autocorrelation (Dormann *et al.* 2007). Unfortunately, generalised least squares models are currently incompatible with the hier.part package I have used.

5.5.7 Conclusions

The independent effects of geographical distance, climate and landcover vary among the metrics and datasets that are used to quantify spatial patterns in β-diversity. Unexplained spatial autocorrelation and spatial autocorrelation due to non-neutral processes makes it difficult to map the variation explained by geographical distance and environmental variables to the relative contributions of niche and neutral processes.

5.6 References

Andrew, M.E., Wulder, M.A., Coops, N.C. & Baillargeon, G. (2012). Beta-diversity gradients of butterflies along productivity axes. Global Ecology and Biogeography, 21, 352–364.

Baselga, A. (2010). Partitioning the turnover and nestedness components of beta diversity. Global Ecology and Biogeography, 19, 134–143.

Baselga, A. (2013). Separating the two components of abundance-based dissimilarity: balanced changes in abundance vs. abundance gradients. Methods in Ecology and Evolution, 4, 552–557.

Baselga, A. (2012). The relationship between species replacement, dissimilarity derived from nestedness, and nestedness. Global Ecology and Biogeography, 21, 1223–1232.Baselga, A., Villeger, S., de Bortoli, J. & Leprieur, F. (2013). betapart: Partitioning beta diversity into turnover and nestedness components. R package version 1.3. http://CRAN.R-project.org/package=betapart.

Beck, J., Holloway, J.D. & Schwanghart, W. (2013). Undersampling and the measurement of beta diversity. Methods in Ecology and Evolution, 4, 370–382.

Beck, J. & Vun Khen, C. (2007). Beta-diversity of geometrid moths from northern Borneo: Effects of habitat, time and space. Journal of Animal Ecology, 76, 230–237.

Borregaard, M.K. & Rahbek, C. (2010). Causality of the relationship between geographic range size and species abundance. The Quarterly Review of Biology, 85, 3–25.

Broome, A., Clarke, S., Peace, A. & Parsons, M. (2011). The effect of coppice management on moth assemblages in an English woodland. Biodiversity and Conservation, 20, 729–749.

Bryant, S.R., Thomas, C.D. & Bale, J.S. (1997). Nettle-feeding nymphalid butterflies : temperature, development and distribution. Ecological Entomology, 22, 390–398.

Buckley, L.B., Waaser, S.A., MacLean, H.J. & Fox, R. (2011). Does including physiology improve species distribution model predictions of responses to recent climate change? Ecology, 92, 2214–2221.

Calderón-Patrón, J.M., Moreno, C.E., Pineda-López, R., Sánchez-Rojas, G. & Zuria, I. (2013). Vertebrate dissimilarity due to turnover and richness differences in a highly beta-diverse region: The role of spatial grain size, dispersal ability and distance. PLoS ONE, 8, 1–10.

Caruso, T., Taormina, M. & Migliorini, M. (2012). Relative role of deterministic and stochastic determinants of soil animal community: A spatially explicit analysis of oribatid mites. Journal of Animal Ecology, 81, 214–221.

Cassey, P., Lockwood, J.L., Olden, J.D. & Blackburn, T.M. (2008). The varying role of population abundance in structuring indices of biotic homogenization. Journal of Biogeography, 35, 884–892.

Chao, A., Chazdon, R.L., Colwell, R.K. & Shen, T.-J. (2006). Abundance-based similarity indices and their estimation when there are unseen species in samples. Biometrics, 62, 361–71.

Chao, A., Colwell, R.K., Lin, C. & Gotelli, N.J. (2009). Sufficient Sampling for Asymptotic Minimum Species Richness Estimators Published by : Ecological Society of America Linked references are available on JSTOR for this article : Your use of the JSTOR archive indicates your acceptance of the Terms & Conditio. Ecology, 90, 1125–1133.

Chase, J.M. & Leibold, M.A. (2003). Ecological Niches: linking classical and contemporary approaches. Chicago University Press, Chicago, Illinois.

Chevan, A. & Sutherland, M. (1991). Hierarchical Partitioning. The American Statistician, 45.

Conrad, K.F., Warren, M.S., Fox, R., Parsons, M.S. & Woiwod, I.P. (2006). Rapid declines of common, widespread British moths provide evidence of an insect biodiversity crisis. Biological Conservation, 132, 279–291.

Conrad, K.F., Woiwod, I.P. & Perry, J.N. (2002). Long-term decline in abundance and distribution of the garden tiger moth (Arctia caja) in Great Britain. Biological Conservation, 106, 329–337.

Davies, Z.G., Wilson, R.J., Coles, S. & Thomas, C.D. (2006). Changing habitat associations of a thermally constrained species, the silver-spotted skipper butterfly, in response to climate warming. Journal of Animal Ecology, 75, 247–256.

Dexter, K.G., Terborgh, J.W. & Cunningham, C.W. (2012). Historical effects on beta diversity and community assembly in Amazonian trees. Proceedings of the National Academy of Sciences, 109, 7787–7792.

Dobrovolski, R., Melo, A.S., Cassemiro, F. a S. & Diniz-Filho, J.A.F. (2012). Climatic history and dispersal ability explain the relative importance of turnover and nestedness components of beta diversity. Global Ecology and Biogeography, 21, 191–197.

Dormann, C.F., Mcpherson, J.M., Arau, M.B., Bivand, R., Bolliger, J., Carl, G., Davies, R.G., Hirzel, A., Jetz, W., Kissling, W.D., Ohlemu, R., Peres-neto, P.R., Schurr, F.M. & Wilson, R. (2007). Methods to account for spatial autocorrelation in the analysis of species distributional data : a review. Ecography, 30, 609–628.

Ferrier, S., Manion, G., Elith, J. & Richardson, K. (2007). Using generalized dissimilarity modelling to analyse and predict patterns of beta diversity in regional biodiversity assessment. Diversity and Distributions, 13, 252–264.

Fitzpatrick, M.C., Sanders, N.J., Normand, S., Svenning, J.-C., Ferrier, S., Gove, A.D. & Dunn, R.R. (2013). Environmental and historical imprints on beta diversity: insights from variation in rates of species turnover along gradients. Proceedings of the Royal Society - Series B: Biological Sciences, 280, 20131201.

Fox, R. (2013). The decline of moths in Great Britain: A review of possible causes. Insect Conservation and Diversity, 6, 5–19.

Fuentes-Montemayor, E., Goulson, D., Cavin, L., Wallace, J.M. & Park, K.J. (2012). Factors influencing moth assemblages in woodland fragments on farmland: Implications for woodland management and creation schemes. Biological Conservation, 153, 265–275.

Harrison, S., Ross, S.J. & Lawton, J.H. (1992). Beta diversity on geographic gradient in Britain. Journal of Animal Ecology, 61, 151–158.

Heikkinen, R.K., Luoto, M., Kuussaari, M. & Poyry, J. (2005). New Insights into Butterfly-Environment Relationships Using Partitioning Methods. Proceedings of the Royal Society - Series B: Biological Sciences, 272, 2203–2210.

Hill, J.K., Griffiths, H.M. & Thomas, C.D. (2011). Climate change and evolutionary adaptations at species’ range margins. Annual Review of Entomology, 56, 143–59.

Hill, L., Randle, Z., Fox, R. & Parsons, M. (2010). A provisional atlas of moths. Butterfly Conservation.

Horn, H.S. (1966). Measurement of overlap in comparative ecological studies. American Naturalist, 100, 419–424.

Hubbell, S.P. (2001). The Unified Neutral Theory of Biodiversity and Biogeography. Princeton University Press, Oxford.

Isaac, N.J.B. & Pocock, M.J.O. (2015). Bias and information in biological records. early view.

Jiménez-Valverde, A., Baselga, A., Melic, A. & Txasko, N. (2010). Climate and regional beta-diversity gradients in spiders: Dispersal capacity has nothing to say? Insect Conservation and Diversity, 3, 51–60.

Jonason, D., Franze, M. & Ranius, T. (2014). Surveying Moths Using Light Traps : Effects of Weather and Time of Year. PLoS One, 9, e92453.

Jones, M.M., Tuomisto, H., Borcard, D., Legendre, P., Clark, D.B. & Olivas, P.C. (2008). Explaining variation in tropical plant community composition: influence of environmental and spatial data quality. Oecologia, 155, 593–604.

Jost, L., Chao, A. & Chazdon, R. (2011). Compositional similarity and β (beta) diversity. Biological Diversity: frontiers in measurement and assessment (eds A.E. Magurran & B.J. McGill), pp. 66–84. Oxford University Press, Oxford.

Keil, P., Schweiger, O., Kühn, I., Kunin, W.E., Kuussaari, M., Settele, J., Henle, K., Brotons, L., Pe'er, G., Lengyel, S., Moustakas, A., Steinicke, H. & Storch, D. (2012). Patterns of beta diversity in Europe: the role of climate, land cover and distance across scales. Journal of Biogeography, 39, 1473–1486.

Koleff, P., Gaston, K.J. & Lennon, J.J. (2003a). Measuring beta diversity for presence-absence data. Journal of Animal Ecology, 72, 367–382.

Koleff, P., Lennon, J.J. & Gaston, K.J. (2003b). Are there latitudinal gradients in species turnover? Global Ecology and Biogeography, 12, 483–498.

Legendre, P. (2008). Studying beta diversity: ecological variation partitioning by multiple regression and canonical analysis. Plant Ecology, 1, 3–8 ST – Studying beta diversity: ecological vari.

Legendre, P., Borcard, D. & Peres-Neto, P.R. (2005). Analyzing beta diversity: Partitioning the spatial variation of community composition data. Ecological Monographs, 75, 435–450.

Lennon, J.J. (2000). Red-shifts and red herrings in geographical ecology. Ecography, 23, 101–113.

McGlinn, D.J. & Hurlbert, A.H. (2012). Scale dependence in species turnover reflects variance in species occupancy. Ecology, 93, 294–302.

Morisita, M. (1959). Measuring of interspecific association and similarity between communities. Memoirs of the Faculty of Science, Kyushu University, Series E: Biology, 3, 65–80.

Morton, D., Rowland, C., Wood, C., Meek, L., Marston, C., Smith, G., Wadsworth, R. & Simpson, I. (2011). Final Report for LCM2007 - the new UK land cover map. Countryside Survey Technical Report No 11/07 logy and Hydrology (CEH Project Number: CO3259).

Mac Nally, R. (2002). Multiple regression and inference in ecology and conservation biology: Further comments on identifying important predictor variables. Biodiversity and Conservation, 11, 1397–1401.

Nychka, D., Furrer, R. & Sain, S. (2015). fields: Tools for Spatial Data. R package version 8.2-1. http://CRAN.R-project.org/package=fields.

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P.M., Stevens, H.H. & Wagner, H. (2013). vegan: Community Ecology Package. R Package version 2.0-10. http://cran.r-project.org/package=vegan.

Paoli, G.D., Curran, L.M. & Zak, D.R. (2006). Soil nutrients and beta diversity in the Bornean Dipterocarpaceae: Evidence for niche partitioning by tropical rain forest trees. Journal of Ecology, 94, 157–170.

Parmesan, C., Ryrholm, N., Stefanescu, C., Hill, J.K., Thomas, C.D., Descimon, H., Huntley, B., Kaila, L., Kullberg, J., Tammaru, T., Tennent, W.J., Thomas, J. a & Warren, M. (1999). Poleward shifts in geographical ranges of butterfly species associated with regional warming. 579–583.

Perry, M. & Hollis, D. (2005). The generation of monthly gridded datasets for a range of climatic variables over the UK. International Journal of Climatology, 25, 1041–1054.

Plotkin, J.B. & Muller-Landau, H.C. (2002). Sampling the species composition of a landscape. Ecology, 83, 3344–3356.

Pocock, M.J.O. & Jennings, N. (2008). Testing Biotic Indicator Taxa: The Sensitivity of Insectivorous Mammals and Their Prey to the Intensification of Lowland Agriculture. Journal of Applied Ecology, 45, 151–160.

Pollard, E. (1988). Temperature, Rainfall and Butterfly Numbers. The Journal of Applied Ecology, 25, 819–828.

Püttker, T., de Arruda Bueno, A., Prado, P.I. & Pardini, R. (2014). Ecological filtering or random extinction? Beta-diversity patterns and the importance of niche-based and neutral processes following habitat loss. Oikos, 206–215.

Qian, H., Badgley, C. & Fox, D.L. (2009). The latitudinal gradient of beta diversity in relation to climate and topography for mammals in North America. Global Ecology and Biogeography, 18, 111–122.

R Core Development Team. (2014). R: A language and environment for statistical computing. Version 3.1.1. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/.

Ricotta, C., Carranza, M.L. & Avena, G. (2002). Computing beta-diversity from species-area curves. Basic and Applied Ecology, 3, 15–18.

Rosindell, J., Hubbell, S.P. & Etienne, R.S. (2011). The Unified Neutral Theory of Biodiversity and Biogeography at Age Ten. Trends in Ecology & Evolution, 26.

Rosindell, J., Hubbell, S.P., He, F., Harmon, L.J. & Etienne, R.S. (2012). The case for ecological neutral theory. Trends in Ecology and Evolution, 27, 203–208.

Siepielski, A.M., Hung, K.L., Bein, E.E.B. & Mcpeek, M. a. (2010). Experimental evidence for neutral community dynamics governing an insect assemblage. Ecology, 91, 847–857.

Siepielski, A.M. & Mcpeek, M. a. (2013). Niche versus neutrality in structuring the beta diversity of damselfly assemblages. Freshwater Biology, 58, 758–768. Retrieved December 19, 2013, from http://doi.wiley.com/10.1111/fwb.12082

Smith, T.W. & Lundholm, J.T. (2010). Variation partitioning as a tool to distinguish between niche and neutral processes. Ecography, 33, 648–655.

Spalding, A. & Parsons, M. (2004). Light trap transects - A field method for ascertaining the habitat preferences of night-flying Lepidoptera, using Mythimna turca (Linnaeus 1761) (Lepidoptera: Noctuidae) as an example. Journal of Insect Conservation, 8, 185–190.

Summerville, K.S. & Crist, T.O. (2004). Contrasting effects of habitat quantity and quality on moth communities in fragmented landscapes. Ecography, 27, 3–12.

Svenning, J.C., Fløjgaard, C. & Baselga, A. (2011). Climate, history and neutrality as drivers of mammal beta diversity in Europe: Insights from multiscale deconstruction. Journal of Animal Ecology, 80, 393–402.

Taylor, M.E. & Morecroft, M.D. (2009). Effects of agri-environment schemes in a long-term ecological time series. Agriculture, Ecosystems and Environment, 130, 9–15.

Tuomisto, H. (2010a). A diversity of beta diversities: straightening up a concept gone awry. Part 1. Defining beta diversity as a function of alpha and gamma diversity. Ecography, 33, 2–22.

Tuomisto, H. (2010b). A diversity of beta diversities: straightening up a concept gone awry. Part 2. Quantifying beta diversity and related phenomena. Ecography, 33, 23–45.

Ulrich, W. & Almeida-Neto, M. (2012). On the meanings of nestedness: back to the basics. Ecography, 35, 865–871.

Walsh, C. & Mac Nally, R. (2013). hier.part: Hierarchical Partitioning. R package version 1.0-4. http://CRAN.R-project.org/package=hier.part.

Warren, D.L., Cardillo, M., Rosauer, D.F. & Bolnick, D.I. (2014). Mistaking geography for biology: inferring processes from species distributions. Trends in Ecology & Evolution, 1–9.

Wennekes, P.L., Rosindell, J. & Etienne, R.S. (2012). The Neutral-Niche Debate: A Philosophical Perspective. Acta Biotheoretica, 60, 257–271.

Whittaker, R.H. (1972). Evolution and Measurement of Species Diversity. Taxon, 21, 213–251.

Whittaker, R.H. (1960). Vegetation of the Siskiyou Mountains , Oregon and California. Ecological Monographs, 30, 280–338.

Chapter 6

Extrapolating insect biodiversity across spatial scales: a synthesis

6.1 Outline

In this thesis I have investigated spatial patterns in insect distributions, using unstructured biological records, simulated species assemblages and local abundance and presence-absence from standardised sampling protocols, whilst explicitly considering issues of spatial scale. I have explored the extent to which opportunistic biological records can be used to explain and predict spatial patterns in biodiversity, despite inherent biases in these data. By focussing on dragonflies and macro-moths, I have gained some ecological insights into these less well-studied taxonomic groups.

The thesis comprised four specific questions. Firstly, can we utilise biodiversity theory describing the functional form of the occupancy-area relationship (OAR) to predict Odonata species occupancies at finer spatial grains than the British atlas data (Chapter 2)? Secondly, can we fill in the gaps in the distribution of an under-recorded British macro-moth using a combination of information on observer effort, species-environment associations and residual spatial autocorrelation (Chapter 3)? In chapters 4 and 5, I moved from single species distributions to examining the multi-species assemblages that emerge from these overlapping distribution patterns. I compiled some desirable and personality properties of a β-diversity metric and examined how these inform the appropriate choice of a metric for quantifying spatial structure in species communities (Chapter 4). Finally, I quantified the independent contributions of geographic distance, climate and landcover in structuring spatial patterns in macro-moth β-diversity (Chapter 5).

In this final chapter I synthesise the findings of chapters 2 to 5 in relation to four broad themes. Firstly, all four chapters have highlighted some of the possibilities and difficulties associated with the scale-dependence of biodiversity. Secondly, these chapters have shown that predicting spatial structure and understanding spatial scaling will require a theoretical framework for quantifying the relative contribution of niche versus neutral processes. Thirdly, I discuss whether a general theory of biodiversity is possible, given the current lack of mechanism and the poor linkage between data and theory. . . Fourthly, I discuss some of the ecological insights that have emerged for dragonflies and macro-moths as a result of these analyses. Finally, I discuss the value of opportunistic biological records like those used in this thesis for addressing a range of questions about spatial patterns in biodiversity, but note that developing methods to deal with the biases in these data should be a priority.

6.2 Spatial scaling of insect biodiversity

This thesis has shown that methods for scaling biodiversity have promising applications in monitoring biodiversity, but it has also highlighted some challenges associated with spatial scale. In this section, I discuss these successes and limitations.

In chapter 2, I tested the predictions of fine-grain occupancy for ten downscaling models and found the results for the Hui model provided satisfactory estimates of distribution size at fine spatial grains and predicted a nonlinear relationship between sampling grain and area of occupancy. If the superior performance of the Hui model can be demonstrated for data sets in other taxa and regions, this would have implications for frameworks like the IUCN, which use restricted or fragmented distributions as criteria to prioritise species for red lists. Red list criteria lack clear guidelines on which spatial scale is appropriate for measuring area of occupancy and for comparing these indices of distribution size between species. The nonlinear OAR slopes that were predicted by the Hui downscaling model may contain a footprint of biologically meaningful scales for measuring species distribution size. Shallower slopes indicate greater levels of intraspecific aggregation within grid cells and may help to guide inferences about the scale of the population for a focal species and the degree of fragmentation of these populations. The significance of the spatial structure that drives the OAR has previously been recognised as an important predictor of past declines and expansions in species distributions using simply the linear relationship between area of occupancy at nested spatial grains (Wilson *et al.* 2004). Extending this kind of analysis to nonlinear OARs across a greater range of spatial scales offers an even more nuanced approach to understanding the patterns left by changes in species distributions size and the scales at which these changes are most extreme.

In contrast to the strong scale-dependence in species distributions observed in chapter 2, in chapter 3 I found no substantial differences in species-environment relationships for the Brindled Green moth at 25 km^2 and 100 km^2 or in the overall predictive success of models fitted at these two spatial grains. Indeed, perhaps we would not expect to see real differences in the effect of climate on the occurrence in grid cells ≤100 km^2 as climate varies over much larger spatial grains. However, elevation and woodland cover are known to vary a great deal within 100 km^2 grid cells, therefore we would have expected to see an improvement in model predictions at finer grains. There are a number of reasons that could explain why this was not the case. Firstly, a key difference between chapters 2 and 3 is that a much narrower window of spatial scales were explored in chapter 3. One possibility is that woodland cover and elevation actually structure the distribution of the Brindled Green at even finer spatial grains than I used, that is the scale of effect was not captured by my chosen scales. By scale of effect, I mean the scale at which the emerging pattern (probability of occurrence) is most strongly affected by the variable of interest (woodland cover or elevation). Indeed it has been observed that the scale of effect is difficult to pinpoint. Even when a broad range of scales are investigated, the effect size is often strongest at the finest or coarsest of these scales, suggesting a broader range of spatial scales are often required to reveal the scales at which this relationship “peaks” (Jackson & Fahrig 2014). A priori estimation of the appropriate range of scales needed to detect the scale of effect is not straightforward. Biodiversity theory provides only very coarse guidelines as to the characteristic scales of the processes driving species distributions (Gotelli *et al.* 2010; McGill 2010a) and our knowledge of how these scales of effect might vary in response to species-level traits like dispersal ability or physiological constraints is very limited.

Perceived scale-dependence (Sandel 2015) was highlighted as potential issue in chapter 1. It describes a situation where scale-dependence emerges from differences in observability of a variable with spatial scale, rather than true pattern shifts. In chapters 2 and 3, perceived scale-dependence may have implications for the validation of model predictions. In chapter 2, our 1km^2 predictions of occupancy were evaluated against observed occurrences of species at the 1km^2 grain in the Dragonfly Recording Network. In chapter 3 predicted probability of occurrence in 25 km^2 cells was evaluated against observed occurrences and abundances in RIS light traps. In both cases, the extent to which these test data can validate the predictions is subject to perceived scale-dependence: observed presence and abundance within these test data reflects only a sample of the species or individuals that are present and may well be biased towards particular habitats. Thus the test data will become an increasingly inaccurate reflection of the true pattern of abundance and occurrence as the scale becomes coarser and fewer of the species and individuals are sampled. Unpicking true scale-dependence from perceived scale-dependence will require not only finding the appropriate scale of effect, but also ensuring that the grain of the predictions matches the grain of the test data. The difficulties with validating the predictions of the Beale observer effort in chapter 3 is an example of the need for clarity about how observed data are related to the conceptual model. Hierarchical Bayesian models are supremely valuable in this regard because there are separate sub-models for the data and the concept. Applying such a model to the test data, as well as the training data is one approach to fully validating the predictions of the Beale observer effort model in chapter 3. Alternatively, field surveys conducted at a grain corresponding to the predictions (e.g. 25 km^2 for the Brindled Green moth and 1 km^2 for Odonata species) and designed to minimise false absences (e.g. by sampling all habitat types within a grid cell) would validate the methods applied in chapters 2 and 3 with greater certainty.

6.3 The challenge of unpicking stochastic and deterministic processes

Chapters 2 to 5 explored the processes shaping dragonfly and macro-moth distributions and the patterns that emerge from the overlap of individual species distributions (e.g. β-diversity). The methods used often provided an adequate description of the data sets used or predicted reasonably well, but a mechanistic understanding of the processes underpinning the observed distributions and abundances has proved challenging. As an example, I discuss some of the difficulties in interpreting the relative importance of niche and neutral processes, using the methods within this thesis, and some examples from the wider ecological literature.

In chapter 2, my results indicated that species with poorer downscaling predictions tended to have a climatic range limit within Britain and tended to have greater dispersal abilities. Both of these traits would make species distributions more likely to be structured by environmental processes: a climatic range limit suggests some physiological tolerance is exceeded in some parts of the range, while high dispersal ability suggests dispersal limitation will leave little spatial footprint on the distribution. The implication is that, while downscaling performs reasonably well using purely spatial information, the inclusion of environmental information models is likely to improve fine grain estimates of distribution size.

In chapter 3, I focus on the distribution of just one species, the Brindled Green moth, and use a species distribution model (the Beale observer effort model) to quantify the associations of probability of occurrence with mean annual temperature, mean annual rainfall, woodland cover and elevation. The model also estimates the residual spatial autocorrelation between neighbouring cells, capturing the extent to which probability of occurrence within a grid cell is greater or less than would be expected based on environmental predictors alone. Encompassed within this estimate are unmeasured environmental covariates, but also neutral processes and the effects of source-sink dynamics, all of which can lead to presences within environmentally unsuitable habitat or absences in environmentally suitable habitat. Therefore, using this approach, it is impossible to quantify the overall contributions of niche versus neutral processes to the distribution of the Brindled Green. All climate and habitat predictors had high relative importance (> 0.7), but highest of all was residual spatial autocorrelation, indicating the combined effects of unmeasured environmental variables, neutral processes and measurement error have the greatest influence on the distribution of the Brindled Green.

Whilst drivers of β-diversity were not the focus of chapter 4, I used simulated species assemblages to test two properties of β-diversity metrics that would be expected to hold if community assembly processes were purely niche (β should be cumulative if turnover is directional, along a simulated linear environmental gradient) or purely neutral (similarity (1-β) should be probabilistic if communities are random draws from a regional species pool). No metric tested performed well under both scenarios, suggesting it may not be straightforward to use such metrics in a null model framework to interpret the contributions of niche and neutral processes.

In chapter 5, I attempted to quantify the relative contributions of landcover dissimilarity, climate dissimilarity and geographic distance to spatial patterns of β-diversity in British macro-moths and found that the independent effects of climate and geographic distance explained broadly similar amounts of β-diversity. The pattern held across a suite of metrics used to quantify β-diversity. However, as in chapter 3, disentangling the effects of unmeasured, spatially structured environmental covariates from purely spatial processes proved impossible as both were encompassed in the explanatory power of geographical distance. This precluded any insights into the relative importance of niche and neutral processes in structuring the distributions of British macro-moths.

In chapter 1, I highlighted an observation in McGill (2010) that theories of biodiversity tend to emphasise the role of either niche or neutral processes in structuring species distributions. The assumption that one process or another will consistently be the dominant effect in shaping species distributions is unlikely. Examples include species of damselfly genera in north-eastern USA, in which the coexistence of genera was largely determined by environmental gradients, but patterns of relative abundance across sites were predominantly neutral. Species abundance distributions (Chust *et al.* 2013) and body-mass patterns (Vergnon *et al.* 2009) in marine phytoplankton communities also show neither niche nor neutral processes prevail. However, all too often, the distribution patterns that cannot be explained by niche processes are mislabelled as evidence of neutrality. The difficulties in unpicking niche and neutral processes in the preceding chapters is perhaps symptomatic of the limitations of a purely statistical approach to understanding of biodiversity patterns. A number of models attempting to integrate niche and neutral theory are being developed (Matthews & Whittaker 2014) and include phase transitions between niche and neutral communities (Fisher & Mehta 2014), emergent neutral theory (Gravel *et al.* 2006) and stochastic niche theory (Kalyuzhny *et al.* 2015). Ecologists have also begun to unpick the role of niche and neutral processes in community assembly by quantifying patterns of spatial variation at multiple hierarchical levels (haplotype to species) and comparing these to the self-similar patterns expected at all hierarchical under purely neutral processes (Baselga *et al.* 2015). Others have explored the use of null models of community assembly, measuring the deviation of observed patterns from those predicted in the absence of neutral and niche processes, to disentangle their contributions (Tucker *et al.* 2015).

Interestingly, spatial scale goes some way towards reconciling the relative importance of niche and neutral processes (Chase 2014), with environmental homogeneity within small spatial extents magnifying the importance of neutral processes, while strong environmental structure over larger spatial extents appears to emphasise niche processes (Garzon-Lopez *et al.* 2014).

Together, the previous chapters indicate that a mechanistic understanding of species distributions and spatial patterns is problematic when using statistical methods to characterise ecological patterns. This has always proved challenging in the field of macroecology (Beck *et al.* 2012). Understanding the sensitivity of species to environmental versus spatial processes is central to choosing the appropriate management, but general rules for predicting species distributions and spatial structure will require a biodiversity theory that incorporates both deterministic and stochastic processes and which provides a framework to unpick the relative contributions of these two sets of predictors. In the following section I discuss some of the obstacles to developing such a general theory of biodiversity and some alternative approaches to predicting and understanding biodiversity patterns over large spatial extents and at fine spatial grains.

6.4 Is a general theory of biodiversity possible?

In the previous section I discuss the difficulties in unpicking niche and neutral effects in ecological models when employing phenomenological, data-derived models. However, starting from a more theoretical position is problematic as biodiversity theory still lacks a traditionally mechanistic framework for understanding large-scale patterns in biodiversity. The unifying principles of current biodiversity theories are rooted in stochastic geometry, as opposed to the deterministic processes we typically recognise as mechanism (McGill & Nekola 2010). This is a key limitation to generalising biodiversity theory across taxa, regions and spatial scale. In disciplines such as community ecology, there have been strong advances in our theoretical understanding of deterministic community assembly processes with examples including Lotka-Volterra models (May 1975), inter-specific competition (Tilman 1982) and meta-community dynamics (Leibold *et al.* 2004). However, these highly mechanistic approaches are data-hungry, requiring a wealth of information about species interactions.

Macroecology as a discipline has been criticised for its lack of progress in understanding mechanism (Brown 1999; Beck *et al.* 2012; Keith *et al.* 2012), progress which some ecologists predict will come only as this relatively 'young' discipline matures (McGill & Nekola 2010). Deducing mechanism has also been elusive due to the fact that the predictions derived from multiple different models, each assuming different mechanisms, are virtually identical, most notably for the species abundance distribution (McGill *et al.* 2007). Until biodiversity theory can generate predictions with sufficient detail to distinguish opposing models, a general theory of biodiversity may not be possible. The poor linkage between data and theory in biodiversity research has perhaps inhibited mechanistic insights into biodiversity patterns, especially over large spatial scales and in species-rich assemblages, where the complexity makes distinguishing very similar predictions even harder to do.

Since McGill (2010b) highlighted three assertions that appeared to unify six theories of biodiversity, only one study has attempted to convert these assertions into quantitative predictions and validate them against multiple observed patterns. These patterns included the species abundance distribution, intraspecific aggregation, the species area relationship and the distance-decay of similarity.

Interestingly, observed patterns of intra-specific aggregation could not be reproduced without the inclusion of species-specific dispersal distances (May *et al.* 2016). Likewise Kalyuzhny *et al.* (2015) and Fung *et al.* (2016) found the predictions of neutral models were improved by including species-level fitness differences in the form of environmental stochasticity. Interestingly, the addition of species-level fitness differences were also able to account for population dynamics, where general theories of biodiversity have typically only succeeded in predicting static patterns. These findings suggest that species differences cannot be ignored when developing set of 'minimally sufficient rules' for a general theory of biodiversity, but these studies do represent some progress towards integrating mechanism into biodiversity theory. It also highlights the potential value of stochastic geometry (a unifying principle of biodiversity theories) as a basic framework that can be extended to generate taxon- and region-specific predictions.

In chapter 1 I considered the effect of species-level traits on downscaling accuracy in an attempt to understand how species differences can explain patterns above and beyond those predicted by stochastic geometry. However, in addition to species differences, there has been an increasing interest in the significance of intra-specific differences in determining biodiversity patterns (Violle *et al.* 2012). An alternative method to stochastic geometry in understanding and predicting biodiversity patterns is individual-based ecology where the properties of ecological systems depend on the patterns emerging from the adaptive behaviour of individual organisms and their interactions with each other and the environment (Grimm & Railsback 2005). The ecological systems that have been explored have typically been populations and communities (Stillman & Goss-Custard 2010; DeAngelis & Grimm 2014), but with sufficient computing power, there is no reason why these same methods cannot be applied to understanding the distributions and abundances of species over large spatial extents. Individual-based ecology uses computer simulation to parameterise models. The approach is highly mechanistic and successful models will depend on the data acquired from field and laboratory studies of individual variation. Linking the adaptive behaviours of individual organisms with their distribution patterns is a promising way of linking ecological subdisciplines from physiology and behaviour through to population ecology, community ecology and biogeography and to understand how and why biodiversity patterns change with spatial scale. If I were to address the questions in this thesis again, this would be the approach I would choose.

6.5 Ecological insights for macro-moth and dragonflies

In chapter 1, I explained that using moths and dragonflies for these analyses had greater potential to yield novel ecological insights. In this section I highlight some of the findings that have emerged from investigating biodiversity patterns in these less well-studied taxonomic groups.

In chapter 1, I observed a sigmoidal relationship of the OAR. This is consistent with our broad understanding of the characteristic scale of effect for some key processes driving species distributions (Pearson & Dawson 2003; Hortal *et al.* 2010). Climate is thought to restrict species distributions at relatively coarse spatial grains and the depressed slope for some Odonata at grains >1600 km^2 is consistent with latitudinal gradients in climate in Britain excluding these species from northerly regions. The steeper slopes I observed at intermediate grains may reflect the distribution of suitable habitat: for Odonata this could well be driven by the fragmented distribution of lotic water bodies needed for reproduction and could even be interpreted as the meta-population-scale. Below these scales, I observed a much shallower OAR, indicating high levels of occupancy within these habitats and possibly beginning to approximate the scale of individual populations. In chapter 2, there was a positive relationship between over-prediction of fine-grain occupancy by downscaling models and the dispersal ability of dragonfly species. This relationship provides evidence that dispersal is associated with reduced distribution size at fine spatial grains (fragmented populations). Put another way, dispersive species occupy fewer 1 km^2 cells within each coarser grain cell than their less mobile relatives. Assuming that less persistent habitats tend to be more fragmented at any given time, our results are consistent with the hypotheses that increased dispersal ability has evolved in species that exploit less stable and predictable habitats in space and time, with consequences including distributions being closer to climatic equilibrium and better tracking of climate change (Hof *et al.* 2012; Grewe *et al.* 2012).

In chapter 3, I focus on the Brindled Green moth and quantified the species' associations with woodland cover, climate and elevation. The distribution of the Brindled Green reaches a range limit in northern Britain, suggesting that climate is a limiting factor. However, one surprising outcome of Chapter 3 is that the Brindled Green is much less likely to occupy grid cells at higher latitudes than our species-environment relationship would predict, suggesting climate, elevation and landcover are not sufficient to explain the northern range limit. Despite the fact that our environmental covariates were chosen to capture as much as possible of what is known about the ecology of the Brindled Green moth, additional factors are clearly shaping the distribution of the Brindled Green that are not captured in our species distribution model. Moreover, there was no clear relationship between mean annual temperature and probability of occurrence for the Brindled Green, despite the fact that temperature is usually a strong predictor of the distribution of butterflies (Warren *et al.* 2001) and moths (Pollard 1988) at their northern range limits. Indeed in chapter 5, climate dissimilarity explained a significant amount of spatial variation in community composition of macro-moths, but clearly not all species contribute equally to this pattern.

6.6 Addressing false absences in biological records

The preceding chapters have demonstrated that biological records can be used to address a range of ecological questions. This is reassuring given the huge volumes of opportunistic biological records that are currently being generated by citizen science projects. In the opening chapter, I discussed the Wallacean shortfall and some of the issues associated with biological records that can bias estimates of species distributions. As spatial patterns in biodiversity have been the focus of this thesis, my main concern has been spatial variation in recording activity, which lead to false absences in species distribution data. In this section I discuss the approaches I used to deal with these false absences, provide some examples of how false absences can affect conclusions and identify some future avenues for improving our use of biological records for understanding species distributions.

When species distributions are mapped at coarser grains, there is less uncertainty about whether absences are true absences or false absences. In chapter 2, I attempted to estimate the occupancy of British Odonata at fine spatial grains, using downscaling models. These models first coarsen species distributions to grains where false absences become less pervasive and then extrapolate the relationship between spatial grain and occupancy to finer spatial grains. A key finding of chapter 2 was that the best performing Hui model was able to make reasonable predictions of fine grain occupancy, suggesting downscaling can go some way to mitigating the false absences in fine grain biological records and thereby improve our estimates of distribution size. A limitation of this approach, however, is that species occurrence records are often point samples, collected with good spatial precision and this information is discarded when the records are aggregated into coarser grain maps. As such there is likely to be limit on how much of this information can be recaptured, especially with no environmental information to guide fine grain predictions.

In chapter 3, I approached the issue of false absences with a different method. Using a hierarchical Bayesian model (Beale observer effort model), I used information that can be easily extracted from biological records to model the relationship between recording effort (number of visits) and the probability of that a species is recorded, given that it was there. A key finding was that the model identified grid cells with high predicted probability of occurrence, but with no records for the Brindled Green moth, potentially indicating models such as these could be a useful tool in guiding recording activity towards areas of high suitability. One avenue for improving this method of filling in the gaps in species distributions would be to use a method which can incorporate information from multiple sources, even when the data are sampled at different spatial scales and with different sampling protocols. For example, abundance data for the Brindled Green from the RIS could be used to inform the predictions using biological records from the NMRS. Such an approach has recently been attempted using a hierarchical Bayesian model combining data from standardised transects in the UK Butterfly Monitoring scheme and opportunistic data from Butterflies for the New Millennium atlas. The model and was able to predict spatial and temporal variation in abundance of the Gatekeeper butterfly over large spatial extents (Pagel *et al.* 2014).

During the course of this thesis, I have also explored how false absences in biological records can affect estimates of β-diversity (chapter 4) and conclusions about the environmental and spatial correlates of β-diversity (chapter 5). In chapter 4, I used simulated species assemblages to test two sampling properties of β-diversity metrics and found that metrics that are more sensitive to turnover in rare species, are also more positively biased by false absences when there is undersampling. In chapter 5, I then applied a selection of these metrics to biological records from the National Moth Recording Scheme (NMRS) and to standardised samples from the Rothamsted Insect Survey (RIS) and modelled spatial patterns in β-diversity as a function of environmental and spatial variables. The most striking finding was the much greater explanatory power of models when standardised recording protocols were used to estimate spatial patterns of β-diversity. Moreover, geographical distance is likely to be strongly associated with spatial variation in recording effort in the Britain in the NMRS. Indeed geographical distance became a much more important predictor of β-diversity in NMRS, suggesting recording effort may be confounded with geographical distance. Together the finding of chapters 4 and 5 underscore that methods to account for false absences are essential for unbiased estimates of spatial patterns of β-diversity (Chao *et al.* 2006) and for our understanding of the environmental and spatial drivers of these patterns (Rota *et al.* 2011; Lahoz-Monfort *et al.* 2014). The hierarchical Bayesian framework for modelling observer effort has yet to be applied when estimating *β*-diversity and would be an important step towards using biological records for this purpose.

6.7 Concluding remarks

The scale-dependence of biodiversity patterns is both a challenge and a promising tool for ecologists. Spatial scale has yet to be fully integrated into biodiversity theory. Moreover, effective conservation measures are limited by uncertainty about the spatial scales at which ecological processes operate and at which species use and respond to their environment. However, spatial-scaling patterns also offer an opportunity to address the gaps in our knowledge of species distributions. Coupled with biological records over large spatial extents and the statistical tools to deal with biases in our data, spatial scaling patterns are one way to link ecological patterns and processes across sub-disciplines in ecology and develop a truly unified theory of biodiversity.

6.8 References

Baselga, A., Gomez-Rodriguez, C. & Vogler, A.P. (2015). Multi-hierarchical macroecology at species and genetic levels to discern neutral and non-neutral processes. *Global Ecology and Biogeography*, **24,** 873–882.

Beck, J., Ballesteros-Mejia, L., Buchmann, C.M., Dengler, J., Fritz, S.A., Gruber, B., Hof, C., Jansen, F., Knapp, S., Kreft, H., Schneider, A.-K., Winter, M. & Dormann, C.F. (2012). What's on the horizon for macroecology? *Ecography*, **35**, 673–683.

Brown, J.H. (1999). Macroecology : Progress and Prospect. *Oikos*, **87**, 3–14.

Chao, A., Chazdon, R.L., Colwell, R.K. & Shen, T.-J. (2006). Abundance-based similarity indices and their estimation when there are unseen species in samples. *Biometrics*, **62**, 361–71.

Chase, J.M. (2014). Spatial scale resolves the niche versus neutral theory debate. *Journal of Vegetation Science*, **25**, 319–322.

Chust, G., Irigoien, X., Chave, J. & Harris, R.P. (2013). Latitudinal phytoplankton distribution and the neutral theory of biodiversity. *Global Ecology and Biogeography*, **22**, 531–543.

DeAngelis, D.L. & Grimm, V. (2014). Individual-based models in ecology after four decades. *F1000prime Reports*, **6**, 39.

Fisher, C.K. & Mehta, P. (2014). A phase transition between the niche and neutral regimes in ecology. *Proceedings of the National Academy of Sciences*, **111**, 13111–13116.

Fung, T., Fletcher, C.D., Ryan, A., Avenue, G. & Ehsan, S.D. (2016). Reproducing static and dynamic biodiversity patterns in tropical forests: the critical role of environmental variance.

Garzon-Lopez, C.X., Jansen, P. a., Bohlman, S. a., Ordonez, A. & Olff, H. (2014). Effects of sampling scale on patterns of habitat association in tropical trees.

Journal of Vegetation Science, **25**, 349–362.

Gotelli, N.J., Graves, G.R. & Rahbek, C. (2010). Macroecological signals of species interactions in the Danish avifauna. *Proceedings of the National Academy of Sciences of the United States of America*, **107**, 5030–5035.

Gravel, D., Canham, C.D., Beaudet, M. & Messier, C. (2006). Reconciling niche and neutrality: The continuum hypothesis. *Ecology Letters*, **9**, 399–409.

Grewe, Y., Hof, C., Dehling, D.M., Brandl, R. & Brändle, M. (2012). Recent range shifts of European dragonflies provide support for an inverse relationship between habitat predictability and dispersal. *Global Ecology and Biogeography*, **22**, 403–409.

Grimm, V. & Railsback, S. (2005). *Individual-based modelling and ecology*. Princeton University Press, Princeton.

Hof, C., Brändle, M., Dehling, D.M., Munguía, M., Brandl, R., Araújo, M.B. & Rahbek, C. (2012). Habitat stability affects dispersal and the ability to track climate change. *Biology Letters*, **8**, 639–643.

Hortal, J., Roura-Pascual, N., Sanders, N.J. & Rahbek, C. (2010). Understanding (insect) species distributions across spatial scales. *Ecography*, **33**, 51–53.

Jackson, H.B. & Fahrig, L. (2014). Are ecologists conducting research at the optimal scale? *Global Ecology and Biogeography*, **24**, 52–63.

Kalyuzhny, M., Kadmon, R. & Shnerb, N.M. (2015). A neutral theory with environmental stochasticity explains static and dynamic properties of ecological communities. *Ecology Letters*, **18**, 572–580.

Keith, S.A., Webb, T.J., Böhning-Gaese, K., Connolly, S.R., Dulvy, N.K., Eigenbrod, F., Jones, K.E., Price, T., Redding, D.W., Owens, I.P.F. & Isaac, N.J.B. (2012). What is macroecology? *Biology Letters*, **8**, 904–6.

Lahoz-Monfort, J.J., Guillera-Arroita, G. & Wintle, B. A. (2014). Imperfect detection impacts the performance of species distribution models. *Global Ecology and Biogeography*, **23**, 504–515.

Leibold, M. a., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J.M., Hoopes, M.F., Holt, R.D., Shurin, J.B., Law, R., Tilman, D., Loreau, M. & Gonzalez, A. (2004). The metacommunity concept: a framework for multi-scale community ecology. *Ecology Letters*, **7**, 601–613.

Matthews, T.J. & Whittaker, R.J. (2014). Neutral theory and the species abundance distribution: Recent developments and prospects for unifying niche and neutral perspectives. *Ecology and Evolution*, **4**, 2263–2277.

May, R.M. (1975). *Stability and complexity in model ecosystems*. Princeton University Press, Princeton.

May, F., Wiegand, T., Lehmann, S. & Huth, A. (2016). Do abundance distributions and species aggregation correctly predict macroecological biodiversity patterns in tropical forests? *Global Ecology and Biogeography*, **25,** 575-585.

McGill, B.J. (2010a). Matters of scale. *Science*, **328**, 575–6.

McGill, B.J. (2010b). Towards a unification of unified theories of biodiversity. *Ecology Letters*, **13**, 627–42.

McGill, B.J., Etienne, R.S., Gray, J.S., Alonso, D., Anderson, M.J., Benecha, H.K., Dornelas, M., Enquist, B.J., Green, J.L., He, F., Hurlbert, A.H., Magurran, A.E., Marquet, P.A., Maurer, B.A., Ostling, A., Soykan, C.U., Ugland, K.I. & White, E.P. (2007). Species abundance distributions: moving beyond single prediction theories to integration within an ecological framework. *Ecology Letters*, **10**, 995–1015.

McGill, B.J. & Nekola, J.C. (2010). Mechanisms in macroecology: AWOL or purloined letter? Towards a pragmatic view of mechanism. *Oikos*, **119**, 591–603.

Pagel, J., Anderson, B.J., O'Hara, R.B., Cramer, W., Fox, R., Jeltsch, F., Roy, D.B., Thomas, C.D. & Schurr, F.M. (2014). Quantifying range-wide variation in population trends from local abundance surveys and widespread opportunistic occurrence records. *Methods in Ecology and Evolution*, **5**, 751–760.

Pearson, R.G. & Dawson, T.P. (2003). Predicting the impacts of climate change on the distribution of species : are bioclimate envelope models useful ? *Global Ecology and Biogeography*, **12**, 361–371.

Pollard, E. (1988). Temperature, Rainfall and Butterfly Numbers. *The Journal of Applied Ecology*, **25**, 819–828.

Rota, C.T., Fletcher, R.J., Evans, J.M. & Hutto, R.L. (2011). Does accounting for imperfect detection improve species distribution models? *Ecography*, **34**, 659–670.

Sandel, B. (2015). Towards a taxonomy of spatial scale-dependence. *Ecography*, **38**, 358–369.

Stillman, R.A. & Goss-Custard, J.D. (2010). Individual-based ecology of coastal birds. *Biological Reviews*, **85**, 413–434.

Tilman, D. (1982). *Resource competition and community structure*. Princeton University Press, Princeton.

Tucker, C.M., Shoemaker, L.G., Davies, K.F., Nemergut, D.R. & Melbourne, B.A. (2015). Differentiating between niche and neutral assembly in metacommunities using null models of *β*-diversity. *Oikos*, **125,** 1–12.

Vergnon, R., Dulvy, N.K. & Freckleton, R.P. (2009). Niches versus neutrality: Uncovering the drivers of diversity in a species-rich community. *Ecology Letters*, **12**, 1079–1090.

Violle, C., Enquist, B.J., McGill, B.J., Jiang, L., Albert, C.H., Hulshof, C., Jung, V. & Messier, J. (2012). The return of the variance: Intraspecific variability in community ecology. *Trends in Ecology and Evolution*, **27**, 244–252.

Warren, M.S., Hill, J.K., Thomas, J. a, Asher, J., Fox, R., Huntley, B., Roy, D.B., Telfer, M.G., Jeffcoate, S., Harding, P., Jeffcoate, G., Willis, S.G., Greatorex-Davies, J.N., Moss, D. & Thomas, C.D. (2001). Rapid responses of British butterflies to opposing forces of climate and habitat change. *Nature*, **414**, 65–69.

Wilson, R.J., Thomas, C.D., Fox, R., Roy, D.B. & Kunin, W.E. (2004). Spatial patterns in species distributions reveal biodiversity change. *Nature*, **432**, 393–396.