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thesis abstract

Analysing and modelling the impact of habitat fragmentation on species diversity: a macroecological perspective

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Abstract. My research aimed to examine a variety of macroecological and biogeographical patterns using a large number of purely habitat island datasets (i.e. isolated patches of natural habitat set within in a matrix of human land uses) sourced from both the literature and my own sampling, with the objective of testing various macroecological and biogeographical patterns. These patterns can be grouped under four broad headings: 1) species–area relationships (SAR), 2) nestedness, 3) species abundance distributions (SADs) and 4) species incidence functions (function of area). Overall, I found that there were few hard macroecological generalities that hold in all cases across habitat island systems. This is because most habitat island systems are highly disturbed environments, with a variety of confounding variables and 'undesirable' species (e.g. species associated with human land uses) acting to modulate the patterns of interest. Nonetheless, some clear patterns did emerge. For example, the power model was by the far the best general SAR model for habitat islands. The slope of the island species–area relationship (ISAR) was related to the matrix type surrounding archipelagos, such that habitat island ISARs were shallower than true island ISARs. Significant compositional and functional nestedness was rare in habitat island datasets, although island area was seemingly responsible for what nestedness was observed. Species abundance distribution models were found to provide useful information for conservation in fragmented landscapes, but the presence of undesirable species substantially affected the shape of the SAD. In conclusion, I found that the application of theory derived from the study of true islands, to habitat island systems, is inappropriate as it fails to incorporate factors that are unique to habitat islands.

Keywords. Fragmentation, functional nestedness, gambin, habitat islands, incidence function, island biogeography, nestedness, species abundance distribution, species–area relationship.

Introduction

Islands have long been considered natural laboratories for ecological research because they are discrete and quantifiable units and cover a wide range of abiotic conditions – thus providing researchers with ideal systems to test and develop ecological theory (Darwin 1859, MacArthur and Wilson 1967, Whittaker and Fernández-Palacios 2007). However, until the late 1960s island biogeography, and island research more generally, was focused primarily on the study of true islands. True islands can be defined as any set of islands surrounded by a matrix of marine water (i.e. continental fragments, continental shelf islands and oceanic islands; see Whittaker and Fernández-Palacios 2007). During the 1970s, the extent of anthropogenic habitat destruction and fragmentation was increasingly becoming the focus of attention (see Harris 1984). The process of habitat fragmentation results in the creation of isolated patches of natural habitat set within in a matrix of human land uses (e.g. agriculture, urban land uses). These isolated patches came to be viewed as habitat islands; isolated in a sea of man-made habitats (Preston 1962, MacArthur et al. 1972). Thus, researchers began to apply island biogeography theory to the study of habitat islands, both from a theoretical and an applied perspective

(Diamond 1975, Wilson and Willis 1975, Harris 1984). Whilst the field has progressed, habitat island research is still largely studied through the lens of island biogeography theory derived from the study mainly of islands in oceans (e.g. MacArthur and Wilson 1967). For example, most meta-analyses of macroecological patterns on islands have incorporated large numbers of such 'real' island datasets (e.g. Ulrich and Gotelli 2007, Triantis et al. 2012), meaning that deriving any inferences of relevance to habitat islands is problematic. Furthermore, traditionally, habitat islands have been the focus of less research effort than true islands in the biogeographical literature.

It has become increasingly realised that habitat islands differ from true islands in many ways (Watling and Donnelly 2006, Laurance 2008), for example in terms of the surrounding matrix, edge effects, habitat connectivity and the main processes driving community assembly (see Laurance 2008). This is not to say that traditional island theory is unsuitable in the context of habitat islands; the interplay between immigration and extinction is a primary determinant of richness dynamics in habitat islands, for instance. Rather, it is the case that there is a need to develop a theory of habitat island biogeography above and beyond that of traditional island biogeography. A necessary first step towards this goal is defining exactly what is meant by the term 'habitat islands' as opposed to true islands.

The difference between true and habitat islands is somewhat subjective. Clearly, the archipelago of Hawaii can be classified as a set of oceanic islands, whilst South American Atlantic forest fragments surrounded by an agricultural matrix are clearly habitat islands. However, in some cases the distinction is not as clear. For example, increasingly many rainforest landscapes have been fragmented by the creation of dams and reservoirs, resulting in the flooding of the surrounding landscape, and the creation of patches of forest surrounded by a matrix of water. Thus, strictly speaking these fragments are true islands in that they are surrounded by water (Whittaker and Fernández-Palacios 2007), but in many ways the islands are more akin to habitat islands, such as in terms of the dominant assembly processes and sizes of the islands. In Matthews (2015), I defined habitat islands as any island of natural habitat not surrounded by a marine water matrix, thus excluding oceanic and continental shelf islands but including flooded forest fragments. I use the same the definition here. The exact classification of true and habitat islands is contentious (see Whittaker and Fernández-Palacios 2007), and it is likely that certain readers will disagree with the definition I have used. However, the use of a slightly different definition would not affect most of the data in my research, and thus would be unlikely to alter the main findings of the thesis.

In order to a develop habitat island biogeography theory it is necessary to determine whether there are any general rules governing species' distributions and diversity patterns in habitat islands (Şekercioğlu and Sodhi 2007). In short, a macroecological perspective is required. However, the majority of habitat island research to date has been undertaken on small to medium scales, generally in single systems. Studying diversity patterns in habitat islands from a macroecological perspective has a number of advantages. For instance, by using a large number of habitat island datasets it is possible to elucidate any general patterns which are consistent across taxa and habitat island types; or to identify any systematic variation across taxa and island types. Researchers have been studying individual habitat island systems for decades (e.g. Brown 1971, Laurance et al. 2002) and a large number of published datasets exist. However, so far it has been rare to bring together such data in any macroecological synthesis. As Whittaker et al. (2005, p. 13) note, "numerous habitat island data sets have been collected, and so what is needed is not necessarily new field efforts, but more concerted efforts in analysis and synthesis, to tease out the scale sensitivity of habitat island data sets, particularly, the form of their [species–area relationship], and their compositional structure."

The overarching aim of my thesis (Matthews 2015) is to develop a macroecological theory of habitat islands through an investigation of different biogeographical and macroecological

patterns (and processes) in multiple habitat island datasets. Through this endeavour, I aim to determine whether (a) there are any general rules/patterns regarding species' distributions in habitat islands, and (b) it is possible to derive any information which can benefit biodiversity management and conservation in patchy landscapes.

Methods

From a comprehensive search of the literature I sourced 207 habitat island datasets, comprising 121 vertebrate, 47 invertebrate and 39 plant datasets. The split by habitat was 127 forest, 12 mountaintop, 16 grassland, 35 urban and 17 'other' datasets. These datasets were sourced from published studies and the source paper citations, along with more extensive information regarding the dataset characteristics (e.g. number of islands) can be found in the appendix of Matthews et al. (2015a). These datasets were combined with four datasets I collected myself through two seasons of fieldwork, sampling birds in forest fragments (approximately 40 in each landscape) in four different fragment landscapes across Europe (Norway, Spain, France and the UK; see Matthews et al. 2015a for full sampling methods). Further data were sourced from colleagues; including a well identified dataset of arthropods (90,000 individuals) in 18 Laurisilva forest fragments in the Azores (Borges et al. 2005, Matthews et al. 2014a).

Using this collection of habitat island datasets I was able to examine a wide variety of different macroecological and biogeographical patterns. These can be grouped under four broad headings:

1. Species–area relationship (SAR). I examined a number of SAR-related questions using a variety of multi-model inference methods (Burnham and Anderson 2002). These questions included: what is the best model/functional form of island SARs in habitat islands (Matthews et al. 2015b)? Is there a threshold habitat island area below which the form of the ISAR changes (Matthews et al. 2014b)? Do habitat generalist species act to modulate the shape of the ISAR (Matthews et al. 2014c)? How do island species–area relationships (ISARs; i.e. the number of species occurring within each of a set of islands plotted against the area of each isolate) differ from species accumulation curves (SACs; i.e. plots of increasing cumulative species number with sampling effort; Whittaker and Matthews 2014)?

2. Nestedness patterns. I was able to undertake a comprehensive evaluation of compositional nestedness (using the NODF metric and the PP null model algorithm; see Ulrich and Gotelli 2012) in the roughly 100 habitat island datasets that included full species lists (Matthews et al. 2015b). Recent methodological advances have enabled workers to test for different types of nestedness, including functional nestedness (i.e. nestedness analysis of species' similarity in terms of their functional traits; Melo et al. 2014). I collected measurements of eight continuous traits for over 1000 bird species, and used these to examine the prevalence of functional nestedness in a subset of 18 habitat island datasets (Matthews et al. 2015c). For both nestedness analyses I also examined the role of island area in explaining any observed nestedness.

3. Species abundance distributions (SADs). The extensive nature of the Azorean arthropod dataset (Borges et al. 2005) allowed me to test various hypotheses regarding species abundance distributions (SADs) in fragmented landscapes. In particular, I assessed whether 'undesirable' species (e.g. introduced species, and those species associated with human land uses) act to change the shape of the SAD, and underpin commonly observed multimodal SADs (Dornelas and Connolly 2008, Matthews et al. 2014d). In addition, I derived the maximum likelihood function for the gambin SAD model (Ugland et al. 2007), integrated it into an R package ('gambin'), and performed an extensive comparative analysis of the fit of gambin against competitor SAD models (Matthews et al. 2014a, Matthews 2015: Chapter 10). I also: a) reviewed the various methods for fitting and comparing SAD models (Matthews and Whittaker 2014a), b) reviewed SADs in the context of neutral theory (Matthews and Whittaker 2014b), and c) argued the case for an increased uptake of SAD models in applied ecological re-

search (Matthews and Whittaker 2015).

4. Species' incidence function analysis. Using my fieldwork datasets, I attempted to answer the question of whether a species' incidence function (i.e. a function specifying the probability of occurrence of species at any island area value; e.g. see Watson et al. 2005) is a constant trait across the species' range, or whether there is some sort of systematic variation in incidence functions across the range (Matthews 2015: Chapter 12). The four landscapes in which I collected field data (see above) were selected such that, for four target bird species, two of the landscapes were situated in the range core of these species, and two landscapes were located in the range edge. Based on the core-abundance hypothesis (see Gaston 2003), I hypothesised that species should be more tolerant of fragmentation at the range core relative to the edge, such that in core landscapes, species would have a higher incidence probability in smaller fragments.

Results

Whilst the identification of clear patterns was problematic, some generalities did emerge from my analyses. For example, convex models, specifically the power model, are by the far the best performing ISAR models, as judged by my habitat island datasets (Matthews et al. 2015a, Matthews 2015: Chapter 5). The *z* value of the power model is related to island type, and increased from habitat islands to oceanic islands, and within habitat islands increased with increasing hostility of the surrounding matrix (Figure 1; Matthews et al. 2015a, Matthews 2015: Chapter 5). I did not find much evidence of thresholds in the ISAR, although various methodological issues were identified that made classification of thresholds problematic (Matthews et al. 2014b, Matthews 2015: Chapter 4). I also found that the ISAR and SAC are not equivalent SAR types, and that the difference between them is linked to the degree of compositional nestedness in the system (Matthews et al. in review, Matthews 2015: Chapter 6). Furthermore, the ISAR was often a poor predictor of the total number of species in an archipelago.

Undesirable species (e.g. invasives and generalists) affected both the slope of the ISAR and the shape of the SAD. I found that generalist species depress the slope of the ISAR, which can mask important patterns of decline in specialist species in habitat islands (Matthews et al. 2014c, Matthews 2015: Chapter 7). Concerning the SAD, I found that a large proportion of the SADs of arthropods in Azorean Laurisilva forest fragments were significantly bimodal, and that this bimodality was largely driven by the amalgamation of different types of species in a sample (e.g. core and satellite species; Matthews et al. 2014d, Matthews 2015: Chapter 11).

Significant compositional nestedness in habitat island datasets was relatively rare, although island area was generally important in accounting for the compositional nestedness that was observed (Matthews et al. 2015b, Matthews 2015: Chapter 8). In addition, I found a strong link between the degree of compositional nestedness in a set of habitat islands and the number of protected areas required in order to represent all species in a dataset at least once (i.e. the answer to the 'minimum set reserve selection problem'; Watson et al. 2011; see Fig. 2). The degree of significant functional nestedness observed was dependent on the null model used, a common finding in nestedness analyses (e.g. Ulrich and Gotelli 2007, 2012), but again island area was important in accounting for functional nestedness (Matthews et al. 2015c, Matthews 2015: Chapter 9).

Finally, the incidence function analyses were inconclusive (Matthews 2015: Chapter 12). For two of the four species, the hypothesised range effect was apparent; that is, for any given small fragment, there was a higher probability of presence in the range core landscapes than in the range edge landscapes. However, the opposite pattern was found for the other two species, and thus the hypothesised range effect cannot be considered universal.

Discussion

Overall, my results indicate that it is difficult to define neat, well-specified generalities that hold in all cases in habitat islands. This is a characteristic of most ecological systems, but seems particularly problematic in habitat islands. Whilst in most instances it was not possible to explicitly test this

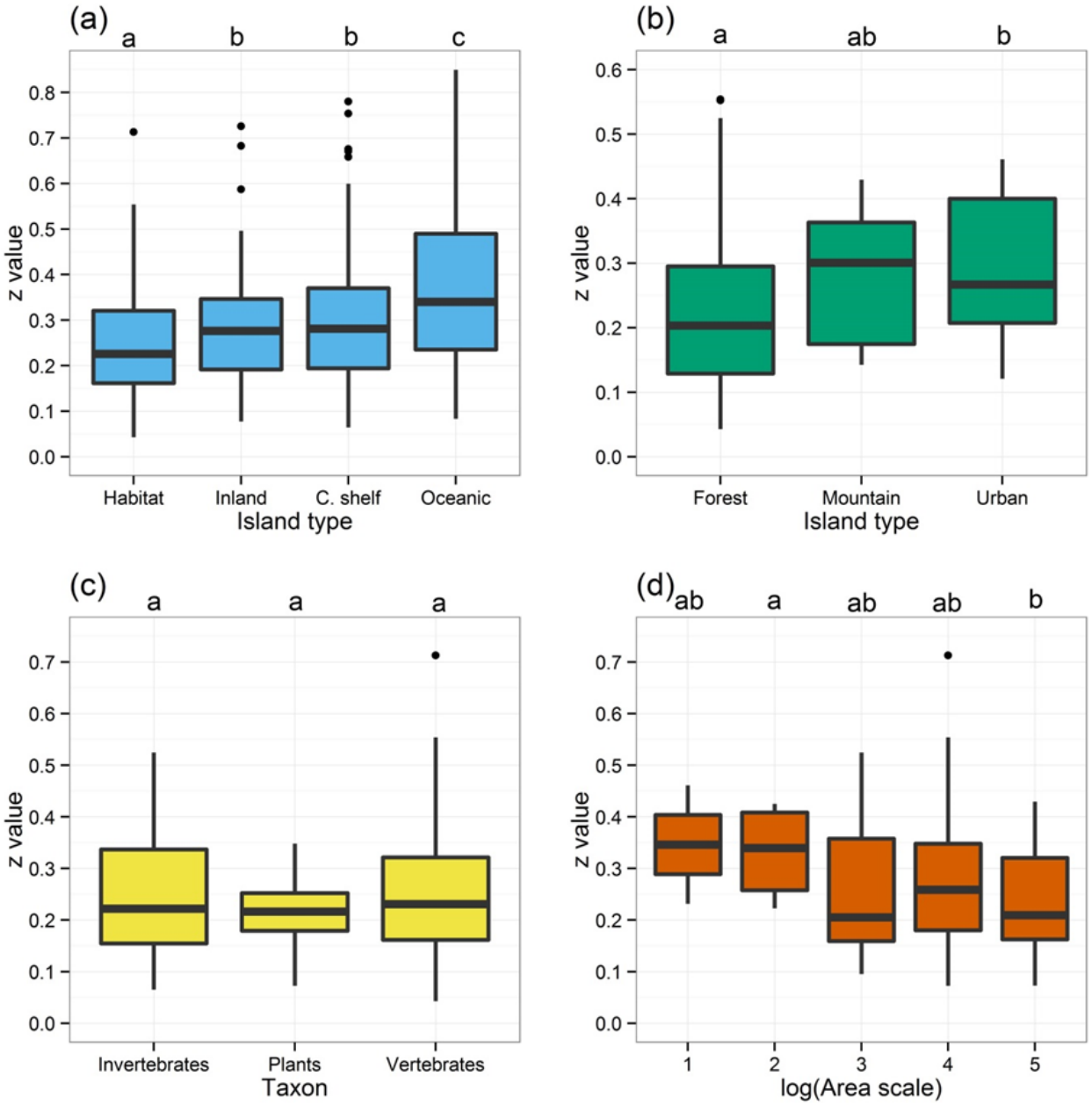

Figure 1. Variation in the *z* parameter of the power (log–log) model across: (a) all island types, (b) different habitat island types, (c) different major taxa, and (d) area scale (natural logarithm of: the area of the largest island in a dataset divided by the area of the smallest island). Note that (b)–(d) were calculated using only habitat island datasets. For all plots, only datasets with significant *z* values ($P < 0.05$) were included. For clarity, the box plots were constructed after omitting the small number of *z* values < 0 (all subsequent statistics were performed using the full set of data). Thus, in (a) there were 132 habitat island, 125 oceanic island, 58 inland water-body ('Inland'), and 277 continental-shelf island datasets ('C. shelf'). In (b) there were 75 forest, 12 mountaintop and 21 urban habitat island datasets. In (c) there were 26 invertebrate, 20 plant and 86 vertebrate datasets. Area scales larger than 5 have been omitted. The box plots display the median (thick black line), the first and third quartiles (thin black box). The whiskers extend from the hinge to the highest value that is within 1.5 multiplied by the inter quartile range, of the hinge. Points beyond the whiskers ('outliers') are indicated by solid dots. Significant differences in *z* values between dataset categories are displayed as different lowercase letters above the box plots. Values that do not significantly differ between categories have the same lowercase letters. Taken from Matthews et al. (2015a).

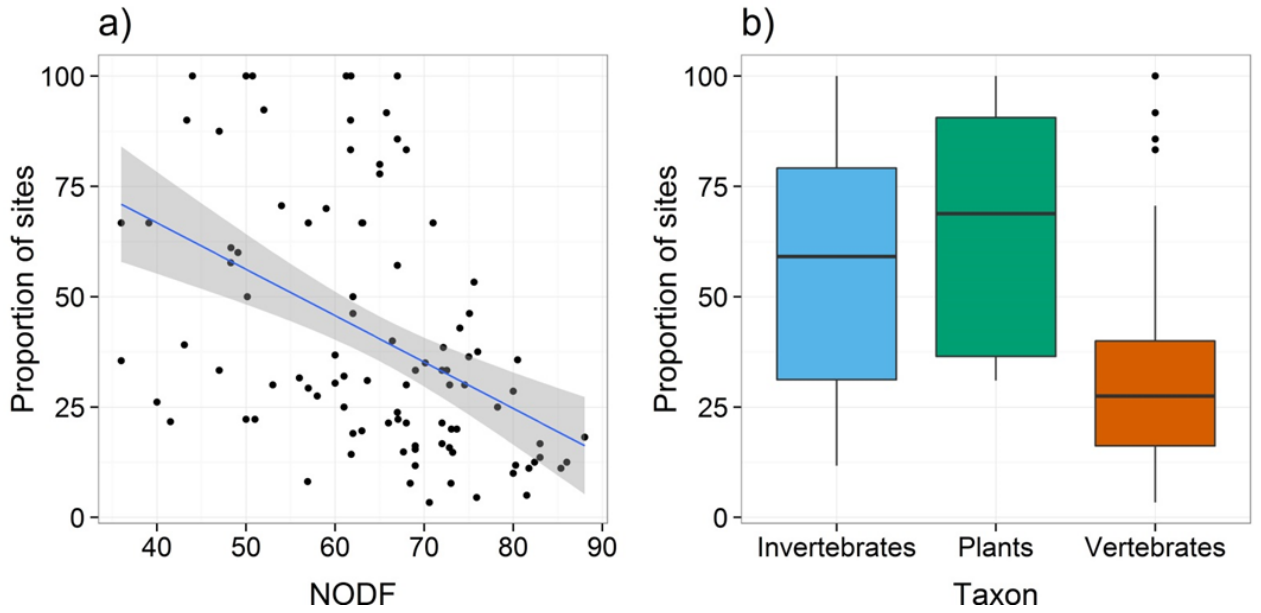

Figure 2. **(a)** The relationship between the smallest proportion of sites required to represent all species in a dataset (i.e. the solution to the minimum set problem) and the NODF value (maximally packed matrix), and **(b)** the variation in this proportion across taxa, for 97 habitat island datasets. To determine the solution to the minimum set problem we first ran an algorithm to determine the smallest number of habitat islands required in order to include all the species in a dataset. This number was then represented as a proportion of the total number of sites in the dataset. In (a), the blue line represents the fit of a standard linear model, and the grey shading represents the 95% confidence interval around this line. The box plots are as explained in Figure 1. Taken from Matthews et al. (2015b).

hypothesis, it appears that a number of confounding variables (e.g. hunting pressure) affect the shape and form of macroecological patterns in habitat islands (e.g. Matthews et al. 2014b, Matthews et al. 2015a). In many ways this is to be expected because by definition most habitat island systems are highly disturbed anthropogenic environments (Fischer and Lindenmayer 2007). It is also apparent that there are many differences between true and habitat islands, not least that the issue of confounding variables appears to be more problematic in habitat islands. As such, it does not appear wise to continue to use the results of studies from islands in oceans to guide habitat island research and conservation (see Laurance 2008).

Many of the macroecological and biogeographical patterns examined in Matthews (2015) are interlinked (Blackburn and Gaston 2001). For example, the majority of habitat island datasets do not appear to be compositionally nested, underpinning the observed differences between the ISAR and the SAC, for a given dataset. Furthermore, one factor contributing to the non-nestedness of most datasets may be the large number of generalist and tourist species present in the smaller patches relative to the larger patches. The presence of these species also acts to depress the slope of the ISAR, and results in the multimodal SAD patterns I observed (Matthews 2015).

The destruction and fragmentation of natural habitat is the leading driver of the current extinction crisis (Wilcove 1987, Sala et al. 2000). My various analyses have shown that macroecological and biogeographical analyses of habitat island datasets can generate useful information for the conservation and management of biodiversity in patchy landscapes (Gaston and Blackburn 2000, Whittaker et al. 2005, Matthews et al. 2014a). For example, the results of Matthews (2015: Chapters 4–7, see also Matthews et al. 2014b, c, Matthews et al. 2015a), in combination with other recent studies (e.g. Guilhaumon et al. 2008, Halley et al. 2013), have enabled the development of a more robust and methodologically sound theory for using SARs in extrapolation exercises (e.g. to predict extinctions), albeit that this remains a work in progress. Furthermore, at a coarse scale, I observed that the *z* value of the ISAR is linked to the type of island, which in turn is linked to the matrix type in

each dataset (Fig. 1), and whilst there was considerable scatter, the slope of the ISAR increased with decreasing matrix permeability, as previously predicted (e.g. Koh and Ghazoul 2010). It follows that improving the quality and permeability of the matrix at fine scales will go some way towards ameliorating the effects of habitat loss and fragmentation (Pereira and Daily 2006). This area of research is the focus of countryside biogeography studies, which, amongst other things, have attempted to adapt traditional island theory in order for it to be more applicable to terrestrial systems and habitat islands (Pereira and Daily 2006, Koh and Ghazoul 2010). To take another example, at various points throughout Matthews (2015) I have highlighted how the SAD can be an important tool in applied ecology, providing information on the commonness and rarity of species that is overlooked when simple metrics such as species richness are used (Matthews and Whittaker 2015).

Although I did not observe the hypothesised systematic variation in incidence functions across the range, it was apparent that incidence function model parameters can vary quite substantially across space for certain species. For example, for robin (*Erithacus rubecula*), the critical island area value (CIV; i.e. the island area value which corresponds to a 50% probability of occurrence, according to the model) in the French landscape was <0.01 ha, whilst the CIV value in the Norwegian landscape was 28.5 ha. This finding reinforces the arguments of previous authors who have called for protected areas and conservation plans for particular species to be focused in areas within a species' range where the species has higher abundance and incidence (Gaston 2003).

As most of the analyses in my research were meta-analyses using published datasets, it is possible that the composition of datasets could have affected my results. First, including studies which used an inappropriate sampling method may result in data that generate or contain spurious patterns. For example, Whittaker (2010) argued that many datasets used in productivity–richness meta-analyses were generated as a by-product of the analyses of the source paper, i.e. the generation of these data was not the primary aim of the study. In such cases, the data are much more likely to contain problems. Thus, in my analyses I attempted to ensure that I did not include data that were generated as a by-product of sampling designed for other purposes. Additionally, where possible, I tried to determine whether studies used proportional sampling or not. Whilst it is possible that others attempting to replicate my analyses may have different opinions on data suitability, I believe that this is not likely to affect more than a handful of the decisions on dataset screening, and that the results presented here should be immune to this particular potential source of bias.

One further issue relates to how I attempted to elucidate variations in different macroecological patterns across taxa. I generally adopted a deconstruction approach, whereby I split the datasets into three broad taxa (i.e. vertebrates, invertebrates and plants) and then analysed patterns within each of these taxa individually. Generally speaking this approach failed to identify interesting taxon-specific patterns (e.g. Fig. 1c, Fig. 2b). Whilst it is possible that no such patterns exist, my approach suffers from the problem that these three categories are very coarse. There is a huge variation within each category, in terms of life history, dispersal ability and scale of perception. However, such coarse groupings were necessary in order to avoid samples sizes too small to enable accurate statistical inference. Thus, future research on these types of macroecological questions should focus on finer-scale taxonomic delineation.

Another limitation of Matthews (2015) is that a majority of habitat island datasets (61%) were classified as 'forest' habitat islands. It is possible that this may have influenced my findings, particularly as the matrix type in most of these studies was the same (agricultural land use). Whilst not ideal, this issue was unavoidable because most habitat island studies focus on forest fragments. Even with this uneven distribution of habitat island types, I found significant differences between island types (e.g. Fig. 1b).

Finally, my research has been largely pattern oriented, with less focus on processes. As

such, a more mechanistic approach to habitat island research is needed in future, because the identification of macroecological patterns, whilst interesting, is of little practical value without the identification of the processes driving the patterns (Gaston & Blackburn 2000). Whilst I have attempted to examine mechanisms where possible, I have been constrained by the lack of available data. In particular, there is a need to collect more environmental data from fragmented landscapes, alongside species lists. Approaches such as process-based models and experimental landscape manipulation should allow future workers to better infer the roles of individual variables in driving diversity dynamics in habitat islands.

Regarding strategic conservation planning (see Watson et al. 2011), I argue that, depending on the data at hand, managers and conservation planners would be better served by avoiding making *a priori* assumptions about species' distributions in habitat islands. In cases where a set of habitat islands is to be destroyed, for example for logging concessions, and an opportunity for conserving a subset of islands is provided, it is likely that surveys will be conducted for at least certain taxa. With such survey data it is relatively simple to construct SACs, compute nestedness metrics, and run minimum set reserve planning algorithms (like that developed in Matthews 2015: Chapter 8) – which may provide a coherent conservation strategy for the region at hand. In cases where there are no survey data, and no time to collect such data, the situation is obviously more problematic. In these cases, my results indicate that, without evidence to the contrary, systems should not be assumed to be nested *a priori*. A sensible strategy would then be to conserve the largest island possible (ideally the largest, but this is unlikely to be an available option in many instances) alongside a small set of smaller islands covering a range of major habitats (i.e. those habitats easily identifiable without site-specific sampling data). It is hoped that the results of Matthews (2015) will act as a catalyst for a more macroecological approach to habitat island research, and a starting point for the development of an integrated theory of habitat islands.

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