Species Diversity in Discrete Habitat Networks

by

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Abstract

Human activities are increasingly fragmenting the natural world. A unifying theme in this thesis is understanding the expected diversity within artificially or naturally discrete habitat networks. I start by testing a common expectation regarding the species composition of small habitat patches, which are usually assumed to support only common species. In a meta-study of 175 published studies, I found that in over 80% of datasets, some species were found only in the smallest patches. Moreover, loss of only the smallest patches comprising less than 20% of total habitat area would remove, on average, 12.7% of species, more than twice the 5.8% predicted from species-area relationships. This suggests that groups of small patches should not be assumed to comprise only common species. I then explored a second commonly held, but little tested, theory - that rapid accumulation of species when patches are combined in small-to-large size order is due to high beta diversity, driven by habitat heterogeneity. Using 38 published abundance datasets, I test competing explanations for the observed difference in the species richness of groups of small patches, relative to the largest patch using path analysis. I found that beta diversity, evenness of species abundance and size-bias in sampling efficiency explain comparable amounts of variation. Both increased and decreased evenness contributed to differences in species richness, suggesting multiple mechanisms contribute to differences in species richness between large and small patches. I conclude that assuming habitat heterogeneity accounts for the rapid accumulation of species when combining patches in small-to-large order is an over-simplification. This chapter also provides the first objective evidence that less effective sampling of larger patches could over-estimate the difference in species richness between groups of small patches and a single large patch. I next used sampling theory to develop and validate a suite of models predicting the expected number of shared species under any spatial and abundance distribution, allowing the effects of sub-division to be distinguished from the effects of habitat loss. The models were validated using empirical and simulated data and predict shared species and total species number in sub-divided habitat with high accuracy ($R^2 > 0.99$, relative root mean square error < 0.05). Using the models, I show that only when individuals are randomly positioned will the number of species be unaffected by sub-division; any amount of intraspecific aggregation results in an increase in the expected species richness of sub-divided, relative to contiguous, habitat of equal total area. In other words, several small patches should contain more species than a single large patch as this is a probable consequence of intraspecific aggregation. Although this does not preclude some independent positive effect of sub-division on species diversity, it is not necessary to invoke such a mechanism to explain the presence of more species in sub-divided habitat. In my final data chapter, I use the new models to explore the effects of habitat loss and sub-division for different spatial and abundance distributions. I simulate the destruction of 20-90% of original habitat area, comparing the number of species that would be present if the remaining proportion of habitat was divided into 1-32 patches. This analysis showed that as the amount of sub-division of a given area increases (i.e., as the remaining habitat is broken into more, but smaller, pieces), the number of additional species reaches a maximum, indicating a diminishing 'benefit'. Second, it showed that under the most even species abundance distributions (hereafter SAD), the loss of 90% of habitat (i.e., 90% of individuals), removed less than 3% of original species, compared with up to 40% under the least even SAD. A general prediction follows, where highly even SAD, (e.g., typical of tropical forest), could suffer few initial extinctions from habitat loss, but be vulnerable to delayed extinction, while less even SAD (e.g., typical of higher latitudes) might face the reverse situation. This thesis makes applied and theoretical contributions to conservation biology by providing insights relating directly to the SLOSS and fragmentation *per se* debates. From an applied perspective, it contributes new understanding relating to rapid species accumulation in small patches. The main theoretical contribution has been the application of sampling theory to predict the expected number of species under sub-division and habitat loss.

Preface

This is an original work by David Charles Deane. Chapter 2 has been published as Deane, D.C. & He, F. (2018) “Loss of only the smallest patches will reduce species diversity in most discrete habitat networks” *Global Change Biology*, Vol. 24 Iss. 12, pp 5802-5814. I was responsible for the concept, all data collation, analysis and interpretation, I prepared the manuscript and was corresponding author. F. He advised on study design, statistical analyses and edited the manuscript.

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I gratefully acknowledge all researchers who made their hard-won datasets available, supporting the types of meta-study undertaken in Chapters 2 and 3. I thank them all for this altruistic contribution to science and hope that my use of their data does this credit.

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I thank He Lab members past and present, but must single out Dingliang for his generosity and willingness to share his encyclopedic technical and theoretical knowledge. I also particularly thank my friends Scott and Pemegul; the former for our countless stimulating conversations ranging from the philosophical to the political and occassionally supernatural; the latter for the laughs, the thoughtful counsel and for occassionally joining us for coffee. From the wider U of A grad student community, I thank my friends April and Baka for their humour, encouragement and inspiration over the many shared drinks both hot and cold. From a personal perspective, I thank my family and friends at home for their support throughout, either by visiting or making time at obscure hours on their weekends to listen with equal patience to my joys and woes. From my heart, I thank all for the wise words you have offered, especially at the most difficult of times. Finally, a special dedication to my Mum, who began her own difficult journey even as this one neared its end for me.

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Context and snapshot of research

At the time of initiating this research, the question of how diversity is affected by sub-division was not only incompletely understood, it was highly controversial. This thesis contributes to resolving this controversy by improving understanding of the expected patterns of diversity in discrete habitat patch networks, both natural and artificial. Central to debate in the contemporary (and historical) literature are two questions: (*i*) the importance – or not – of small patches of habitat for biodiversity conservation and (*ii*) whether the effects of sub-division on species diversity can be interpreted as positive or negative. I address both. After reviewing the theoretical landscape in Chapter 1, I present four chapters, formatted for publication, that address both theoretical and applied aspects of the questions.

- In Chapter 2, I demonstrate that the commonly held notion that small patches contain only common species is typically not correct. The implication is that the loss of groups of small habitat patches – whether naturally occurring or created by fragmentation – can be expected to reduce species representation across habitat networks.
- In Chapter 3, I consider a well-known ecological pattern where groups of small patches usually contain more species than a single large patch of equal total area. I test the most common explanation - beta diversity due to environmental heterogeneity – against three alternative hypotheses. I illustrate the potential for some largely ignored, alternative explanations to contribute to this pattern and show richness differences could be over-estimated due to a size-dependence in sampling efficiency.
- In Chapter 4, I develop an analytical modelling approach to identify the expected effects of habitat sub-division on diversity (as distinct from habitat loss) and validate it using simulated and empirical data. I show that common patterns of species accumulation

among sub-divided habitat are a statistical expectation when intraspecific aggregation is present. I discuss the importance of this finding for the fragmentation *per se* debate.

- In Chapter 5, I apply the modelling framework of Chapter 4 to demonstrate the relative effects of spatial and abundance distributions adding several additional insights to those of Chapter 4.

Finally, in Chapter 6, I review the overall implications of my research for the expectation of species richness in sub-divided habitat. I highlight future directions for investigation and discuss some limitations and uncertainties.

Chapter One: Introduction

1.1 Species conservation in an increasingly patchy world

It has been estimated that by the end of the 20th century, more than half of the terrestrial land surface had become dominated by human land uses (Ellis et al., 2010). As a result of this burgeoning human geographical footprint, it has been argued that conservation reserves will not determine the future of biodiversity (Chazdon et al., 2009, Kareiva and Marvier, 2012, Mendenhall et al., 2014). Rather it will depend on how well diversity can persist in these mixed 'countryside landscapes' (Daily et al., 2001, Pereira and Daily, 2006), where self-assembling pockets of semi-natural habitat persist, immersed in a landscape matrix dominated by human land uses.

My research interests are inspired by recognition that there exists, within those human-dominated landscapes, many different networks of discrete patches of semi-natural habitat. Among these are formerly continuous biomes (e.g., woodland, forest, grassland) that now find themselves as isolated patches, surrounded by other contrasting land cover. But there are also those habitat types, whose patches have always existed in isolation from one another, such as lakes and wetlands. When species' populations within these discrete habitat networks are connected via dispersal, they are referred to as metacommunities (Hanski and Gilpin, 1991, Wilson, 1992). Classical metacommunity ecology essentially emerged as an umbrella framework that integrates many different ecological theories relevant to patchy habitats, including niche theory, mass effects, patch dynamics and competition theory (synthesised in Leibold et al., 2004). Within the metacommunity framework, these theories are understood via their position along three major axes of variation: ecological equivalence of species, dispersal and environmental heterogeneity (Leibold et al., 2004, Logue et al., 2011, Winegardner et al., 2012). What emerges at the intersection of these axes is the distribution of individuals in space and time that determines the patterns of diversity we observe.

Although the metacommunity framework is conceptually appealing, it is not clear how the many constituent theories can be used to understand the effects of habitat sub-division in a predictive sense. In this thesis, my focus is instead on testing the role of different spatial patterns and abundance distributions in leading to the patterns of diversity we observe in sub-divided habitat. In the first two data chapters, I consider all types of discrete habitat networks, natural or artificial, including continental, oceanic and inland island archipelagos, habitat islands and remnant fragments. However, the intensity of debate in the current literature, provided a clear imperative to understand the role of fragmentation (or more neutrally ‘sub-division’) on diversity. Within the context of habitat loss and sub-division, I explore how variations in spatial and abundance distributions affect our expectation for species diversity in sub-divided habitat. It is my belief that such understanding holds the potential to resolve much of the controversy around the effects of habitat sub-division on diversity.

In the remainder of this introductory chapter, I define some important terminology, before reviewing some of the controversies at the heart of recent (and not so recent) debate over the effects of sub-division on diversity (section 1.3) and illustrating how my research fits within this ecological milieu (section 1.4).

1.2 Defining ‘diversity’ for the purposes of this thesis

There are many elements to biological diversity (Magurran, 2009, Maurer and McGill, 2011). In this thesis, I have intentionally focussed on the simplest and most widely used measure; the number of species present, or species richness. Although richness is an incomplete measure of diversity that can be problematic to estimate (Gotelli and Colwell, 2011, Maurer and McGill, 2011, Chao and Jost, 2012), it is also an intuitive and iconic metric that is meaningful to scientists, politicians, policy makers and the general public alike (Magurran and McGill, 2011). It is also the most widely available type of species data.

More importantly, it is arguable that research into the determinants of species richness has been heavily weighted towards patch-scale patterns, with the great majority of effort focused on understanding the mechanisms determining local scale (alpha) diversity; or, how compositional change (beta diversity) arises among the sampling units at which alpha diversity is quantified. Fragmentation research has also been weighted toward local (patch) scale diversity (Haila, 2002, McGarigal and Cushman, 2002) at the expense of patterns that emerge in networks of habitat patches (Fahrig, 2017, Fahrig, 2019, Lindenmayer, 2019). My research focuses on understanding how landscape-scale species richness of discrete habitat networks is shaped by spatial and abundance distributions, within the constraints of patch number and size. A theoretical expectation for this has been lacking in the context of interpreting the effects of habitat sub-division on diversity.

1.3 A brief review of controversy in habitat sub-division research

If controversy over the effects of habitat sub-division on species richness could be traced to a single source, it would probably be the application of Macarthur and Wilson's (1967) equilibrium theory of island biogeography to conservation reserve design. This came to a head with the publication of a set of design principles partially attributed to island biogeography theory claiming a large reserve will hold more species at equilibrium than a small reserve (Diamond, 1975b). Others disagreed that this conclusion followed inevitably from island biogeography theory, arguing it makes no prediction of the total diversity among a group of smaller islands of equivalent total area (Simberloff and Abele, 1976, Higgs and Usher, 1980). The total number of species, they argued, will depend on species overlap among the small patches and empirical evidence tended to support more species being present in a group of smaller sites (Simberloff, 1976, Simberloff and Abele, 1976). These exchanges ignited the well-known controversy over conservation reserve design referred to as the 'single-large-or-several-small' (SLOSS) debate. Rather than ever being resolved, the SLOSS debate seems to have ended up as a general consensus that there exists no 'one size fits all' geometric basis for designing conservation reserves (e.g., Shafer, 1990, Lomolino, 1994, Ovaskainen, 2002, Hokkanen et al., 2009, Tjørve, 2010). In fact, as I suggest below, it is arguable that it has simply re-emerged under a different name.

Another major piece of the habitat-subdivision-controversy jigsaw was put in place by Quinn and Harrison (1988), who introduced a graphical method to compare the accumulation of species with area in discrete habitat networks (islands and habitat islands; see Chapter 3). Their method involved building species accumulation curves in patch size order – from the smallest to the largest and the reverse - and plotting them on a common set of axes. The resulting pair of curves allows comparison of the rate of accumulation of species with area when adding small, relative to large, patches. In an analysis of 30 datasets, they found 29 in which the small-to-large curves approached asymptote (i.e., total species richness of all patches) at a smaller accumulated area than the large-to-small curve (Quinn and Harrison, 1988). This pattern, partially established as an empirical expectation by Simberloff and others at the onset of the SLOSS debate, has been repeatedly demonstrated in diverse habitat types (island, fragments, habitat islands) and taxa (e.g., Robinson and Quinn, 1992, Baz and Garcia Boyero, 1996, Tscharntke et al., 2002b, Peintinger et al., 2003).

The typical explanation offered for more rapid accumulation of species through combining the smallest patches is that it is probably due to increased environmental heterogeneity as the small patches are distributed over a wider extent than a single consolidated patch (Gilpin and Diamond, 1980, Kitchener et al., 1980, Fahrig, 2017). I have however found only two, very recent, explicit tests of this hypothesis, both in freshwater island systems (Liu et al., 2018, MacDonald et al., 2018b). Other possible explanations exist (see Chapter 3). In my view, attempting to understand why this curiously ubiquitous macroecological pattern arises would be more productive than arguing the merits of the pattern for informing conservation.

Irrespective of the cause, one of the important interpretations of the small-to-large pattern is that it suggests small patches are not depauperate in diversity (Fahrig, 2017, Fahrig, 2018, Fahrig et al., 2019). This assertion has been central in the most recent incarnation of the ‘how does habitat sub-division affect diversity’ controversy, known as the ‘fragmentation *per se*’ debate (Fahrig, 2017, Haddad et al., 2017, Fahrig, 2018, Fletcher et al., 2018, Fahrig et al., 2019). At a time when action is urgently needed to address biodiversity decline to offset the expansion of human activity (Brooks et al., 2002, Butchart et al., 2010, Pereira et al., 2010, Newbold et al., 2015), policy-makers are faced with conflicting views on how best to preserve diversity. Despite decades of research effort on the effects of fragmentation (reviews in Wilcox and Murphy, 1985, Shafer, 1990, Saunders et al., 1991, Andrén, 1994, Fahrig, 2003, Fischer and Lindenmayer, 2007, Didham et al., 2012, Fahrig, 2017), ecologists are arguably as far as ever from reaching consensus.

1.4 Setting the scene: competing paradigms for the organization of species diversity across discrete habitat networks

To a useful generalization, the entire debate over habitat sub-division can be summarised as a tension between two equally well supported theoretical paradigms (Fahrig, 2017). Rather than truly distinct theoretical paradigms, they represent convenient end points for illustration; there is certainly overlap of ideas within and among them. However, by simplifying them in this way, they help to emphasise the contrasting views embodied in the habitat sub-division debate. I will refer to them as the ‘spatial coexistence’ and ‘extinction-colonisation’ paradigms. The research in this thesis can be mapped onto some points of conflict for these two theoretical paradigms, within the context of the predictions they make for the effects of sub-division on species composition and richness (Fig. 1.1).

What I call the ‘spatial coexistence’ paradigm is a body of research that has focussed on explaining how coexistence is achieved by spatial partitioning of species. It emphasises the role of niche theory in determining where species live; the optimal environmental conditions for different species are separated in space (or time), which supports their coexistence (Hutchinson, 1957, Macarthur and Levins, 1967). It also includes theories that explain species coexistence across patches through escaping superior competitors, such as the competition-colonization theory (Levins and Culver, 1971, Tilman, 1994). Spatial coexistence theory then, largely provides explanations for patterns of beta diversity (here meaning differences in composition among habitat patches) in discrete habitat networks (Fig. 1.1).

In contrast, the paradigm I refer to as ‘extinction-colonization’ emphasises the role of demographic rates in determining the persistence of populations and therefore species coexistence in space. This includes an influential set of theories such as nested subsets, metapopulations and island biogeography (MacArthur and Wilson, 1967, Patterson and Atmar, 1986, Hanski, 1999). Among the predictions from this view of sub-divided habitat is that small patches provide poor habitat, being prone to higher extinction due to supporting only small populations. Species assembly within patches under this paradigm is largely assumed to be a more-or-less neutral function of dispersal and extinction rates, meaning the most common and abundant species have the highest probability of being present in the smallest patches (Fig. 1.1).

Classical metacommunity theory (Leibold et al., 2004) largely integrates the bodies of theory I refer to as the spatial coexistence and extinction-colonization paradigms. In contrast, sampling theory does not (necessarily) make any specific claim about the roles of niche, competitive, demographic or other ecological processes. Rather it uses the different patterns of distribution that arise as a result of the integration of these processes to predict the resulting species diversity patterns in space (Kobayashi, 1985, He and Legendre, 2002, Plotkin and Muller-Landau, 2002, Green and Ostling, 2003, Harte et al., 2008, Kitzes and Harte, 2014, Kitzes and Harte, 2015). Spatial sampling theory has advanced understanding and expectation for how species diversity assembles, and scales, with area. However, there have been few attempts to use sampling theory to directly address the question of sub-division (Harte and Kitzes, 2012, Hanski et al., 2013). One of the useful contributions spatial sampling theory could make to the debate over the effects of sub-division is providing an expectation for what diversity in sub-divided habitat should look like. Attempts to date have tended to focus on establishing upper and lower bounds (Arnillas et al., 2017, Chisholm et al., 2018).

Among my contributions in this thesis is the application of sampling-theory-based methods and predictions to the question of how sub-division affects species richness (Chapters 4-5). By so doing, I hope to resolve some of the uncertainties over the way that diversity should be *expected* to assemble in discrete habitat patches, given different spatial and abundance distributions in continuous habitat.

1.5 Hypotheses under test

Having set out the broad theoretical scene, I can explain the relevance of my thesis chapters within this context, shown diagrammatically in Fig. 1.1.

In **Chapter 2**, I test the hypothesis that small patches typically contain only common species. I reason that if this were true, then the destruction of only the smallest patches would not reduce the number of species found across the network of discrete habitat patches. In contrast, were some species distributed only within the smallest patches then removing patches in order of increasing size will reduce the total number of species. I use a database of 175 published datasets to test the hypothesis by removing all patches to a maximum of 20% of the total area of all patches. I then analyze proportional species loss using regression. I anticipated that the loss of only the smallest patches would reduce total species number, particularly for plants and invertebrates in aquatic habitat islands such as wetlands.

In **Chapter 3** I challenge the most-common explanation for the rapid accumulation of species among several small patches relative to individual large patches of equivalent area: that it is due to increased beta diversity. I pose three alternative hypotheses (*i*) that a shift in competitive hierarchies could produce the same effect by altering species abundance distributions in the small patches; (*ii*) that size-dependent disproportionate sampling effort could be underestimating richness of the large patches; and, (*iii*) that it depends on taxonomic group. Using 38 published abundance datasets I use individual-based null models and confirmatory path analysis to test support for the four hypotheses to explain the difference in richness within the single largest patch and the combined smallest patches (to a lesser or equal total area). I anticipated that both sampling and evenness in abundance will contribute to differences and that small-to-large dominance in richness will differ among taxa.

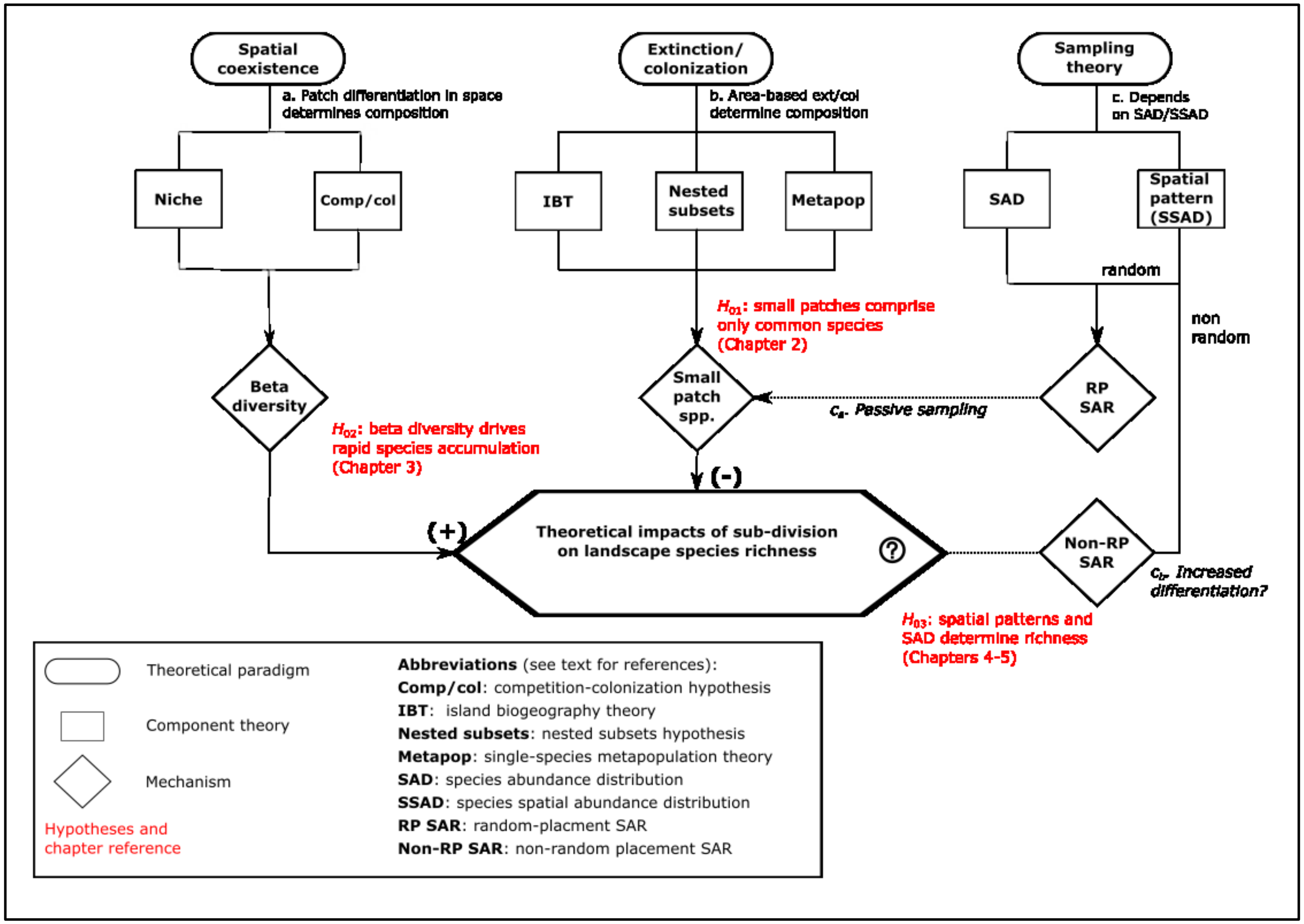

Figure 1.1 Thesis outline showing hypotheses under test within the context of relevant ecological theory

In **Chapter 4** I develop a modelling framework to test how sub-division (fragmentation *per se*), as opposed to habitat loss, affects species diversity. To achieve this, I combine the sampling theory used to derive species-area relationships from species abundance distributions (Fig. 1.2) and spatial patterns (Fig. 1.3) to model zeta diversity (the expected number of species shared among all sites) of multiple patches of habitat. I validate the model using empirical and simulated data. The validated framework introduces a novel means to investigate the effects of sub-division on species richness analytically.

In **Chapter 5** I apply the modelling framework developed in Chapter 3 to simulated landscapes to test the hypothesis that total species numbers across multiple patches depend on the relative evenness of their species abundance distributions and their spatial distributions. I created landscapes that combine four different species abundance distributions of increasing evenness (approximating the range of the niche pre-emption to the broken stick species abundance models) with four different spatial patterns (three levels of aggregation and random placement) in a factorial experiment. I then destroyed increasing fractions of habitat (20-90%) and compared the diversity patterns as the remaining areas were sub-divided into 1-32 patches of equal size. Simulations explain some commonly observed patterns in sub-divided habitat and pose some new hypotheses.

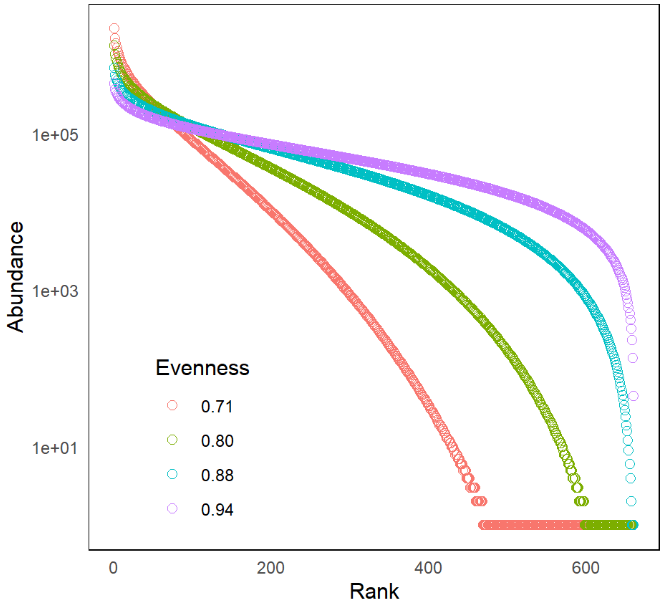

Figure 1.2 Rank abundance distributions contrasting in evenness. Each curve represents a different species abundance distribution (SAD), with Pielou's evenness shown in the legend. If all species had equal abundance, the SAD would be a horizontal line with evenness of 1.

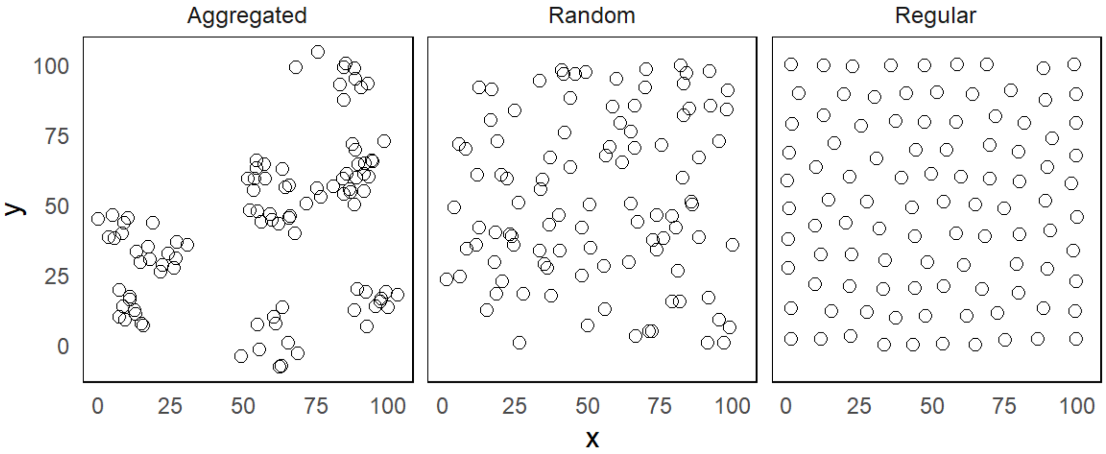

Figure 1.3 Contrasting intraspecific spatial patterns. Each panel illustrates the location of 100 individuals from a single species distributed according to a spatial pattern shown in the panel heading.

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Chapter Two: Loss of only the smallest patches will reduce species diversity in most discrete habitat networks

2.1 Abstract

Under many global-change scenarios, small habitat patches are the most vulnerable to destruction. For example, smaller ponds are at greater risk in a drying climate and their loss would remove any obligate aquatic individuals present. I asked what proportional loss of species diversity from metacommunities comprised of discrete habitat patches should be expected from attrition (complete loss) of only the smallest patches under such a premise. I analyzed 175 published datasets for different taxonomic groups (vertebrates, invertebrates and plants) and habitat types (islands, habitat islands and fragments). I simulated the destruction of only the smallest patches to an approximate 20% of total area (range 15.2 – 24.2%) and analyzed species loss. Mean [±95% CI] species loss was 12.7% [10.8, 14.6], although 18.3% of datasets lost no species. Four broad patterns of species loss were evident, reflecting underlying differences in minimum area requirements and spatial turnover among patches. Regression modeling showed species loss increased with greater species turnover among patches (β_{SIM}) and decreased with greater slope of the power-law species-area relationship. Losses also increased with greater numbers of single-patch endemics and with increasing proportions of patches destroyed. After accounting for these predictors, neither taxonomic group nor habitat type explained variation in species loss. Attrition of the smallest patches removed species in >80% of metacommunities, despite all larger patches and >75% of total area remaining intact. At both 10 and 20% area reduction, median species loss across all datasets was around 50% higher than predicted from methods based on the species-area-relationship. I conclude that any mechanism of global change

that selectively destroys small habitat patches will lead to imminent extinctions in most discrete metacommunities.

2.2 Introduction

Networks consisting of discrete patches of habitat arise naturally from environmental heterogeneity and artificially through human habitat fragmentation. Species accumulation curves can be built for such networks by combining patches in order of their size – either from the smallest to the largest or the reverse. When the two curves are compared to determine the number of species accumulated for a given amount of area, the small-to-large ordering typically accumulates many more species (e.g., Quinn and Harrison, 1988, Cook, 1995). Early interest in this pattern was largely driven by controversy over conservation reserve design (i.e., the SLOSS debate; Diamond, 1975b, Simberloff and Abele, 1976) but the plotting of size-ordered species accumulation curves remains a popular means to compare the diversity of groups of smaller sites (e.g., Fischer and Lindenmayer, 2002, Le Roux et al., 2015, Richardson et al., 2015) or to explore differences in this pattern among groups of species or management areas (e.g., Peintinger et al., 2003, Mitsuo et al., 2011, Gavish et al., 2012). There is however a conservation implication of this pattern that has been largely ignored: how would the systematic *loss* of the smallest patches affect the species diversity of discrete habitat networks?

This is an important question given the conservation value of small patches for a diverse range of taxonomic groups and discrete habitat types, including reptiles, birds and plants in forest and grassland fragments (Turner and Corlett, 1996, Fischer and Lindenmayer, 2002, Rosch et al., 2015, Lion et al., 2016), invertebrates and vascular plants in lakes and wetlands (Virolainen et al., 1998, Peintinger et al., 2003, Scheffer et al., 2006, Richardson et al., 2015) and invertebrates on oceanic and continental islands (Borges and Brown, 1999, Dapporto and Dennis, 2008).

For many metacommunity types, the loss of patches in approximate order of increasing size is plausible under different global-change scenarios. For example, smaller terrestrial remnants are more susceptible to complete loss (attrition) following landscape fragmentation (Forman, 1995). In tropical rainforest fragments, reduction in biomass and recruitment at patch edges (Laurance et al., 1997) can result in an inward contraction of the patch, with small patches at greater risk of attrition (Gascon et al., 2000). Smaller forest fragments are also more prone to on-going clearance for agriculture as they often lack formal conservation protection (Piquer-Rodriguez et al., 2015). Aquatic metacommunities are perhaps at even greater attrition risk, with the loss of smaller ponds and wetlands occurring during agricultural expansion (Serran and Creed, 2016), landscape drainage (McCauley et al., 2015) or in drying climates (Zacharias and Zamparas, 2010). For wetlands in an agricultural landscape in southern Australia, loss of patches in small-to-large size order would result in a near-worst-case loss of vascular plant species from the metacommunity (Deane et al., 2017a).

Habitat loss from fragmentation is unequivocally detrimental for biodiversity (Fahrig, 2003, Haddad et al., 2015), yet in heavily modified landscapes, any remnant patches of native habitat become critical for biodiversity conservation (e.g., Tscharntke et al., 2002a, Lindborg et al., 2014, Decocq et al., 2016). Even if current trends of fragmentation could be halted immediately, the legacy of decades of land clearance still need to be understood and managed (Haddad et al.,

2015) and there is increasing interest in understanding the consequences of different patch loss patterns on fragmented landscapes (e.g., Economo, 2011, Mouquet et al., 2013, Arnillas et al., 2017, Chisholm et al., 2018, Resetarits et al., 2018). Quantifying the risk to biodiversity associated with loss of smaller patches from discrete habitat 'archipelagos' of all types is an important step toward planning any necessary conservation interventions.

Destruction of smaller patches would result in the lowest - possibly zero - loss of species from a landscape where the species composition of smaller sites comprised subsets of the species found in larger sites – that is, under strong nestedness on a gradient of patch area (Darlington, 1957, Patterson and Atmar, 1986, Worthen, 1996). For this to occur, habitat diversity, quality and availability would all need to scale predictably with patch area (Simberloff and Martin, 1991, Wright et al., 1998, Honnay et al., 1999). However, the commonly observed pattern of rapid small-to-large species accumulation (Quinn and Harrison, 1988), coupled with the low tendency for island, or habitat island, biota to form nested subsets by richness or area (Matthews et al., 2015) suggests this is probably rare in nature. With destruction of the smallest patches, I expected the more random cooccurrence patterns of invertebrates (Baz and Garcia Boyero, 1996, Boecklen, 1997, Scheffer et al., 2006) and the tendency for rare plants to occur in small terrestrial and wetland patches (Simberloff and Gotelli, 1984, Richardson et al., 2015, Deane et al., 2016) would result in higher proportional loss of species among invertebrate and plant metacommunities. In contrast, the larger minimum area requirements, greater mobility and more nested matrix structures of mammal and bird metacommunities (Patterson and Atmar, 1986, Watling and Donnelly, 2006, Matthews et al., 2016) should lead to lower species loss.

Using published data, I modeled the loss of species following the destruction of the smallest patches to represent an approximate 20% reduction in total habitat area. This is half the maximum acceptable habitat loss threshold suggested by Yin et al. (2017) but consistent with a loss of habitat that might occur with attrition of only the smallest patches under the global-change scenarios described above. I compared observed species loss against a null model assuming random placement of species among patches and modeled the loss of species as a function of predictors quantifying nestedness on gradients of area and richness, area-scaling relationships, species turnover and cooccurrence patterns. Results confirmed my general expectations and demonstrated that overall diversity in more than 80% of metacommunities would be reduced following destruction of only the smallest patches.

2.3 Methods

2.3.1 Simulating patch attrition and quantifying species loss

For each dataset, I ranked patches in increasing size order and simulated destruction of patches constituting a target proportion of 20% of the total area of all patches in the metacommunity. As patches were irregularly sized, it was usually not possible to select patches that removed precisely 20% of area. Instead I removed the number of patches that resulted in an area loss between 15 and 25%, selecting the closest value to 20%. For 11 datasets it was not possible to obtain a percentage of total area within this window, leaving 164 datasets for analysis at a notional 20% area reduction (Table 2.1, Appendix A.1). I included the exact proportional area removed as a covariate in all models to account for variation in this value. I also tested for any sensitivity in proportional species loss to the integer number of removed patches, the proportion of total area these constituted and the proportion of total patch number. I found no evidence for proportional area (Pearson's $r = 0.05$, $t_{161} = 0.51$, $p = 0.60$), or number of patches removed ($r = 0.09$, $t_{161} = 1.2$, $p = 0.22$). However, the proportion of total patches removed to achieve a 20% reduction in area had a weak, yet statistically significant, positive association with the proportion of species removed ($r = 0.23$, $t_{161} = 3.0$, $p = 0.002$). I included both the integer number and proportion of total sites removed as predictors (see *Predictor Variables*). While selection of 20% was effectively an arbitrary proportion of area to remove, I was guided by a recently proposed maximum acceptable loss threshold of 40% (Yin et al., 2017) and chose this as a realistic amount of habitat that might be destroyed. I re-ran the same analysis by removing a notional 10% of area (actual range 5.3-14.9%; results presented in Table 2.5, Section 2.8) but that did not qualitatively change the results of 20% removal. I conclude that the results provide broad inference on the risk of species loss that could be expected following destruction of the smallest patches while retaining 80% of total area in the largest patches in a diverse range of taxonomic groups and discrete habitat types.

Prior to analysis, I tested for any evidence that differences in sampling effort across the studies might affect estimates of species loss. I was particularly concerned that studies using only a single census might underestimate species incidence relative to studies that collated surveys from multiple studies or repeated sampling events, but found little evidence of any effect of survey methods on proportional species loss at 10% (Wilcoxon rank sum test; $W = 3163$, $p = 0.85$) or 20% ($W = 2527$, $p = 0.20$) area loss.

2.3.2 Sources of data

I compiled data from published sources providing near-complete census data for discrete habitat patch networks. I included ‘true’ islands (i.e. terrestrial habitat surrounded by water, whether marine or freshwater), habitat islands (which I define as naturally occurring patches of habitat surrounded by a hostile matrix, e.g., lakes, wetlands, montane or ‘sky’ islands) and fragments of vegetation of any type. I included hilltop islands created by flooding during the creation of water reservoirs. Data were compiled from the following three sources: (1) “Web of Science” literature searches, January 2017, (using keywords: NESTED*; SPECIES AREA; INCIDENCE; OCCURRENCE; DIVERSITY; ISLAND; HABITAT ISLAND; FRAGMENT*, (2) citation tracking and by reviewing reference lists from comparable meta-studies (e.g., Quinn and Harrison, 1988, Cook, 1995, Matthews et al., 2015), and (3) the original sources of datasets provided with the software program of Atmar and Patterson (1995). Through this approach I identified 175 datasets providing minimum information on patch area and presence-absence (or abundance) of each species within each patch (see Appendix A.1 for a list of data sources).

Table 2.1 Distribution of datasets among discrete habitat types and taxonomic groups for a 20% reduction in area. 'Inland archipelagos' are either lake or hilltop islands isolated by flooding following reservoir creation; 'Continental archipelagos' are marine islands located on the continental shelf or within bays near to contiguous mainland areas; 'Oceanic archipelagos' are found in the open ocean far from any continental mainland areas; 'Forest fragments' were predominantly tropical, but include some sub-tropical and temperate woodlands; 'Patchy vegetation' consists of structurally defined natural habitat islands of vegetation isolated by a contrasting vegetation matrix, e.g., naturally occurring forest patches (capões) in Brazilian grasslands; 'Montane (sky) islands' are high elevation sites in mountain ranges isolated by intervening non-mountainous areas; 'Wetlands and lakes' were permanent or semi-permanent waterbodies but include some riverine floodplain wetlands and lake systems periodically connected via river systems. Taxonomic groups were: invert = invertebrates, plant = vascular plants and fungi; vert NV = non-volant vertebrates; vert V = volant vertebrates.

Patch type	**Taxonomic group**				**Total count:**
	invert	plant	vert NV	vert V	
Inland archipelagos	1	2	3	3	*9*
Continental archipelagos	16	1	9	6	*32*
Oceanic archipelagos	2	5	1	8	*16*
Forest fragments	13	6	12	16	*47*
Grass/shrubland fragments	5	3	6	3	*17*
Montane (sky) islands	-	-	5	7	*12*
Patchy vegetation	1	-	1	3	*5*
Wetlands and lakes	14	8	2	2	*26*
Total count:	*52*	*25*	*39*	*48*	*164*

2.3.3 Comparison of species loss with the random-placement model

To provide a null model to compare loss of species with area I used the random-placement species-area model (Arrhenius, 1921, Coleman, 1981). This model predicts the number of species found in sub-area *a* of larger area *A*, assuming species are randomly located in space. The random-placement species-area curve and its variance are (Coleman, 1981):

$$S_a = S - \sum_{i=1}^{S} \left(1 - \frac{a}{A}\right)^{n_i} \tag{2.1}$$

$$\sigma_a^2 = \sum_{i=1}^{S} \left(1 - \frac{a}{A}\right)^{n_i} - \sum_{i=1}^{S} \left(1 - \frac{a}{A}\right)^{2n_i} \tag{2.2}$$

where n_i is the abundance of species *i*. The probability of presence within sub-area *a* is the complement of the probability of absence and the equivalent endemics-area relationship predicting species found only in a given sub-area is (Green and Ostling, 2003):

$$E_a = \sum_{i=1}^{S} \left(\frac{a}{A}\right)^{n_i} \tag{2.3}$$

with corresponding variance:

$$\sigma_a^2 = \sum_{i=1}^{S} \left(\frac{a}{A}\right)^{n_i} - \sum_{i=1}^{S} \left(\frac{a}{A}\right)^{2n_i} \tag{2.4}$$

For these data, I lacked knowledge of species abundance, but instead used the distribution of species incidence (presence-absence) on patches to estimate the random placement model. I first calculated the column sums of each site by species presence-absence matrix and then used this incidence vector in equations 2.3 and 2.4 in place of the abundance vector n_i. I was not aware of prior application of the random-placement model using incidences across discrete habitat patches and so first verified equations 2.3 and 2.4 using a re-sampling approach. I removed patches in random order and recorded accumulated species and area lost at each increment. I repeated this process many times and averaged over both species lost and area removed to produce a smooth curve. As shown in Figure 2.3 (Section 2.8), equation 2.1 closely predicts expected loss of species based on removing patches in random order, while an interval of 2 standard deviations above and below the expectation calculated with 2.2 closely coincide with 95% empirical confidence limits from re-sampling.

In this analysis, I used the random-placement endemics-area model in two ways. First, I subtracted the observed species loss at the notional area reduction threshold with two standard deviations above the random placement prediction based on 2.2. This takes a positive value if the observed species loss exceeds the upper 95% confidence interval of the random placement model. I used this value (denoted ‘rp20’) as a response variable in regression modeling as described in the following section. Second, I used the random placement prediction as a qualitative null model, comparing the observed pattern of small-to-large species-loss curve against the null model to identify differences among datasets. I grouped these into a minimum number of pattern types and used this to help infer possible mechanisms that could restrict some species to smaller patches that would result in their loss were those patches all to be destroyed.

2.4 Regression analyses

I used regression modeling to explore variations in species loss among datasets following destruction of small patches. I built two sets of models each using different response variables (*i*) proportional species loss (spr20, the ratio of observed species loss and overall diversity) and (*ii*) deviations from the random-placement model prediction (rp20, calculated as described in the previous section). These provide complementary information as spr20 quantifies absolute species loss, while rp20 indicates the difference in species loss from a null expectation under a hypothesis of random placement of species among patches after having accounted for differences in the incidence distribution among datasets.

As predictor variables, I required measures to compare different matrix characteristics. Two broad approaches have been used to analyze the internal matrix structure for presence absence data. The most common approach historically has been to analyze individual measures such as cooccurrence or nestedness (e.g., Diamond, 1975a, Patterson and Atmar, 1986). More recently there has been interest in classifying metacommunities within a framework according to their degree of coherence, turnover and boundary clumping (Leibold and Mikkelson, 2002, Presley et al., 2010). As my interest was in understanding how matrix structures affect species loss rather than classification, I used a combination of individual measures of matrix structure quantifying cooccurrence, β-diversity and nestedness, while accounting for differences in matrix dimensions (Ulrich et al., 2018).

For cooccurrence, I calculated the *C*-score, which measures the number of checkerboard pairs of species occurrences (Diamond, 1975a) relative to the maximum possible number, with the matrix ordered by marginal totals (Stone and Roberts, 1990). *C*-scores that take higher values indicate lower cooccurrence of species pairs, and a matrix that is, on average, more segregated. I used two measures of β-diversity, proportional turnover ($\beta_P = 1 - \alpha/\gamma$ where α is mean species richness of patches and γ represents overall metacommunity species richness) quantifying the proportion of species among all patches not found in a single patch (Tuomisto, 2010); and, β_{SIM}, the multiple-site generalization of Simpson's pairwise dissimilarity measure quantifying species turnover among sites independently of differences in species richness (Simpson, 1943, Baselga, 2010). For nestedness, I used the NODF metric of Almeida-Neto et al. (2008), calculated along gradients of species richness ($NODF_{SR}$) and patch area ($NODF_{AR}$). The overall NODF statistic is the weighted average of two separate components representing paired overlap among sites and species. For a gradient of species richness, these quantify overlap in composition of species found in depauperate and speciose sites, and cooccurrence of narrowly distributed species with those found more widely. Ulrich et al. (2018) show raw scores for individual measures of internal structure depend non-linearly on matrix dimensions and suggest the use of effect sizes based on null model comparisons and the use of the number of sites and species as statistical covariates in regression. For each matrix I calculated normalized effect sizes as the raw metric score minus the mean of 1000 null communities simulated using the fixed-fixed algorithm (Ulrich et al., 2018) for the *C*-score and NODF metrics (based on both patch area and species richness gradients) using R-package vegan (Oksanen et al., 2017).

In addition to the measures of matrix structure described above, I was interested in how the scaling of species number with area affected the importance of smaller patches for metacommunity diversity. If species number increases more rapidly with increments in area, then smaller patches are likely to contain relatively small proportions of overall diversity. To provide a measure of differences in this scaling relationship between richness and area I fit the power-law island species-area model, $species = c \times Area^z$, where *c* and *z* are parameters and larger positive values for the exponent *z* indicate higher rates of species accumulation with increasing area (Connor and McCoy, 1979). I fit the power-law model to each dataset and used the fitted z as a predictor in regression modeling, expecting that higher values for *z* would be more likely to result in lower proportional species loss for removal of small sites as they would contain relatively few species. I also included the proportion of species that were found in only one patch (single-patch endemics) as a predictor expecting the loss of species would increase for larger proportions of endemic species.

Finally, to test for any intrinsic variation attributable to life form or patch isolation, I included three categorical descriptors of the datasets. The first captured broad differences among taxonomic groups following comparable meta-studies (e.g., Gotelli and McCabe, 2002, Matthews et al., 2016), while retaining adequate sample size within factor levels: taxonomic group (comprising four levels: invertebrates, volant vertebrates, non-volant vertebrates and plants; plants here included both vascular plants, lichen and fungi, which I grouped together as sessile organisms). The second categorical predictor was based on differences in phase contrast between the matrix and the habitat patch as suggested by Watson (2002) (comprising three levels: water-terrestrial, terrestrial-terrestrial, terrestrial-water). Finally, I tested for differences in species loss among habitat types (comprising three levels: true islands, habitat islands and fragments).

My final predictor set for the regression modeling comprised (*i*) 8 continuous variables: normalized effect sizes for the *C*-score (Cs) and the two nestedness statistics on gradients of species richness and area ($NODF_{\mathrm{SR}}$, $NODF_{\mathrm{AR}}$); the two β-diversity measures (β_{P} and β_{SIM}); the exponent of the power-law species-area model (z_{SAR}); the proportion of species found in only one patch (prEnd); the proportion of total site number removed (prSite); (*ii*) three categorical predictors (matrix contrast, CT; taxonomic group TG; and patch type PT); and, (*iii*) three continuous statistical covariates proportional area destroyed (area), log-transformed overall number of species (lnSpp) and number of sites (lnSite). I also tested for differences in the proportion of species among the categorical predictors using the Kruskal-Wallis statistic and did post hoc comparisons using Fisher's least significant difference with a Type I error probability of 0.05, implemented with R-package `agricolae` (de Mendiburu, 2017).

2.4.1 Model and predictor selection and uncertainty

I modeled proportional species loss for notional area reductions of 20% (spr20; also repeated for a 10% reduction - Table 2.5) using binomial generalized linear mixed models (GLMM). Following Warton and Hui (2011), the random effect in the model is a normally distributed intercept for each dataset to account for overdispersion in the binomial response (a global model including all predictors had a ratio of residual deviance to degrees of freedom of 2.3). I then fit a global model using only linear combinations of all predictors and used all subsets selection based on Akaike's Information Criterion corrected for small sample size (AIC_c) to select the top-ranked model and quantify model selection uncertainty among the candidate set. Modeling was done using R-packages lme4 (Bates et al., 2015) and MuMIn (Barton, 2017). I calculated pseudo-R^2 for the top-ranked model based on a likelihood ratio test against a model containing only an intercept (Nagelkerke, 1991).

For the response variable measuring deviation from the random-placement model (rp20) I used multiple linear regression and followed the same model selection approach described above. All predictors used in regression modeling were standardized to allow for comparison of coefficients as a measure of effect size.

2.5 Results

Across all datasets, proportional species loss for destruction of the smallest patches at a notional 20% loss of area (range: 15.2 – 24.2) was 0.127 [0.108, 0.146] (mean ± [95 % CI]). The number of species removed exceeded the upper 95% confidence limit for the random-placement model in 75 datasets (45.7% of the total number), while no species were removed in 30 datasets (18.3%). There were statistically detectable differences in proportional species loss among the different taxonomic groups (Kruskal-Wallis $\chi^2 = 21.0$, df = 3, $p < 0.001$) and contrasts in matrix phase ($\chi^2 = 8.6$, df = 2, $p = 0.014$), but not among patch types ($\chi^2 = 0.3$, df = 2, $p = 0.86$). Invertebrates and plants had higher proportional loss than groups of volant vertebrates and non-volant vertebrates, while aquatic habitat surrounded by a terrestrial matrix was higher than terrestrial habitat in a terrestrial matrix but neither differed from terrestrial habitat in a water matrix (Fig. 2.1).

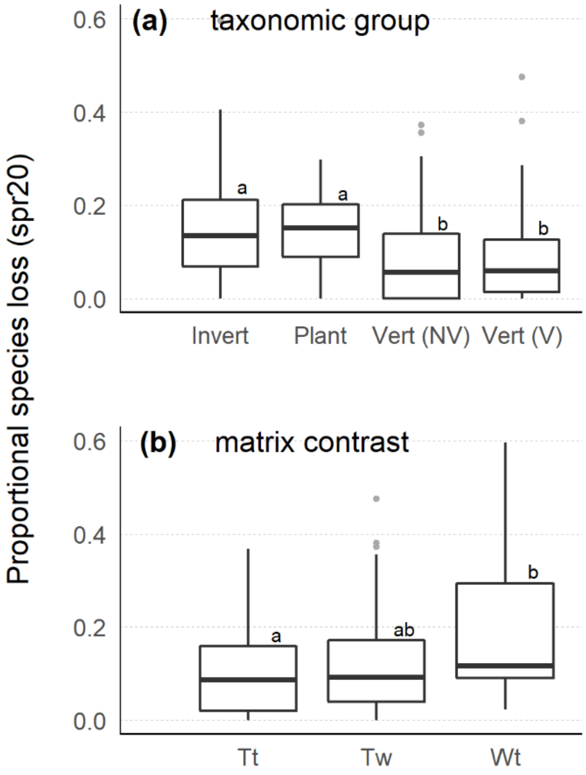

Figure 2.1 Proportional species loss for 20% area reduction a. taxonomic groups (Invert = invertebrates, Plant = vascular plants and fungi; Vert (NV) = non-volant vertebrates); Vert (V) = volant vertebrates) and b. differences in phase contrast between the habitat and the matrix (Tt = terrestrial habitat, terrestrial matrix; Tw = terrestrial habitat, water matrix; Wt = aquatic habitat, terrestrial matrix). Boxplots show the distribution of proportional species loss among groups and those with the same letter code do not differ at the 5% level based on Fisher's least significant difference.

Although proportional species-loss as patches were removed in small-to-large order did not typically follow a smooth curve, four broad patterns were evident (Fig. 2.2; Table 2.2; Appendix

A.2). In threshold patterns, species loss commenced only after some patch-size was exceeded (Fig. 2.2a) and commonly resulted in zero species loss at 20% area reduction. Random patterns (Fig. 2.2b) were consistent with the random-placement model and typically resulted in low, but non-zero, proportional species loss for a 20% area loss. Step patterns emerged where destruction of most small patches led to no species loss but removing a limited number of sites did (Fig. 2.2c). In some cases, this pattern produced proportional loss of species exceeding the random-placement prediction, although most small sites did not contribute to this. A linear pattern of species loss occurred where the loss of most small patches contributed to species loss from the metacommunity, resulting in a proportional loss of species that clearly exceeded the upper confidence limits of the random placement prediction (Fig. 2.2d).

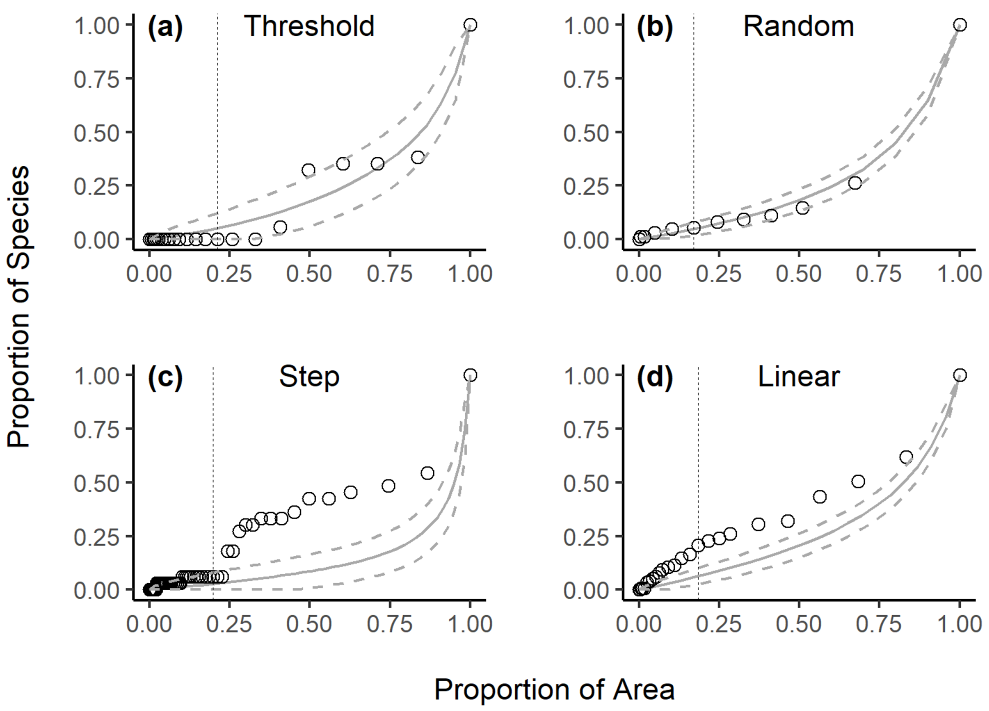

Figure 2.2 Example datasets illustrating four patterns of species loss from metacommunities as patches are removed in small-to-large size order. The solid line is the random placement endemics-area curve, with dashed lines indicating an approximate 95% confidence limit. Points show the cumulative loss of species associated with the removal of each patch and all patches smaller than it. The vertical dashed line shows where species loss was for the notional 20% loss of area; patterns illustrated refer to the area to the left of this line. See also Table 2. a). Threshold pattern (~20% of datasets): destruction of small patches results in no species loss, which occurs only after removal of patches exceeding some size threshold. Data: mammals in montane islands of the U.S. Great Basin (Brown, 1978); b). Random pattern (~9% of datasets): species loss follows the random-placement model. Data: birds in natural forest patches in southern Brazil (Dos Anjos and Bocon, 1999); c). Step pattern (~44% of datasets): species loss occurs in a stepwise manner, with destruction of most small patches not removing species while a select few did. Data: orthopterans in grassland fragments, Austria (Essl and Dirnbock, 2012); d). Linear pattern (~27% of datasets): loss of most small patches results in species loss with the accumulated

proportion removed consistently exceeding the upper 95% confidence limit of the random placement model. Data: spiders in vegetation fragments, Israel (Gavish et al., 2012).

Table 2.2 Proportion of datasets for different life form groups that followed each species-loss pattern at 20% area loss. See Table 1 for a breakdown of datasets by patch type and Fig. 2 for a description of the species-loss patterns. Bolding indicates the most common pattern for each life form. See also Appendix A.2 for size-ordered species-loss curves for all datasets.

Life form	**Threshold**	**Random**	**Stepped**	**Linear**
Invertebrates	0.04	0.13	0.40	0.43
Plants	0.04	0.21	0.33	0.38
Non-volant vertebrates	0.35	0.02	0.51	0.07
Volant vertebrates	0.27	0.06	0.42	0.23

For regression models of proportional species loss at a 20% habitat reduction (i.e., spr20) there was little uncertainty in model selection, with five models in a 95% confidence set (Table 2.3). The top ranked binomial GLMM ($w\mathrm{AIC}_c = 0.5$; pseudo-$R^2 = 0.67$; Tables 2.3, 2.4) contained a total of eight predictors, although three of these were statistical covariates. Of the five retained by model selection, four were retained in all models (Table 2.3). The strongest effect size based on standardized coefficients was for the multiple-site species turnover measure, β_{SIM}, which had a positive effect (Table 2.4). The exponent of the power-law species-area relationship (z_{SAR}) and the proportion of single-patch endemics had effects of similar magnitude but were opposite in their effects: larger z_{SAR} was associated with lower species loss, while species loss increased with an increasing proportion of endemic species (Table 2.4). A larger proportion of patches destroyed was also associated with higher species loss. *C*-score was the final predictor in the top-ranked model but had a small coefficient value (Table 2.4) and was one of four predictors found in only one model in the 95% confidence set, the others being nestedness by area (NODF_{AR}, 2nd ranked model, $w\text{AIC}_c = 0.16$), nestedness by species richness (NODF_{SR}, 5th ranked model, $w\text{AIC}_c = 0.08$) and the categorical predictor indicating the phase contrast between the habitat and the matrix (CT, 4th ranked model, $w\text{AIC}_c = 0.12$).

Regression models for a notional 10% loss of area (range = 5.3 - 14.9%) produced results qualitatively similar to that of the 20% reduction described above (Table 2.5). The number of datasets losing no species was higher (23.4% of datasets) while mean (± [95 % CI]) species loss was lower at 0.080 [0.067, 0.093]. The proportion of datasets exceeding the random-placement prediction at the 5% level was also slightly lower (42%). Model selection results for 10% area reduction were consistent with a 20% loss (spr20), with each of the six models comprising the 95% confidence set containing the same four predictors common to all models for 20% area loss (i.e., prEnd, prSite, z_{SAR} and Cscor; Table 2.5). There were some changes in their relative effect size though, with the proportion of single-patch endemics having the largest coefficient values at 10% area reduction (Table 2.5). Model uncertainty was also higher, with the top-ranked model having a weight of support ($w\text{AIC}_c$) of 0.33.

Table 2.3 Model selection results for the 95% confidence set of binomial GLMM (i.e., for spr20), ranked by Akaike's Information Criterion corrected for small sample size (AICc). Model structures and selection statistics are shown in rows, each representing a model in order of decreasing weight of support. Inclusion of predictors in each model are shown by the symbols, with open circles denoting negative coefficients. Predictor codes refer to the following measures (see Methods): βSIM = multiple-site measure of overall species turnover; zSAR = the exponent of the power-law island species-area relationship; prE = proportion of endemics (species found in only one patch); prS = proportion of sites removed; Cs = normalized effect size for the C-score; NA = normalized effect size for NODF nestedness statistic on a patch area gradient; NS = normalized effect size for NODF nestedness statistic on a patch species richness gradient. Model selection statistics: df = model degrees of freedom; LL = log likelihood; ΔAICc is the difference in AICc compared with the top-ranked model of lowest AICc; wAICc is the weight of support for the model. Statistical covariates included in all models were the total number of sites and species in the metacommunity (both log-transformed) and proportional area removed.

Rank	**Predictors**								***df***	***LL***	**ΔAIC_c**	**$wAIC_c$**
	β_{SIM}	z_{SAR}	*prE*	*prS*	*Cs*	N_A	N_S	CT				
1	●	○	●	●	○				10	-386.2	-	0.50
2	●	○	•	●		●			10	-387.4	2.2	0.16
3	●	○	●	●					9	-386.5	2.5	0.14
4	●	○	●	●				●	11	-388.1	2.9	0.12
5	●	○	●	●			●		10	-386.3	3.6	0.08

When the deviation from the random placement model prediction (rp20) rather than proportional species loss was used as the response variable in regression models, results were again similar (Table 2.6, Chapter 2 Supporting information). Model uncertainty was much greater in this analysis, with 35 models in the 95% confidence set. The most notable difference for rp20 from the species-loss models (spr20) was the absence of the proportion of local endemics (prEnd) among the predictors in the five models receiving at least 5% support (Table 2.6). This is readily understood as the random-placement model is based on the incidence distribution and large numbers of rare species increase the expected loss of species, removing their influence on the resulting deviation from the model. Other predictors were as for the proportional species loss for 20% area reduction (spr20), with the two largest effect sizes being a negative influence of the power-law island SAR exponent (z_{SAR}) and a positive effect from increasing multiple-site species turnover (β_{SIM}), which together accounted for 66% of explained variation (Table 2.6).

Table 2.4 Standardized coefficients for top-ranked spr20 model (*w*AIC$_c$ = 0.5, see Table 3) for proportional species loss when removing patches in size order to a total of 20% area destroyed. Pseudo-R^2 = 0.67. Est. = estimated coefficient, SE = standard error, *z*-stat = *z*-statistic for each coefficient; *P*(>|*z*|) = Type I error probability. Note *lnSite*, *lnSpp* and *area* were included in all models to account for differences in matrix dimensions and proportional area removed. Other predictors selected based on all-subsets selection from a global model including 8 continuous and 2 categorical predictors. Standard deviation for random term accounting for overdispersion = 0.36.

Code	Description of predictor	Est.	SE	*z*-stat	*P*(>|*z*|)
Int	Intercept	-2.27	0.06	-36.8	<0.001
β_{SIM}	multi-site species turnover	0.57	0.10	5.8	<0.001
z_{SAR}	exponent of power-law SAR	-0.47	0.05	-9.3	<0.001
prEnd	proportion of endemic species	0.47	0.07	6.6	<0.001
prSite	proportion of total sites	0.33	0.05	6.3	<0.001
Cscor	*C*-score (normalized effect size)	-0.13	0.06	-2.2	0.03
area	proportion of area removed	0.04	0.05	0.7	0.48
lnSpp	total number of species (log)	0.06	0.06	1.0	0.31
lnSite	total number of sites (log)	-0.29	0.08	-3.4	<0.001

2.6 Discussion

2.6.1 Loss of only the smallest patches would reduce diversity in most metacommunities

Rapid accumulation of species diversity when patches are combined in small-to-large size order is a well-known phenomenon (e.g., Quinn and Harrison, 1988, Cook, 1995, Peintinger et al., 2003), yet there has been little interest in quantifying how the loss of small patches would impact overall diversity in metacommunities (although see Deane et al., 2017a). I found that sequential destruction of the smallest patches would remove at least some species in over 80% of metacommunities, even if the largest patches (containing > 75% of total area) remained intact.

Theoretical and experimental studies are increasingly concerned with how various landscape configurations or patterns of patch-loss could impact overall metacommunity diversity (Economo, 2011, Mouquet et al., 2013, Arnillas et al., 2017, Chisholm et al., 2018, Resetarits et al., 2018); given the size-related attrition risk facing many discrete habitat types under global change, it seems prudent to understand the importance of small patches in this context. Although I found that plants and invertebrates systems lost a significantly higher proportion of species, these differences can be attributed to differences in species turnover and area-scaling of diversity (Fig. 2.4, Chapter 2 Supporting information), which largely determined the proportional loss of species. After accounting for these patterns, neither taxonomic group nor matrix contrast explained any additional variation. Although individual size-ordered species-loss curves differed considerably, four distinct patterns were evident, suggesting a limited number of ways the loss of small patches would impact overall diversity.

2.6.2 Accounting for the different patterns of patch-size-ordered species loss curves

Small habitat patches in discrete networks are generally assumed (and often found) to be dominated by generalist species (e.g., Bender et al., 1998, Sfenthourakis and Triantis, 2009, Capizzi et al., 2015). If small patches support *only* these widespread generalist species, their destruction would not reduce overall species diversity. I observed this in the threshold pattern, for around 20% of metacommunities. Predictably, this was most common in vertebrates, particularly non-volant groups, which tend toward nested distributions and large minimum area requirements (Patterson and Atmar, 1986, Wang et al., 2010). However, 68% of vertebrate datasets lost at least one species for a 20% reduction in total area, suggesting the impact from small patch destruction for these groups is lower, but not entirely negligible.

I found a stepped pattern of species loss was the most common response, where loss of most small patches removed no species yet removal of a select few did. This indicates that some rare species were found only within small patches, though most were more widespread. There are at least two biological explanations. First, if some species were actively colonizing the smallest patches, cumulative loss of those patches might remove these species. Both amphibian and invertebrate taxa have been found to actively colonize smaller patches to avoid predatory fish (Chesson, 1984, Resetarits and Wilbur, 1989, Resetarits and Binckley, 2014). Second, if certain environmental conditions were associated only with smaller patches, these might support species not found in larger sites. This is consistent with a species sorting metacommunity (Leibold et al., 2004), a commonly identified paradigm in both terrestrial and aquatic systems (Cottenie, 2005, Logue et al., 2011, Heino et al., 2015). Historical or evolutionary factors can also produce unique species composition in small habitat patches. In the Azores, for example, the number of endemic arthropod species depends more on geological age than island area (Borges and Brown, 1999).

In about 25% of datasets, loss of most small patches reduced overall diversity. I refer to this as the linear pattern although the actual shape of the response differed widely among datasets (see Appendix A.2 for all species loss curves). The linear pattern was most common in vascular plant and invertebrate metacommunities, which tend toward more segregated (Wellborn et al., 1996, Gotelli and McCabe, 2002, Scheffer et al., 2006) less nested matrix structures (Boecklen, 1997, Peintinger et al., 2003). These matrix characteristics favor increased spatial turnover and higher numbers of locally endemic species, both of which were positively correlated with species loss in this study. Post hoc analyses suggest these predictors also explained much of the variation in species loss among taxonomic groups (Section 2.8.1, Chapter 2 Supporting information).

The spatial turnover component of β-diversity (β_{SIM}) represents replacement, rather than loss, of species among sites (Baselga, 2010) and is therefore a measure of how likely it is that patches will contain different species. Spatial turnover depends on environmental, spatial and organismal characteristics (Nekola and White, 1999) and these are difficult to disentangle. However, in heterogeneous environments, rates of dispersal differentiate the metacommunity paradigms of mass effects and species sorting (Leibold et al., 2004, Logue et al., 2011). High rates of dispersal would be expected to homogenize composition (Mouquet and Loreau, 2003), reducing endemicity and allowing species to persist within (or re-colonize) sink habitats with low or negative population growth rates by immigrating from source populations (Brown and Kodric-Brown, 1977, Shmida and Ellner, 1984, Pulliam, 1988). In contrast, intermediate dispersal favors increased turnover due to spatial niche separation, where each species occupies optimal environmental conditions (Leibold et al., 2004). The linear pattern of species loss appears to be favored under greater among-patch environmental heterogeneity and moderate dispersal. The differences I observed in species loss among taxonomic groups are likely to be due to the different scales at which they experience heterogeneity.

In around 10% of datasets, I found species loss for small patch removal consistent with the random placement of species across patches (Connor and McCoy, 1979, Coleman, 1981, Andrén, 1994). This pattern occurred in a diverse set of metacommunities subject to cyclical disturbance, including long-distance migratory birds of Finnish taiga-forest fragments (Haila et al., 1993), invertebrates of temporary natural ponds or artificial water storages (Urban, 2004, Markwell and Fellows, 2008) and weedy plants in vacant urban lots (Crowe, 1979). Bird metacommunities from naturally-occurring forest patches in Brazil (Dos Anjos and Bocon, 1999) and fragmented temperate British (McCollin, 1993) and US (Blake, 1991) woodland fragments also followed this pattern.

2.6.3 The role of area-scaling of diversity and patch number

The exponent (z-value) for the island species-area relationship (ISAR) had a negative correlation with proportional species loss from smaller patches though the distribution of values did not differ among life forms (Section 2.8.1). When species-area curves are built in a cumulative fashion by adding only those new species encountered as the sampled area increases, larger exponents indicate higher species turnover in the metacommunity (Tjorve and Tjorve, 2008) and there should be a high positive correlation between species turnover and exponents. However, this relationship does not hold for island species-area relationships (e.g., the Pearson correlation between β_{SIM} and z_{SAR} for my data was -0.08), because they are built from discrete samples and compositional overlap among sites is unknown (Simberloff and Abele, 1976). For ISAR, smaller exponents simply mean there is less disparity in local species number between small and large patches. If fewer species are present in small patches relative to large ones, there should also be fewer rare species and the impact of small patch loss on overall diversity should in general decrease as ISAR exponents increase as I found.

Island species-area relationships themselves have a long, though controversial, history of use in area-based extinction prediction (reviewed in Lewis, 2006). Although I do not use ISAR to predict species loss directly, it is interesting to place modeled species loss within this historical context. A traditional power-law species-area estimate assuming a *z*-value of 0.25 (e.g., May et al., 1995) would suggest losses of ~4 and 7% of species for the destruction of 15 and 25% of total area, respectively. This is around 50% lower than median proportional species loss across all datasets (~ 6 and 10%). The shortcomings of this approach are however well known and improving extinction predictions in fragmented landscapes is an active area of research (e.g., With, 2016, Arnillas et al., 2017, Chisholm et al., 2018).

Species loss also increased with the destruction of larger proportions of total patch number. Since all species occupy a finite number of patches, increasing the proportion of patches destroyed must increase the probability of overall species loss – unless only widespread species are present in those patches. Even when area is controlled for, the number of species accumulated often increases with patch number (e.g., Simberloff and Gotelli, 1984, Baz and Garcia Boyero, 1996, Hu et al., 2012). Hu et al. (2012), found that this pattern was driven by rare plant species, their number increasing monotonically with the number of reservoir-lake islands accumulated, while all common species were sampled at around half total island number. Deane et al. (2016) reported a similar pattern for rare plant species in seasonal wetlands of an agricultural landscape in southern Australia, which increased the number of wetlands required to represent all species by 50%. The importance of patch number in this analysis suggests metacommunities comprising few large and many small habitat patches might lose a greater proportion of species from any process resulting in small-to-large size-ordered patch attrition.

2.6.4 Uncertainties and limitations

My scenarios model imminent (or immediate) extinction - where all individuals of a species are contained within destroyed habitat (Kinzig and Harte, 2000). From a conservation perspective, this considers only species representation, not persistence (Margules and Pressey, 2000). Similarly, I ignore any impact of small patch loss on species committed to extinction from reduced habitat area (i.e. extinction debt; Diamond, 1972, Tilman et al., 1994). Small patch loss could have on-going effects on population dynamics affecting persistence and extinction debt, for example by reducing colonization success where patches provide stepping-stones that facilitate dispersal (MacArthur and Wilson, 1967, Semlitsch and Bodie, 1998, Lindborg et al., 2014). Extinction debt can comprise a large proportion of extant diversity (Triantis et al., 2010, Halley et al., 2014) and small patch loss might also expedite this by imminent extinction of already rare species and by reducing the number of occupied patches. Any such longer-term impacts remain unknown.

Methodologically, my analysis is limited by not incorporating information on environmental constraints, landscape structure and variations in species functional traits (e.g., dispersal ability) supporting a detailed understanding of metacommunity structures (Ulrich et al., 2017). Although I analyzed matrices of different dimensions, I used these as statistical covariates and normalized effect sizes to counter any bias (Ulrich et al., 2018). I also tested for bias due to differences in census techniques (Methods) or study extent (Section 2.8.1) but found no evidence of this. One possible source of bias I could not quantify arises from researchers avoiding small sites known to be of low or zero biodiversity. Such bias is quite probable and would reduce the impact of small patch loss. On the other hand, under many global change scenarios (e.g., drought, sea level rise) loss of smaller patches would not occur in isolation but with concurrent reduction in the size of larger patches. This would further increase the risk of imminent and on-going species extinction. While I lack the data to investigate such impacts, it is important that future research considers the consequences of patch-size reduction across the metacommunity in addition to the complete loss of the smallest patches.

Finally, I emphasize that the impacts of habitat loss on landscape biodiversity are well established (Wilcox and Murphy, 1985, Fahrig, 2003, Haddad et al., 2015). I consider only the species diversity contained within networks of discrete habitat patches and no comparison with the diversity that would be maintained within large extents of contiguous habitat can be inferred.

2.6.5 Conclusions

In this chapter I have tested a common assumption for small habitat patches that relates most directly to the extinction/colonization theoretical paradigm introduced in Chapter 1. In general, the results suggest that groups of small patches will typically contain some species not present in larger patches. Three of the four patterns adopted by the species loss curves, can be roughly assigned to what might be expected under the two theoretical paradigms, the threshold and random models aligning with extinction/colonization and the linear model with that of spatial coexistence theory. The prevalence of these among datasets suggest roughly similar support for the two theoretical paradigms in controlling the composition of small patches in discrete habitat networks. The step model – the individually most commonly observed – has elements of both paradigms suggesting a combination of both paradigms is usually involved.

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2.8 Supporting Information for Chapter 2

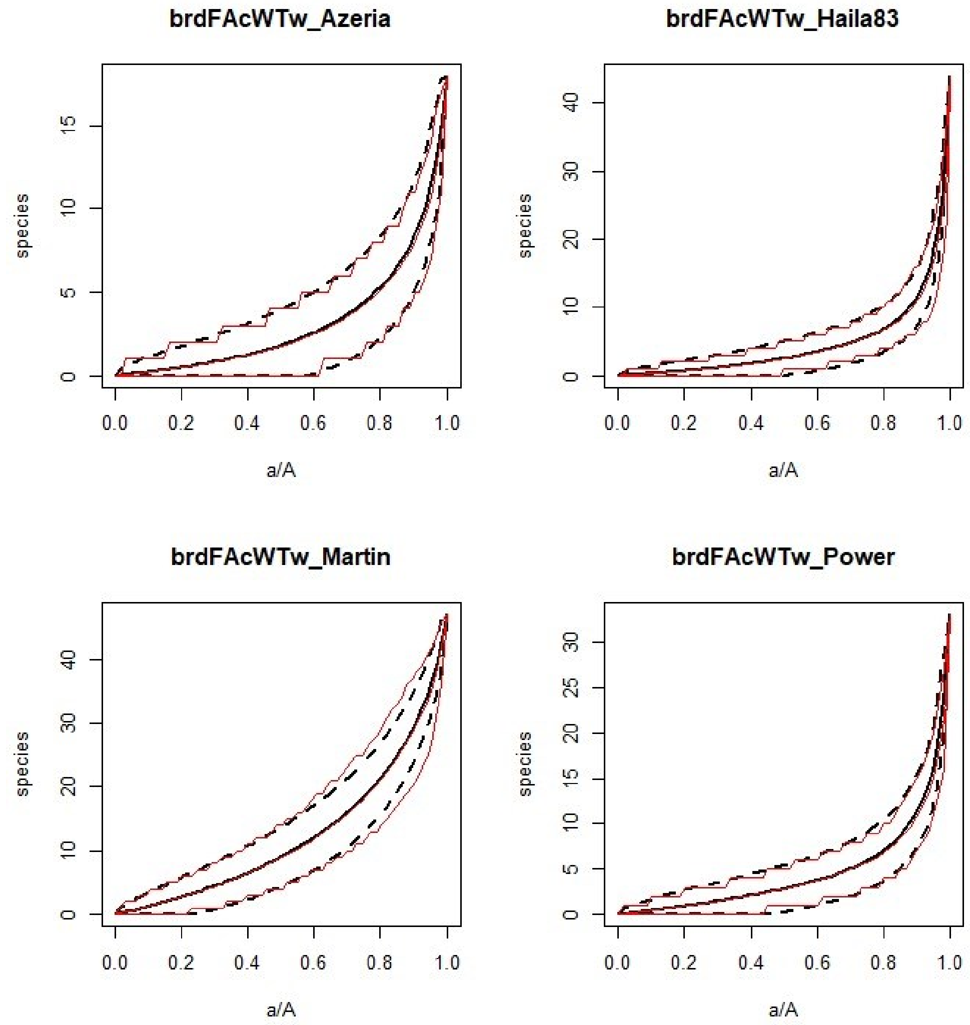

Figure 2.3 Comparison of random placement model and variance with resampling based patch removal. Resampling (red) curves are the mean number of species removed over 2000 iterations of removing patches in random order and calculating both the area and species number. Random placement (black) curves were calculating using equation 2a and 2b from the main text, solid line is the estimate, dashed lines show the estimate ± 2SD

Table 2.5 Model selection results for proportional species loss at 10% loss of total area. Shown are the 95% confidence set of all Binomial GLMM models ranked by Akaike's Information Criterion corrected for small sample size (AIC$_c$). Model structures, standardized regression coefficients and selection statistics are shown in rows, each representing a model in order of decreasing weight of support. Predictor codes: *area* = proportion of total area removed; *lnSite* = logarithm of number of sites (patches); *lnSpp* = natural logarithm of total metacommunity species richness; β_{sim} = ; β_{P} = ; *C-score* = checkerboard score (normalized effect size); *CT* = matrix phase contrast (categorical predictor); NODF$_{\mathrm{A}}$ = nestedness on a gradient of patch area (normalized effect size for NODF metric); NODF$_{\mathrm{S}}$ = nestedness on a gradient of species richness (normalized effect size for NODF metric); *prE* = proportion of local endemics; *prS* = proportion of sites removed; z_{SAR} = the exponent of the power-law island species area relationship. Selection statistics: *df* = model degrees of freedom; *LL* = log likelihood; ΔAIC$_c$ is the difference in AIC$_c$ vs. top-ranked model; *w*AIC$_c$ = weight of support.

Rnk	**Predictors**													**Selection statistics**				
	Int	*area*†	*lnSite*†	*lnSpp*†	β_{sim}	β_{P}	*C-score*	CT	NODF$_{\mathrm{A}}$	NODF$_{\mathrm{S}}$	prE	*prS*	z_{SAR}	*df*	*LL*	AIC$_c$	ΔAIC$_c$	*w*AIC$_c$
1	-2.82	0.074	-0.228	0.023	0.45	-	-	-	-	-	0.551	0.316	-0.465	9	-348.5	716.1	-	0.33
2	-2.82	0.075	-0.206	0.045	0.44	-	-0.051	-	-	-	0.558	0.328	-0.469	10	-348.1	717.5	1.4	0.17
3	-2.89	0.076	-0.26	0.035	0.43	-	-	+	-	-	0.527	0.33	-0.458	11	-347.0	717.6	1.5	0.16
4	-2.82	0.072	-0.227	0.026	0.45	-	-	-	-0.030	-	0.546	0.314	-0.465	10	-348.4	718.1	2.0	0.12
5	-2.82	0.074	-0.241	0.021	0.42	0.058	-	-	-	-	0.528	0.308	-0.479	10	-348.4	718.2	2.1	0.12
6	-2.82	0.074	-0.228	0.023	0.46	-	-	-	-	-0.006	0.549	0.315	-0.465	10	-348.5	718.4	2.3	0.11

† statistical covariates included in all models to account for variations in actual area destroyed and differences in matrix dimensions

Table 2.6 Model selection results for deviation from random placement model (rp20) at destruction of 20% of total area. Shown are all models with at least 5 % of support, ranked by Akaike's Information Criterion corrected for small sample size (AIC_c). Model structures, standardized regression coefficients and selection statistics are shown in rows, each representing a model in order of decreasing weight of support. Predictor codes: *area* = proportion of total area removed; *lnSite* = logarithm of number of sites (patches); *lnSpp* = natural logarithm of total metacommunity species richness; β_{SIM} = species turnover component of the multiple site beta diversity partition (Baselga, 2010); C_N = normalized effect size for *C*-score (Stone and Roberts, 1990); *CT* = matrix contrast, categorical predictor based on phase of habitat (i.e. terrestrial or water) and that of the surrounding matrix; $NODF_{AR}$ = NODF metric (Almeida-Neto et al., 2008) on a gradient of patch area; *prS* = proportion of sites removed; z_{SAR} = the exponent of the power-law island species area relationship. Selection statistics: *df* = model degrees of freedom; *LL* = log likelihood; ΔAIC_c is the difference in AIC_c vs. top-ranked model; $wAIC_c$ = weight of support.

Rnk	Predictors										Selection statistics				
	Int	*area*†	*lnSite*†	*lnSpp*†	β_{SIM}	β_P	C_N	CT	$NODF_{AR}$	prS	z_{sar}	*df*	*LL*	AIC_c	ΔAIC_c	$wAIC_c$
1	0.001	-0.002	-0.015	0.012	0.022	-	-0.008	-	-0.006	0.010	-0.024	10	348	-674.6	-	0.34
2	0.002	-0.002	-0.017	0.009	0.014	0.011	0	-	-0.005	0.008	-0.028	10	347.858	-674.3	0.28	0.30
3	0.002	-0.002	-0.017	0.010	0.016	0.010	-0.005	-	-	0.010	-0.027	10	347.319	-673.2	1.36	0.17
4	0.002	-0.002	-0.018	0.008	0.015	0.010	-	-	-	0.009	-0.027	9	345.574	-672.0	2.58	0.09
5	-0.001	-0.002	-0.018	0.011	0.020	-	-	+	-0.006	0.011	-0.023	11	347.851	-672.0	2.6	0.09

† statistical covariates included in all models to account for variations in actual area destroyed and differences in matrix dimensions

2.8.1 Post hoc tests

Influence of regressors on species loss

After regression analysis showed taxonomic group did not contribute to explained species loss after accounting for other predictors, I tested which, if any, of the three most influential regression predictors accounted for this. I found that species turnover ($\beta_{SIM;}$ Kruskal-Wallis χ^2 = 21.2, df = 3, $p < 0.001$) and the proportion of single-patch endemics (Kruskal-Wallis χ^2 = 20.9, df = 3, $p < 0.001$) largely explained the different species loss patterns among taxonomic groups (Fig. 2.4). In contrast, exponent values for the island species-area relationship did not differ among taxonomic groups (Kruskal-Wallis χ^2 = 3.4, df = 3, $p = 0.34$).

Sensitivity of results to study extent and latitudinal range

Given the differences among datasets in terms of their geographical scope I tested for any sensitivity of the proportional species loss observed (spr20) to log-transformed study extent (Pearson's $r = 0.07$, $t = 0.88$, df = 163, $p = 0.38$) and latitudinal range ($r = 0.06$, $t = 0.75$, df = 163, $p = 0.45$) and conclude that the loss of species from small patches was not influenced by variation in either variable among studies.

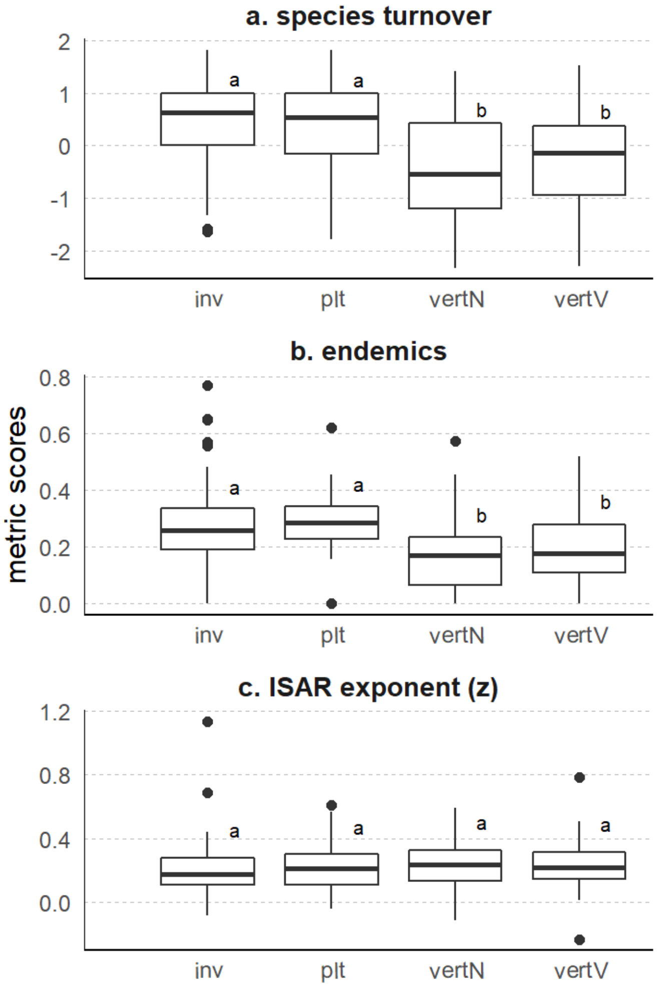

Figure 2.4 Distribution of predictor metrics as a function of taxonomic group. a. β_{SIM} b. proportion of species found in only one patch (single-patch endemics); c. power-law island species area relationship exponent. Compare Fig 2.1, main text. Groups marked with the same letter do not differ at the 5% level.

Chapter Three: Changes in the evenness of species abundance distributions and sampling bias contribute to the SLOSS pattern of species richness in discrete habitats

3.1 Abstract

Paired species-accumulation curves, ordered from small-to-large and large-to-small (aka SLOSS analysis), often suggest several small patches contain more species than a single large patch of comparable area. This is most often attributed to higher beta diversity driven by increased environmental heterogeneity in sub-divided habitat. However, few tests of this, or competing explanations, have been attempted. Here I test four competing hypotheses to explain the difference in species richness between groups of small patches and a single large patch: (*i*) beta diversity (BD); (*ii*) changes in the evenness of species abundance (EV); (*iii*) decreased sampling efficiency in larger patches (SE); and, (*iv*) intrinsic taxonomic characteristics. Using 38 published abundance datasets from discrete faunal habitat networks (fragments, islands and habitat islands), I test the direct and indirect effects of each hypothesis on the observed richness differences using confirmatory path analysis. Broad taxonomic grouping (invertebrates > birds = non-volant vertebrates) directly accounted for most of the variation in richness difference but BD, EV and SE had comparable effect sizes (standardized coefficients = 0.32, 0.25 and -0.22 respectively), each accounting for 16-18% of explained variation. Taxonomic group and EV also mediated the strength of BD. These results suggest that, for animal taxa, changes in the distribution of species abundance across multiple small patches and less effective sampling of larger patches are plausible alternative explanations to beta diversity for observed differences in species richness between several small and single large patches. Limited prior consideration of these possibilities could have contributed to the SLOSS and related debates.

3.2 Introduction

Whether or not small habitat patches contribute to biodiversity conservation, is perhaps the most controversial and enduring unresolved question in conservation biology (e.g., Diamond, 1975b, Simberloff and Abele, 1976, Fletcher et al., 2018, Fahrig et al., 2019). Originally, this question divided opinion on conservation reserve design principles - whether a single large (SL) or several small (SS) reserves protect more species (i.e., the SLOSS debate; Diamond, 1975b, Simberloff and Abele, 1976, Gilpin and Diamond, 1980, Higgs and Usher, 1980). More recently, the conservation value of small patches has been a key point of difference in debate over the impacts of fragmentation *per se* (Fahrig, 2017, Fletcher et al., 2018, Fahrig et al., 2019). Probably no other method of data presentation has been more influential to both debates than the comparison of species accumulation curves ordered according to patch size: from the smallest to the largest and the reverse (Fig. 3.1). As noted by Quinn and Harrison (1988) when introducing the method (hereafter QH curves), comparing the curves usually implies that a collection of small patches will contain more species – often many more – than the equivalent area contained in a single large patch (e.g., Quinn and Harrison, 1988, Peintinger et al., 2003, Arroyo-Rodriguez et al., 2009, Richardson et al., 2015, Rosch et al., 2015). Despite its prevalence and the enduring controversies surrounding the pattern, its causes remain poorly understood (Fahrig, 2017, Liu et al., 2018). Establishing the underlying mechanisms could inform debate over reserve design and fragmentation and contribute to understanding assembly of species diversity in metacommunities.

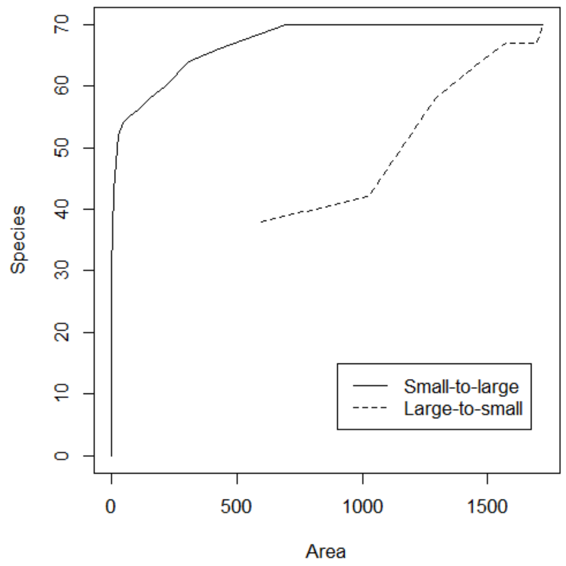

Figure 3.1 Example of a Quinn-Harrison type curve. Each curve represents a species accumulation for the same dataset with the only difference being the order in which the sites (patches, islands, etc.) are accumulated. The small-to-large curve starts with the smallest patch and combines sites in increasing size order, the large-to-small curve does the opposite. Data are birds in mangrove fragments from Australia (Mohd-Azlan and Lawes, 2011)

In metacommunity theory (Leibold et al., 2004), spatially discrete habitat networks within a landscape are generally conceptualized as organizing along three main axes: species equivalence, environmental variation, and dispersal (Logue et al., 2011). Explanations for patterns of diversity in spatially discrete habitats should reflect the influence of these processes and the ways in which they are mediated by the characteristics of the landscape (Fournier et al., 2017, Rybicki et al., 2018). Given differences in life histories, minimum area requirements, mobility and body size among taxonomic groups, one might expect large differences in their QH curves. Empirical evidence from published studies using QH curves in fact suggests the pattern of rapid initial increase in richness under small-to-large accumulation of patches is quite consistent across taxa.

It is widely reported for plants and invertebrates (e.g., Quinn and Harrison, 1988, Tscharntke et al., 2002b, Peintinger et al., 2003, Gavish et al., 2012, Richardson et al., 2015, Rosch et al., 2015, Liu et al., 2018) and has also been demonstrated in birds (Baldi and Kisbenedek, 2000), herpetofauna (McCoy and Mushinsky, 1994, Oertli et al., 2002) and mammals (Quinn and Harrison, 1988, Robinson and Quinn, 1992). Despite this apparent consistency among taxa, it seems reasonable to expect that differences in life history traits will affect their relative accumulation within and among patches (Qian and Ricklefs, 2012) and at least partially contribute to observed patterns of species accumulation.

The most common explanation for higher species richness among groups of smaller patches than within a single large patch is increased environmental heterogeneity (e.g.,Kitchener et al., 1980, Simberloff and Gotelli, 1984, Tscharntke et al., 2002a, Rosch et al., 2015, Fahrig, 2017). This is essentially distance-decay in environmental similarity (Nekola and White, 1999), where the much wider spatial extent over which groups of smaller patches are distributed relative to a single patch of comparable area is likely to encompass a broader range of environmental conditions (Kitchener et al., 1980). As environmental heterogeneity accumulates more rapidly, this drives higher beta diversity and greater number of species among the smaller patches (Tscharntke et al., 2002b, Fahrig, 2017). Just such a relationship has been demonstrated for artificially-fragmented plant communities on islands within a water-supply-reservoir lake in China (Liu et al., 2018) and in natural lake islands in Canada (MacDonald et al., 2018b). However, smaller patches are also thought to be more susceptible to stochastic influences such as ecological drift or priority effects (Chase, 2003, Fukami, 2004), which could also lead to differentiation in the composition of small patches. Irrespective of whether it is driven by deterministic and/or stochastic influences, higher beta diversity is the leading explanation offered for the SLOSS pattern.

Without necessarily specifying a mechanism, species-area sampling theory provides a complementary way to consider the question: any process that increases the evenness in species abundance, or decreases intraspecific clustering (i.e., spatial aggregation), should increase the number of species observed in a given area (He and Legendre, 2002). In contrast, when these two variables move in the other direction (decreased evenness and increased aggregation), the effect is to decrease compositional similarity and higher endemicity (Plotkin and Muller-Landau, 2002, Green and Ostling, 2003). If the latter conditions prevail, this then must increase beta diversity and result in more species being present among groups of smaller patches than a single large patch (Kobayashi, 1983). As habitat sub-division alters the evenness of species abundances both within and among groups of patches (Quinn and Robinson, 1987, Wilson et al., 1999, Cushman and McGargal, 2003, Marini et al., 2014), this could provide a competing, though not necessarily independent, explanation for more rapid accumulation of species among vs. within patches. Thus, changes in evenness of abundance in discrete patches could act directly by increasing within patch species number or indirectly via altering the strength of beta diversity and increasing among-patch species accumulation.

However, another important source of uncertainty in the use of QH curves are the data themselves. The method requires near-complete census data for each patch, which is problematic in patches of different size because of a confounding of patch size and sampling effort (Hill et al., 1994, Rosenzweig, 1995, Gavish et al., 2012). Difficulty in obtaining a complete census should also increase with patch area, meaning rare species might be more likely to be encountered in smaller patches (Deane and He, 2018). It is unknown whether such a sampling bias contributes to the more common SLOSS observation of more species in groups of smaller patches. Unlike species density, the density of individuals in a plant or animal assemblage tends to remain constant across different sampling areas (Connor et al., 2000, He et al., 2002). This is often an assumption in ecological theory (MacArthur and Wilson, 1967, Hubbell, 2001, Harte et al., 2008). If the proportion of individuals sampled in a patch declines with patch size, it seems probable that smaller patches will represent a more reliable census than larger patches. If individual density is assumed to be constant, a simple proxy measure of sampling bias within a given study system could then be based on the proportion of total individuals sampled from each habitat, allowing a test of its influence on the SLOSS pattern.

Here I use 38 published faunal abundance datasets from discrete habitat networks to test support for four possible explanations for more rapid accumulation of species in several small patches relative to a single large patch: taxonomy, beta diversity, evenness of species abundances, and size-dependent sampling efficiency. I found some support for all of these, suggesting that automatically assuming it is driven by beta diversity alone might be an over-simplification.

3.3 Methods

3.3.1 Data sources and pre-processing

Although size-ordered species accumulation curves only require presence-absence data in discrete habitats (such as islands, insular habitats such as wetlands, or fragments of formerly continuous biomes), to test inference on diversity and fragmentation using QH curves, to test the four competing explanations for differences in species richness, abundance data in each habitat patch are needed. Such data allow us to use individual-based methods to test for differences in species number and diversity among samples drawn from smaller and larger patches and determine possible size-related differences in sampling density. I used a subset of datasets that were compiled using literature searches and citation tracking in Chapter 2 (see also Deane and He, 2018), limiting analysis to those datasets presenting either the number of sampled individuals, or relative and total abundances from which this could be calculated, yielding 38 datasets (Appendix B). Datasets were mostly from fragmented forests, woodlands or grasslands (n = 27) but also included some from islands (n = 5) and habitat islands (n = 6). All represented taxa were animals, predominantly birds and invertebrates (n = 16 each) but also included were mammals (n = 3) and amphibians (n = 3). For analysis purposes, I simplified this to three broad taxonomic groups: invertebrates, birds and non-volant vertebrates. Appendix B lists the sources and provides metadata on each included study.

3.3.2 Confirmatory path analysis

As a response variable I used a literal test of the ‘single large or several small’ pattern. I calculated the arithmetic difference in the number of species contained within the single largest patch and all smallest patches up to an equivalent (or smaller) area (Fig. 3.2). To account for differences in overall species richness among datasets, I normalized the difference by total number of species observed across all patches (i.e., gamma diversity for the study).

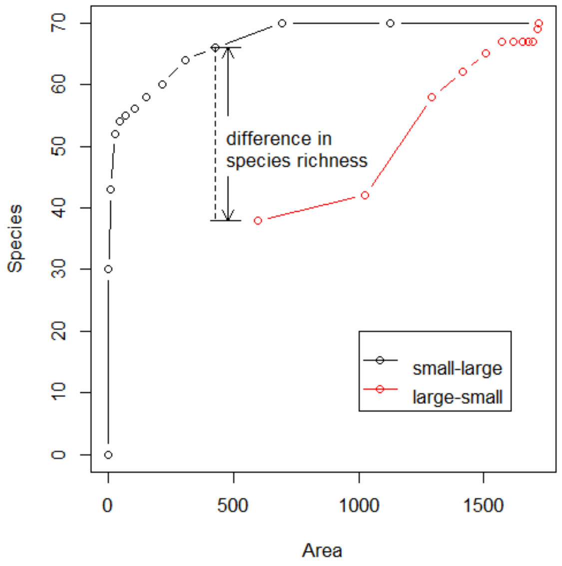

Figure 3.2 Calculation of the response variable. The number of species found in the group of smallest patches whose area was closest to, while still less than, the area of the single large patch was subtracted from the number of species found in the latter. The difference was then adjusted for differences in diversity among datasets by dividing by the observed number of species across all patches (here 70 species). Data as per Fig. 3.1.

To test support for the four competing hypotheses in explaining the difference in species richness, I used confirmatory path analysis (Shipley, 2000, Shipley, 2009). Like structural equation modelling (SEM), confirmatory path analysis is graphically based, using two or more equations to represent hypothesised direct and indirect causal links between dependent and independent variables. Typically, the equations are implemented in a multiple regression framework, with model coefficients indicating the direction and magnitude of different predictors. Traditional structural equation models solve all equations simultaneously, estimating coefficients with a single variance-covariance matrix that requires independence of observations and normally distributed errors. Piecewise structural equation modelling (Lefcheck, 2016) instead estimates coefficients within each equation separately and these are combined at a later stage of analysis to infer support for hypothesised causal pathways explicit within the model equations. This approach allows for the use of models incorporating multilevel designs (Shipley 2000, 2009), as is the case here.

I encoded the four hypotheses proposed to explain differences in species richness within and among patches into a simple confirmatory path analysis, which is based on a conceptual diagram illustrating the ways in which they might act to moderate species richness directly and indirectly (Fig 3.3). Four regression models were needed to implement the full path analysis:

$$SRd \sim Bdev + EVd + SE + Taxa \quad (1)$$

$$Bdev \sim Taxa + EVd \quad (2)$$

$$EVd \sim Taxa \quad (3)$$

$$SE \sim Taxa \quad (4)$$

where *SRd* is the difference in species richness between the group of smallest patches and the single large patch, taking a positive value if more species were found in the group of small patches; *Bdev,* and *EVd* are predictors quantifying observed beta diversity and evenness of abundance in the small patches relative to null models for each (see Sections 3.3.3; 3.3.4). In each case, a positive value indicates small patches had higher beta diversity or were more even than null model predictions. *SE* indicates the sampling efficiency for the dataset, with more positive values implying less difference in sampling effectiveness for small, relative to large, patches. Model 1 describes the direct effects of the four predictors, while models 2-4 describe the indirect effects of various predictors on one another.

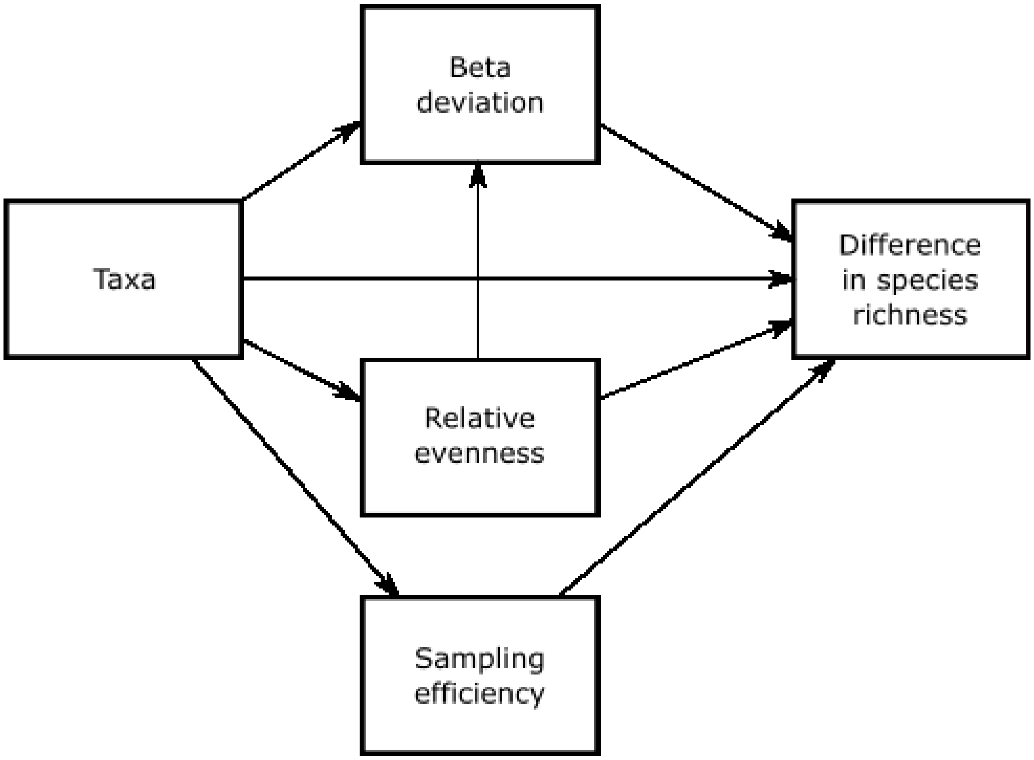

Figure 3.3 Conceptual model for the factors influencing the difference in observed species in a collection of small patches relative to the largest patch. Taxonomy, beta diversity, evenness in species abundance distributions and sampling efficiency are all theorised to have a direct influence. Taxonomy also has indirect effects via the influence of different life history characteristics such as fecundity, mobility and body size in mediating beta diversity, species abundance distributions and, via differences in detectability, on sampling efficiency.

As four studies provided more than 1 dataset (range 2-4; Appendix B), I implemented the individual regressions with a two-level linear mixed model that included a random intercept to account for within- and among-study variation. Model fits were assessed using the coefficient of determination, evaluated separately for marginal (R^2m; accounting for the variance explained in the response relative to a model containing only an intercept for the fixed effects) and conditional contributions (R^2c; which includes variation accounted for by both fixed and random effects) as described in Nakagawa and Schielzeth (2013). Additionally, I tested for any confounding effects of possible covariates specific to different studies. For example, each dataset inevitably differed in the total area for the group of small patches and the area of the single largest patch in the dataset used to compare species richness. They also differed in the number of small patches that were combined to compare with the largest patch. To test for any sensitivity in the results to these variations, I calculated the Pearson correlation between each covariate with model residuals. I found no evidence that these differences among datasets accounted for any unexplained variation in results (all $p > 0.38$).

After fitting the full path analysis (4 models), I iteratively tested alternative structures, adopting the model with the lowest AIC (ΔAIC to second ranked model >10). I tested the overall path model fit using Shipley's directional separation (d-sep) test, which tests whether the causal independence among predictors implied in the graphical model are supported (Shipley, 2000). For example, the path model assumes beta diversity and sampling efficiency are independent (there is no path between them; Fig. 3.3). The d-sep test is used to verify these assumptions in model structure. The test statistic for directional separation is Fisher's C which has a χ^2 distribution with $2k$ degrees of freedom, where k is the number of tests of independence (Shipley 2009).

To establish the strength of support for each hypothesis, I used standardized coefficients. As no single path coefficient can be calculated for categorical predictors in confirmatory path analysis I instead used ANOVA to identify the overall statistical significance for taxonomy and calculated marginal means for each level (invertebrates, birds, non-volant vertebrates) to indicate the direction of effects (Lefcheck, 2016). To test for any difference in coefficients between the levels of categorical predictors, I did pairwise *post hoc* tests using the Tukey-Kramer method to correct for multiple tests. As an alternative effect size for the direct effects of each predictor in Model 1, I used Cohen's (1977) effect size index f^2, where for predictor B: $f_B^2 = \frac{R_{AB}^2 - R_A^2}{1 - R_{AB}^2}$, where R_{AB}^2 and R_A^2 are the proportion of variance explained by the fixed effects for models including all predictors and that omitting the predictor of interest (here predictor B), respectively. Thus, f_B^2 provides the proportion of explained variation by predictor B, relative to the proportion of unexplained variation in the full model.

3.3.3 Quantifying beta diversity among the small patches

As a predictor of the strength of beta diversity in regression analysis, I used an individual-based null model to calculate a beta deviation statistic, thematically following Kraft et al. (2011). First, I calculated the observed beta partition for only the smallest patches, $\beta_{SS} = (1 - \bar{\alpha}_{SS}/\gamma_{SS})$, where $\bar{\alpha}_{SS}$ and γ_{SS} are the mean richness per a small patch and the total richness among the all small patches, respectively, and β_{SS} is the observed beta diversity. This takes values from 0 – 1 and represents proportional turnover (Tuomisto, 2010), where in this application it is the turnover within the small patches.

As each study differed in total diversity and the number of patches, I used an individual-based null model to determine how widely the observed turnover differs from that expected based on the characteristics of each dataset. The null model re-sampled the same number of individuals for each patch as in the observed data from the overall ("regional") species abundance distribution of the grouped patches. The probability of sampling an individual from a given species in the null model algorithm depends on its relative abundance in the regional SAD. This sampling procedure simulates the expected distribution of species across the patches if individuals are randomly positioned within them. A beta deviation statistic is then calculated for each dataset as the observed beta β_{SS} minus the mean β_{SS} of the simulated null communities, divided by the standard deviation β_{SS} of the simulations. Thus, a positive value for the beta deviation means the observed species turnover among small patches is greater than the expected (i.e., assuming individuals were randomly distributed among patches and the overall SAD for the dataset represents the true landscape SAD). I calculated beta deviation from 1000 null model simulations.

3.3.4 Quantifying evenness in species abundance distributions (SAD)

I quantified evenness using Pielou's (1975) measure; the ratio of the Shannon diversity and the log of total species number (hereafter evenness). This measure (also known as Shannon evenness) is among the best measures of the evenness property of species abundance distributions and is the most reliable measure of this property for smaller sample sizes (McGill, 2011). To quantify the relative evenness in abundance distributions among the small patches, I again used a null model approach. I assumed the regional SAD (the sum of abundances of every species across all patches) reflects the underlying distribution of abundances for the landscape. I pooled the abundances for the small patches only and calculated their observed evenness. I then simulated null abundance distributions by drawing the same total number of individuals as were observed in the pooled small patches from the regional SAD and calculated evenness for each of these. The evenness deviation statistic was calculated as for the beta deviation as the observed evenness minus the mean evenness of the simulated small patch SAD divided by the standard deviation in the null simulations. I again simulated 1000 null communities. Thus, a positive value for the evenness deviation indicates an observed distribution of abundance among the small patches that is higher (closer to a horizontal rank abundance distribution) than would be expected for the number of individuals given the regional SAD.

3.3.5 Testing for patch size-dependence in sampling efficiency

I also included a predictor intended to reflect differences among the studies in their efficiency in sampling larger sites. My hypothesis here is that size bias in sampling (where smaller patches received proportionally more sampling effort) will increase the likelihood that the richness of the smaller patches is disproportionately sampled. To create a predictor, I assume constant faunal density across patches (Connor et al., 2000) and therefore, that the strength of any negative correlation between sampling density (which I define as the number of individuals comprising the sample for that patch divided by its area) and the area of the patch also reflects how strongly proportional sampling effort decreased with patch size within that study. For each dataset, I estimated faunal density for each patch as the ratio of the number of sampled individuals and the patch area. Finding a strong non-linear pattern in most datasets, I calculated the Pearson correlation coefficient of sampling density with the log of patch area. I used this as a proxy measure of the likely magnitude of disproportionate sampling as a function of patch area.

All statistical analyses were done with R-3.6.1 (R Core Team, 2019) with custom packages nlme (Pinheiro et al., 2019), piecewiseSEM (Lefcheck, 2016) and emmeans (Lenth, 2019) used respectively for regression modelling, confirmatory path analysis and *post hoc* tests among levels for the taxonomy categorical predictor.

3.4 Results

3.4.1 Trends in richness and predictors within and among taxa

The difference in species richness between a group of the smallest patches and the single largest patch was positive for 27 (71%) of 38 datasets, with a mean difference between them equal to 23.5% of overall (gamma) diversity. Richness differences were highest among invertebrates $\left(\overline{SRd}_{inv} = 0.46\right)$ and lowest for birds $\left(\overline{SRd}_{birds} = 0.04\right)$. Across all datasets, beta deviation had a mean value of 1.25 (units = standard deviation in the null model distribution), indicating the observed beta partition in most datasets was higher than expected if species had assembled within the smallest patches at random. Invertebrates had the highest mean beta deviation $(\overline{BD}_{inv} = 1.91)$, birds the least $(\overline{BD}_{birds} = 0.77)$. Evenness deviation had a mean value of -1.65, indicating abundances were typically less even among small patches than expected given the regional distribution. Mean deviations from the regional SAD were least negative for non-volant vertebrates $(\overline{EV}_{vert} = -0.20)$ and most negative for invertebrates $(\overline{EV}_{inv} = -2.34)$. I found there was a significantly negative correlation (P-value <0.05) between log area and sampling density (number of individuals sampled/area of patch) in 30 of 38 datasets and the mean correlation across all datasets was -0.62. Invertebrates had the most negative mean correlation with patch area ($\overline{SE}_{inv} = -0.72$), non-volant vertebrates the least negative ($\overline{SE}_{vert} = -0.52$).

3.4.2 Confirmatory path analysis modelling

The path model with the most support included all direct effects but did not include an indirect influence of taxa on evenness or sampling efficiency (Fig. 3.4). All independence claims were supported by directional separation tests (Fisher's *C* = -1.23, *df* = 7, *p* = 0.26). The direct effects including all four hypothesised predictors explained 73% of the variation in species richness differences (Fig. 3.4), which increased to 94% when the additional variance accounted for by the inclusion of the random effect (different data sources) in the model (Intraclass correlation coefficient = 0.75; Fig. 3.4, Tables 3.1, 3.2).

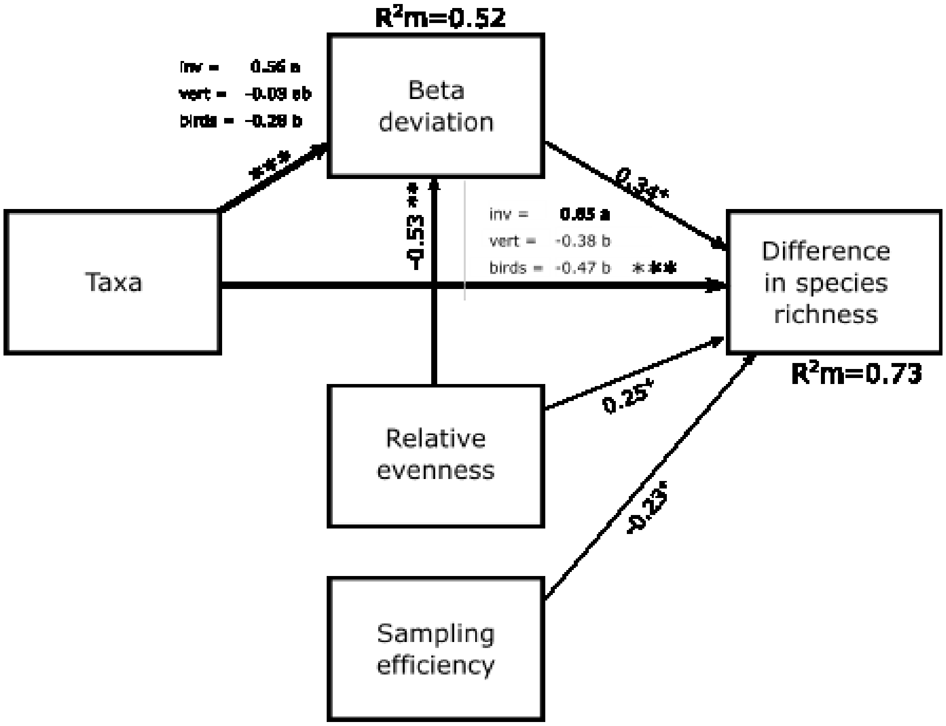

Figure 3.4 Results of confirmatory path analysis. Coefficients are only shown for pathways with Type I error probabilities < 0.05 (* = $p < 0.05$; *** = $p < 0.001$). For the effects of taxa, least squares means for each factor level is shown along with compact letter display of pairwise differences significant at the 5% level using the Tukey-Kramer method to adjust for multiple comparison; factor levels with the same letter are not significantly different from one another. R^2m = variance explained only by the fixed effects in the model. For the main pathway, the conditional variance in species richness difference explained (i.e., including the random intercept for source study) R^2c = 0.94 (see also Tables 3.1, 3.2).

Table 3.1 Overall results of confirmatory path analysis. The structure for the final path model (Fig. 3.4) included regression equations 1 and 2 ('Model' see Methods). Response SRd is the difference in species richness between the group of small patches and the single largest patch for each dataset, while response BD is the beta deviation. EV is the evenness of abundance distributions, SE is the implied size-dependence in sampling efficiency TAXA is a categorical predictor with levels INV= invertebrates, BIRDS and VERTn = non-volant vertebrates. Shown are the estimated coefficient in the path model, along with the standard error, degrees of freedom critical value and type I error probability.

Model	**Response**	**Predictor**	**Estimate**	**Std. Err.**	**df**	**Crit. value**	***P*-value**
1	SRd	BD	0.342	0.146	6	2.34	0.058
		SE	-0.226	0.099	6	-2.27	0.064
		EV	0.249	0.118	6	2.10	0.080
		TAXA			2	24.93	<0.001
		INV	0.654	0.173	28	3.78	<0.001
		VERTn	-0.377	0.235	26	-1.60	0.122
		BIRDS	-0.469	0.189	26	-2.48	0.020
2	BD	EV	-0.529	0.109	8	-4.86	0.001
		TAXA			2	9.65	<0.001
		INV	0.561	0.189	28	2.97	0.006
		VERTn	-0.027	0.289	26	-0.094	0.926
		BIRDS	-0.281	0.229	26	-1.23	0.230

After accounting for all predictors, invertebrate taxa had a larger mean difference in species richness than either birds or non-volant vertebrates, while birds and non-volant mammals did not differ from one another (Fig 3.4; Table 3.1). The categorical predictor for taxa directly accounted for the most individual variation explained by any predictor relative to the unexplained variation ($f_{taxa}^{2} = 0.93$). The other three hypotheses accounted for similar amounts of explained, relative to unexplained, variation ($f^2_{BD} = 0.18$; $f^2_{EV} = 0.164$; $f^2_{SE} = 0.166$; Fig 3.4; Table 2). Taxonomic grouping and evenness deviation had indirect effects on richness differences, both via their influence on beta diversity ($R^2m = 0.52$). Beta deviation was more positive for invertebrates than birds but did not differ between either of those groups relative to non-volant mammals. More even distribution of abundance among the small patches had a strong negative effect on beta deviation (Fig 3.4; Table 3.1).

Table 3.2 Type III ANOVA table for contribution of each predictor in confirmatory path analysis (see also Table 3.1, Fig. 3.4). SRd = difference in species richness between the several small patches and the single largest patch. Other predictors are as for Table 3.1.

Response	Predictor	Test Stat	df	P-value
SRd	EV	6.5	1	0.022
SRd	BD	6.5	1	0.011
SRd	SE	6.5	1	0.014
SRd	TAXA	6.5	1	<0.001
BD	TAXA	9.7	2	0.008
BD	EV	9.7	2	0.396

3.5 Discussion

More rapid accumulation of species when sites are combined in small-to-large size order is a very common observation for a wide range of taxa (Quinn and Harrison, 1988, Robinson and Quinn, 1992, Cook, 1995, Peintinger et al., 2003, Richardson et al., 2015). This has been among the evidence used to argue that sub-division has neutral to positive effects on species diversity (Fahrig, 2017, Fahrig et al., 2019), although this conclusion remains controversial (Haddad et al., 2015, Fletcher et al., 2018). The most common explanation for greater species richness in groups of smaller patches is that increased environmental heterogeneity in sub-divided habitats promotes beta diversity among them (e.g., Quinn and Harrison, 1988, Tscharntke et al., 2002b, Fahrig, 2017). While this has recently been demonstrated empirically for plants and butterflies on lake reservoir islands (Liu et al., 2018, MacDonald et al., 2018b), few direct tests of this or competing explanations exist. It seems reasonable to consider other possibilities, as the distribution of diversity in any landscape reflects not only environmentally or stochastically driven species turnover, but the interaction of many possible competitive and other assembly mechanisms (e.g., Shmida and Wilson, 1985, Tilman, 1994, Hubbell, 2001, Fukami, 2004, Leibold et al., 2004).

In addition to the spatial distribution of species, which determines beta diversity in continuous and discrete habitats, the commonness and rarity pattern of a community as described by species-abundance distributions can also influence diversity patterns (He and Legendre, 2002, Plotkin and Muller-Landau, 2002, Harte et al., 2008). This study shows that after accounting for intrinsic differences among taxa, evenness of species abundance distributions directly explained a similar amount of variation in richness differences as beta diversity. As expected, evenness of abundance among the small patches also moderated the observed beta diversity (Plotkin and Muller-Landau, 2002). Results also suggest that disproportionate sampling efficiency in larger patches could over-estimate the richness differences between large patches and groups of small ones. It is perhaps surprising that these factors have not been more widely considered in addressing the SLOSS debate. The omission of these factors in past studies, particularly given their opposite effects on the richness difference, has likely contributed to the controversy.

3.5.1 Sub-division could affect species richness by altering species abundance distributions

How global change processes such as fragmentation affect the relative commonness of species is not yet well understood, especially in mobile taxa (Marini et al., 2014). At the scale of individual fragments, decreasing area tends to result in less even species abundance distributions in plants (Wilson et al., 1999) and mobile insects (Marini et al., 2014). However, when the abundances across multiple discrete patches are combined, the opposite pattern has emerged, at least for experimental plant communities (Quinn and Robinson, 1987) and birds in forest fragments (Cushman and McGargal, 2003). One explanation offered is priority effects, where the colonization history of the site determines which species become dominant in smaller patches (Cushman and McGargal, 2003, Fukami, 2004, Chase, 2010).

Increases in the evenness of pooled abundances among small habitat patches should increase local richness but decrease beta diversity (He and Legendre, 2002, Plotkin and Muller-Landau, 2002). These results suggest the effect of increasing local richness can be large enough to explain elevated diversity in groups of small patches. For example, some patch-size-dependence in evenness would explain Simberloff and Gotelli's (1984) observation that small patches of vegetation in the prairie-forest ecotone consistently contained more species than null model predictions, while larger patches contained fewer. On the other hand, as expected (Plotkin and Muller-Landau, 2002, Green and Ostling, 2003), decreased evenness among small patches increased beta diversity, the usual explanation for higher richness in sub-divided habitat. However, while elevated beta diversity could arise from drift or environmental heterogeneity (Tscharntke et al., 2002b, Chase, 2003, Liu et al., 2018), this discounts a possible role for changes in competitive or mass effects (Levins and Culver, 1971, Shmida and Wilson, 1985, Tilman, 1994), which will also change with sub-division.

The role of evenness in this analysis thus raises some questions for future investigation. First it suggests a need to quantify, and to better understand, the mechanism of changes in evenness within and among patches following habitat sub-division. Second, it suggests that SLOSS type differences in richness following land clearance and sub-division could depend on the pre-fragmentation distribution of abundance. For example, as most temperate taxa are less evenly distributed than those in the tropics (Alroy, 2015), within a taxon and habitat type, the strength of dominance in richness for groups of small patches might increase with latitude.

3.5.2 Taxonomic grouping dominated explained variation in SLOSS

I found richness differences in groups of small patches relative to a single large patch were most strongly associated with taxonomic group, which directly accounted for most of the explained variation among datasets. In this analysis, all ten datasets where the single largest patch contained more species were either birds (8/16 datasets) or mammals (2/3 datasets). However, I doubt this provides reliable general SLOSS inference for these taxa. For non-volant vertebrates, I clearly had too few datasets (n = 6) to draw any wider inference. Even though replication for birds was higher (n = 16), these included 7 datasets on high-latitude migratory birds from just two studies (Haila, 1983, Haila et al., 1993) and both studies showed colonization among patches to be consistent with random placement of species. Under random placement, the probability a species is present in a patch depends only on the number of individuals and the proportion of total habitat area constituted by the patch (Coleman, 1981). Random spatial patterns decrease beta diversity among, and endemicity within, patches of all sizes (Plotkin and Muller-Landau, 2002, Green and Ostling, 2003). Quinn-Harrison type curves under perfect random placement will be identical, but nestedness in species distribution across natural habitats tends to result in large patches containing more species than groups of small patches. Such was the case here for 6 out of 7 high latitude migratory bird datasets. Among other bird datasets, the species richness of the largest patch exceeded that of the group of several small patches in 1 of 9 datasets.

Although Quinn & Harrison's (1988) metastudy showed a strong small patch dominance of richness for most island and habitat-island datasets regardless of taxa, far less SLOSS related evidence has been presented for vertebrates - particularly mammals. For example, Fahrig (2017) in a meta-analysis of the SLOSS literature identified 60 relevant studies: 77% were either plants or invertebrates, 13% were birds and 10% were other vertebrates (2 fish, 4 herpetofauna). The combination of an unbalanced literature and my own non-representative data sources make it difficult to draw any general taxonomic inference for the SLOSS pattern as implied by QH curves. However, consistent with the lower probability of observing rare species in small patches (Deane and He, 2018), evidence suggests birds and mammals are less likely to have greater richness in groups of small patches than plants and invertebrates, as the former groups in general require large habitat areas to maintain viable population sizes (Patterson and Atmar, 1986, Crooks et al., 2001, Gibson et al., 2013).

3.5.3 Uncertainties

A major limitation with this analysis is the small number of datasets and the resulting wide range of taxa lumped within my broad taxonomic groupings. I recognize the enormous scope for variation within each group and the unequal representation of non-volant vertebrates limit the generality. I also acknowledge the complete lack of data for sessile organisms. Another source of variability was the different habitat types (islands, habitat islands and fragments) from which the data were collected. In my analysis, this variability probably accounts for most of the 20% of variation explained by the random intercept term in the regression models, which represented the different data sources. I was also unable to include differences in landscape properties but such factors as the matrix land use, connectivity and remaining habitat in the landscape are likely to affect species coexistence in metacommunities and, therefore, the assembly of diversity (Fournier et al., 2017, Rybicki et al., 2018).

Finally, while my main interest has been in understanding the macroecological pattern of small patch dominance in species richness, my results cast new doubt on the reliability of inference obtained from QH curves. Specifically, I question whether it is reasonable to expect that similarly complete species lists can be obtained from patches that often differ in size by several orders of magnitude. Related problems associated with the confounding of sampling effort with patch size have been noted (Gavish et al., 2012), although careful study design can support analyses that control for this (Liu et al., 2018, MacDonald et al., 2018a, MacDonald et al., 2018b). Overall, I agree it is doubtful that QH curves can provide reliable inference (Ramsey, 1989, Mac Nally and Lake, 1999, Alberto and Manly, 2006, Gavish et al., 2012) and direct tests of potential competing mechanistic explanations (e.g., Liu et al., 2018) seem to present a more promising means to understand the assembly of diversity in sub-divided landscapes.

3.6 Conclusions

In this chapter I have elaborated on the complexity underlying the relationship between sub-division and diversity in discrete habitat networks. I have confirmed that relative evenness of abundance is a reliable predictor of species richness differences in the SLOSS debate and the effects of sub-division on diversity, including increased beta diversity, are mediated by changes in evenness. Importantly, I have demonstrated a likely role for differential sampling efficiency in over-stating the differences, although the modest effect size suggests this is not adequate to entirely explain observed differences.

3.7 References

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Chapter Four: A shared species model to determine the expected effects of habitat loss and fragmentation on species diversity

4.1 Abstract

Understanding the effects of habitat fragmentation on species diversity is an enduring problem in ecology and conservation biology. Species-area relationships derived from sampling theory describe the scaling of species richness with area under varying patterns of aggregation and species abundance distributions but do not predict the effects of habitat sub-division. I use sampling theory to instead derive a model for the expected number of species shared in multiple samples (zeta diversity), allowing the effects of sub-division on diversity to be determined analytically. Under random placement of individuals, the model is parameter-free. For non-random spatial distributions, it can be modelled at the cost of a single fitting constant, which scales with sampling area according to a power function. In both cases, zeta diversity models can be used to calculate values such as gamma diversity and the number of species found in only a single patch (single-patch endemics; SPE) allowing the effects of sub-division to be predicted. I validate model predictive performance in simulated sub-divided landscapes using empirical and simulated data under random and non-random placement of individuals, comparing observed gamma diversity and SPE against the predictions of the analytical model and those based on the equivalent area within a single fragment. The model accurately re-produces emergent properties of diversity in sub-divided habitat, showing the relative number of species in several small vs a single large patch depends on intraspecific spatial patterns; aggregated distributions result in greater diversity in sub-divided habitats while the number does not differ under random

placement. Through the shared species model, I provide a framework for quantifying the effect of landscape fragmentation on species diversity.

4.2 Introduction

What, if any, difference in species richness should be expected between a single continuous patch of habitat and a group of discrete habitat patches of equal total area? Application of this question to conservation reserve design sparked debate that has remained unresolved since it emerged during the 1970s (Diamond, 1975b, Simberloff and Abele, 1976, Gilpin and Diamond, 1980, Higgs and Usher, 1980, Quinn and Harrison, 1988). More recently, it has been re-invented as conflicting opinion on the biodiversity impacts of fragmentation *per se* (Fahrig, 2017, Haddad et al., 2017, Fletcher et al., 2018, Fahrig et al., 2019). Essentially, it is a problem of spatial turnover: how species composition changes with area. Spatial sampling theory approaches this question by combining two macroecological patterns: species abundance and spatial distribution patterns. This approach can predict both important diversity patterns (He and Legendre, 2002) and how compositional similarity changes among pairs of sites (Plotkin and Muller-Landau, 2002). Here I use sampling theory to derive a model for the expected number of species shared among multiple sites – the zeta diversity (Hui and McGeoch, 2014). From zeta diversity, a range of different diversity measures can be calculated (Hui and McGeoch, 2014, Arita, 2017, Lu et al., 2019); I use this to predict expected species richness patterns under any combination of patch number and size.

The simplest way to compare the species composition of any number of discrete samples, or habitat patches, is to ask how many species they share. While the absence of a species at a site does not provide conclusive evidence that the site is not suitable for that species, its presence is evidence that it is able to live at the site (Legendre and Legendre, 2012). This must be the case even if viability of that population occasionally (or entirely) depends on propagules from outside sources (Brown and Kodric-Brown, 1977, Shmida and Wilson, 1985, Pulliam, 1988). The number of species shared between two samples is also central to the calculation of measures of pairwise association and dozens of alternative similarity (and dissimilarity) metrics have been developed (reviewed in Jost et al., 2011, Legendre and Legendre, 2012). Each of these measures provides slightly different information about the compositional patterns demonstrated by two or more samples (Tuomisto, 2010, Legendre, 2014). More recently, interest has extended to consider how diversity is shared among multiple sites in a network (e.g., Diserud and Ødegaard, 2007, Chao et al., 2008, Arita, 2017, Lu et al., 2019). The concept of zeta diversity – the number of species shared among any number of samples (Hui and McGeoch, 2014) – unifies similarity theory, showing shared species are a fundamental unit of currency from which multiple diversity patterns can be derived (Hui and McGeoch, 2014, Arita, 2017, Lu et al., 2019). Typically, zeta diversity is calculated from occupancy data but here I illustrate how it can be calculated using spatial sampling theory.

The species-area relationship (SAR) bears a strong relationship with measures of compositional similarity, as both describe turnover in space (Lande, 1996, Harte and Kinzig, 1997, Koleff et al., 2003, Tjørve and Tjørve, 2008, Pan, 2015). The SAR has been an important means for exploring how species number scales with area (e.g., Arrhenius, 1921, Preston, 1962, Coleman, 1981, He and Legendre, 2002, Wilber et al., 2015). It has also been used to derive an expected species overlap among areas, allowing its use in predicting the impacts of habitat loss (Harte and Kinzig, 1997, Harte et al., 1999, Tjørve, 2002, Tjørve, 2010), or sub-division, usually under an assumption of a power law form (Simberloff and Abele, 1976, Higgs and Usher, 1980, Tjørve and Tjørve, 2008, Tjørve, 2010, Hanski et al., 2013, Rybicki and Hanski, 2013). The power law SAR has also been adapted for use in fragmented habitat by incorporating an extra term derived from metapopulation theory (Hanski et al., 2013).

Unlike SAR based on the power law though, species-area models derived from spatial sampling theory depend only on species abundance and spatial distributions and have shown how variations in these fundamental ecological characteristics affect the way in which local diversity scales with area (He and Legendre, 2002, Green and Ostling, 2003, Tjørve et al., 2008, Kitzes and Harte, 2014). Similarly, Plotkin and Muller-Landau (2002) derived the expectation for patterns of similarity between two sites under different species abundance distributions and spatial patterns. The same basic sampling theory can be used to ask how the expected number of species shared among – or endemic to - multiple samples should change based on ecological (species abundance distributions and spatial patterns) and geometric (sampling area and number) constraints.

With the expected number of shared species among samples (their zeta diversity) established, general formulae for a range of incidence-based diversity measures can be calculated (Hui and McGeoch, 2014, Lu et al., 2019). For example, if ζ_2 denotes zeta diversity of order 2 (the expected number of species shared in two samples), then Jaccard's pairwise similarity index is $\zeta_2/(2\zeta_1 - \zeta_2)$ (Hui and McGeoch, 2014). Similarly, a formula for the total number of species in a group of samples can be derived based on their zeta diversity (Methods). Rather than using species incidence as in the original derivation of zeta diversity (Hui and McGeoch, 2014), here I use abundance data to calculate the expected number of shared species, and demonstrate the use of the general formulae based on the zeta diversity partition accurately predicts the expected effects of sub-division on diversity.

My aims for this chapter are to (*i*) derive a model to predict the number of shared species in equal-sized sampling areas for random and non-random placement of individuals; (*ii*) validate the model predictions for a range of spatial and abundance distributions; (*iii*) use the models to demonstrate how shared species should be expected to change under different constraints, both ecological (abundance and spatial distributions) and geometrical (patch area and number).

4.3 Methods

4.3.1 Shared species under random placement

Species-area relationships have been shown to be ultimately determined by the abundance of individuals of each species and their spatial pattern (He and Legendre, 2002). Assuming random and independent placement of the individuals of each species in space, the expected number of species found in subarea *a,* of total area *A,* is given by the sum over all species of the probability that at least one individual of the species is present (Arrhenius, 1921, Coleman, 1981):

$$\bar{s} = \sum_{i=1}^{S} p_i = \sum \left[1 - \left(1 - \frac{a}{A}\right)^{N_i}\right] \qquad (4.1)$$

Retaining the assumptions of independent and random spatial distribution, if two independent samples of size *a* are obtained from the same community, the expected number of species in common is the sum over all species of the product of the probabilities that at least one individual of each species is present in each sample. More generally, among *m* samples, each equal to subarea *a* of total area *A*, the expected number of shared species $SS_{m|a}$ should follow:

$$E\left(SS_{m|a}\right) = \sum_{i=1}^{S} P_{1,i} \cdot P_{2,i} \cdot \ldots \cdot P_{m,i} = \sum \left[1 - \left(1 - \frac{a}{A}\right)^{N_i}\right]^m \qquad (4.2)$$

Thus, assuming random placement of individuals, the expected number of species present in repeated samples of a given area from an assemblage depends only on the abundance vector N_i. As species abundance distributions become more even, the number of shared species increases, (Plotkin and Muller-Landau, 2002).

4.3.2 Shared species under non-random placement

Eq. 4.2 predicts the number of species shared among *m* samples of area *a*, provided individuals from each species are randomly located in space. However, it is most common for species to be clustered (aggregated) in space (He et al., 1997, Condit et al., 2000). Intraspecific aggregation has the effect of decreasing the expected number of species in sub-area *a* (He and Legendre, 2002) and in decreasing the expected compositional similarity of two samples (Plotkin and Muller-Landau, 2002). He and Legendre (2002) adapted the sampling SAR for aggregated species spatial distributions based on the negative binomial distribution. Using the same logic as for the random placement of individuals, this suggests a model for expected shared species in *m* samples under non-random placement:

$$E\left(SS_{m|a}\right) = S\left[1 - \left(1 - \frac{a}{A}\right)\right]\left[\sum_{i=1}^{S}\left(1 + \frac{N_i a}{A k_i}\right)^{-k_i}\right]^m \tag{4.3}$$

where: *S* is the total number of species in the assemblage, N_i is a vector of the abundance of each species and k_i is a parameter describing the spatial distribution of species *i* in sub-area *a* of total area *A*. The term $(1 - a/A)$ is required to ensure the number of species is zero when $a = 0$, and *S*, when $a = A$ but is only a statistical modification with no theoretical justification (He and Legendre, 2002). In the study of fragmented landscapes, the main interest is in understanding how small to moderate sized fractions of the original habitat area are affected. This suggests that values of the remaining fraction near 0 or *A* will not be relevant and the correction factor $(1 - a/A)$ is unnecessary and can thus be omitted from Eq. 4.3.

The value of k_i depends on the mean abundance of species *i* in area *a*. If μ_i is the mean density of species *i* in area *a*, k_i varies over the intervals $(-\infty, -\mu_i)$ and $(0, \infty)$. Negative values of *k* represent the probability of presence of a species in sub-area *a* derived from a binomial distribution; as k_i approaches $-\mu_i$ from the negative side, this describes an increasingly regular spatial distribution (He and Legendre, 2002). Positive values of *k* represent the probability of presence of the species derived from the negative binomial distribution, varying over the interval $(0, \infty)$, where values approaching 0 reflect increasingly aggregated spatial patterns (He and Legendre, 2002).

Parameter k can be generalized using a constant scaling factor, *c*, for all species to convert mean density to k. Although every species in the community typically follows a distinct spatial pattern (He et al., 1997, Condit et al., 2000), the value for *c* that gives the best fit to all species in an assemblage can be obtained using maximum likelihood or other optimization methods (Plotkin and Muller-Landau, 2002). One advantage of using a single community-level estimate for *c* at each grain is the area-scaling of the term can be explored (Plotkin and Muller-Landau, 2002). Conceptually, scaling factor *c* represents the attraction of intraspecific individuals within area *a*; under aggregated spatial distributions intraspecific individuals have an attractive effect, meaning *c* takes positive values, while in regular spatial patterns the effect of conspecifics is inhibitory, resulting in a negative value for *c* (Zillio and He, 2010).

An alternative interpretation of *c* is as a model parameter that can be used to fit Eq. 4.3 to observed data: $k_i = N_i a/Ac$. Removing the unnecessary term constraining the estimated number of species shared at extreme area values (0 and *A*), results in a non-random model for the number of species shared in *m* samples:

$$E(SS_{m|a}) = \sum_{i=1}^{S}(1-(1+c)^{-k_i})^m \tag{4.4}$$

where all notation is as described above.

An alternative to omitting the constraining term in Eq. 4.4, is to base the shared species probability calculation on the finite negative binomial distribution derived by Zillio and He

(2010). This is the correct probability distribution for spatial aggregation in a finite population and removes the need for the constraining term. Based on the finite negative binomial distribution (Zillio and He, 2010) the expected number of shared species in m samples of area a, is:

$$E\left(SS_{m|\alpha,k,N}\right) = \sum_{i=1}^{S}\left[1 - \frac{\Gamma(N_i + k_i\ /\ \alpha - k_i)\Gamma(k_i\ /\ \alpha)}{\Gamma(N_i + k_i/\alpha)\Gamma(k_i/\alpha - k_i)}\right]^m \tag{4.5}$$

where $\alpha = a/A$; m, k_i, and N_i have the same interpretation as Eq. 4.4; and, $\Gamma(n) = (n - 1)!$ is the gamma function. As with Eq. 4.3 and 4.4, parameter k adjusts the expected mean density of each species in area a according to its spatial distribution and has the same derivation and interpretation as for Eq. 4.4 (He and Legendre, 2002, Zillio and He, 2010). Compared to Eq. 4.4, Eq. 4.5 is more complex and requires additional computational effort due to the large numbers required for the gamma function. Unless the predictive performance represents a substantial improvement, the additional complexity might not be warranted. Thus, in this chapter I compare the performance of the two non-random shared species models, eq. 4.4 and 4.5, using *c* as a fitting constant to validate model predictions against empirical and simulated data. I also explore the scaling of *c* with area in both models (Eq. 4.4, 4.5) under different ecological constraints (SAD and spatial pattern).

4.4 Diversity modelling

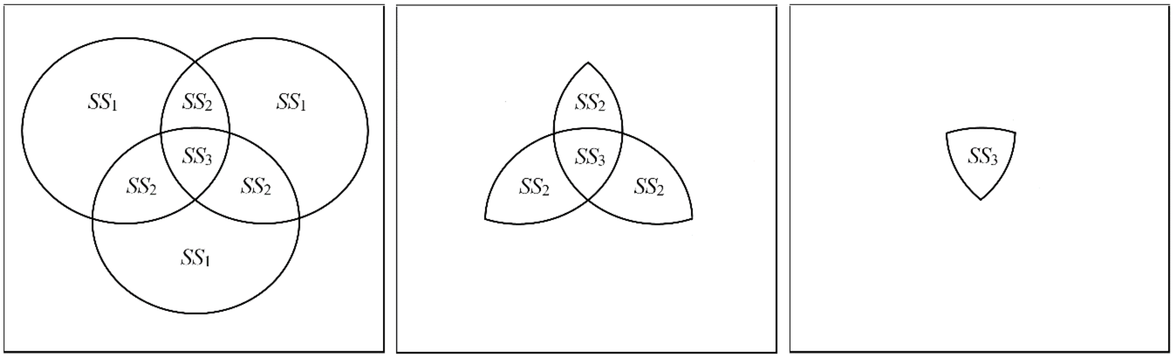
The expected number of species shared among m patches has recently been defined as the zeta diversity of order m (Hui and McGeoch, 2014). With this information, a number of useful diversity values can be calculated for the patches based on these shared components (Hui and McGeoch, 2014). Having obtained estimates for zeta diversity from the shared species models, I use the relationships derived for zeta diversity to calculate the total number of expected species in all patches combined (i.e., gamma diversity) and the number of species found in only a single patch (single-patch endemics). Thus, the shared species models can be used to predict expected patterns of diversity in landscapes comprising any number of samples (or fragments), m, of area a, provided complete knowledge of species abundances and spatial distributions in the original study extent of interest A are available. Although this is rarely the case in actual datasets, it allows for analytical tests of the effects of fragmentation on landscapes by intentionally manipulating the abundance distributions and spatial patterns according to known or theorised values.

4.4.1 Estimating gamma diversity for **m** *fragments of size* **a**

The number of species expected in one sample of area a (alpha diversity) is calculated using the shared species formulae, with $m = 1$. The expected number of species shared (zeta diversity) among any number of samples m of size a can be determined. From the expected shared species, gamma diversity in m samples of area a can be calculated recursively following the inclusion-exclusion formula given in Hui and McGeoch (2014):

$$\gamma_{m,a} = \sum_{j=1}^{m} (-1)^{j+1} \binom{m}{j} SS_j \tag{4.6}$$

where: $\gamma_{m,\,a}$ = the total number of species contained in m samples of area a and SS_j = the number of species shared in j samples (j = 1, 2,…, m). Referring to Fig. 4.1, the derivation of Eq. 4.6 can be illustrated for 3 sites of area a.



$$\gamma_{m,a} = \binom{3}{1} SS_1 - \binom{3}{2} SS_s + \binom{3}{3} SS_3$$

Figure 4.1 Venn diagram illustrating the recursive calculation of gamma diversity from shared species (zeta diversity) components using Eq. 4.6. Each panel shows the area of 'species space' represented by each term of the recursion for three sites shown below the figure.

Each sample has a total richness equal to the alpha diversity for area a (i.e., the average number of species shared in 1 site = SS_1). Ignoring species shared among 2 or more sites, the maximum possible total number of species = $\binom{3}{1}$ SS_1(left panel). To obtain total number of species across the three samples (gamma diversity), the species shared among 2 (SS_2) and 3 (SS_3) sites must be corrected for. There are three possible ways to share species among 2 sites (centre panel), so these are excluded from the total count (i.e., the second term in the summation: $-\binom{3}{2}$ SS_2). As the number of species shared in three sites (right panel) has been completely removed with the exclusion of the species shared in 2 sites, this must be replaced = $\binom{3}{3} SS_3$. The recursion can be easily extended to additional sites (Hui and McGeoch, 2014).

4.4.2 Estimating beta diversity for **m** *fragments of size* **a**

As alpha and gamma diversity can be obtained as described above, Whittaker's (1960) multiplicative, or Lande et al's (1996) additive, beta diversity partitions can be calculated directly.

4.4.3 Single patch endemic species

Single-species metapopulation theory predicts that extinction risk is a function of the number of occupied patches (Hanski, 1999). The species most at risk of extinction from a metacommunity then should be those maintaining only a single sub-population (hereafter, single-patch endemics). This can be calculated from zeta diversity as a function of the number of sites sampled, m, according to the formula (Hui and McGeoch, 2014) $S_m – S_{m-1}$, where S_m and S_{m-1} are calculated from shared species using either Eq.4.4 or 4.5. Note that the number of species expected to be endemic to any number of fragments can be calculated as the difference between the shared species in one less sample.

4.5 Model validation

Model validation consisted of comparing observed values for shared species, gamma diversity and single-patch endemic species obtained from sub-sampling simulated and actual landscapes (hereafter validation landscapes) for different combinations of patch area, a, and patch number, *m*. To provide a point of reference, I also sampled the landscape at the total pooled sampling area (i.e., observed species richness at area a x m), allowing comparison of observed and modelled species number in sub-divided habitat with that found in a single continuous patch of equivalent total area.

I compared the mean observed shared species, gamma diversity and single-patch endemics with the predicted value for the random, and for both non-random, shared species models (Eq. 4.4 and 4.5). Goodness of fit was assessed using the coefficient of determination (R^2) and relative root-mean-square error (rRMSE) between observed and predicted values for shared species, gamma diversity and single-patch endemics in each landscape for each model. Model fit was also assessed graphically, with predicted values falling within 95% confidence limits in observed mean of simulated data considered to represent adequate performance.

4.5.1 Validation landscapes

To validate models, I used both simulated and empirical datasets representing 50-ha landscapes with species distributed according to different abundance distributions and spatial patterns (hereafter 'validation landscapes'). Empirical data were from the 50-ha Barro Colorado stem-mapped forest plot (Hubbell et al., 2005), 2005 census (211845 live stems and 301 tree/shrub species). In simulated landscapes, I independently varied the spatial pattern while retaining a common species abundance distribution and varied the species abundance distribution under a constant set of spatial constraints.

To validate model performance under contrasting spatial patterns, I used the observed data and also simulated three landscapes (as described below) using the BCI empirical SAD, but with individuals positioned (*i*) at random, (*ii*) adopting more aggregated intraspecific clustering than observed at BCI; and, (*iii*) with more regular (dispersed) spatial patterns than at BCI. To simulate random placement landscapes, I used the empirical SAD, but rather than using the observed *xy* locations from the stem-mapping, I randomly positioned individuals in 50-ha space. To validate the non-random shared species models I simulated one regular and two aggregated 50-ha landscapes using the Strauss and Thomas point pattern processes respectively. The Thomas process requires two parameters, one controlling the number of parent nodes (μ), the other representing the standard deviation of the dispersal kernel and thus controlling the strength of clustering of intraspecific individuals (σ). Simulated landscapes used parameter values of μ that increased with the abundance of the species (<100 = 5; 100 - 1000 = 10; > 10000 = 20) and σ values of 25 and 50-m. The Strauss point pattern process has three parameters, β, controlling the intensity of the effect; r, the inhibition radius within which conspecifics are excluded; and, the inhibition strength, γ, which determines how strongly the inhibition radius is enforced. Parameter r was assigned a value that depended on the abundance of the species, setting this to $A/\sqrt{N_i}$ (the distance between individuals in a lattice). Inhibition strength takes values from 0-1, with low values leading to strong enforcement of the inhibition distance. I set this value to 0.1, providing a more regular than random spatial distribution for each species. Regular landscapes were simulated using a Metropolis-Hastings algorithm, with both aggregated and regular spatial patterns simulated using R package ‘spatstat’ (Baddeley et al., 2015).

To validate model performance under different species abundance distributions, I simulated four landscapes with intraspecific clustering similar to that of the empirical data (see following paragraph), but with species abundances distributed according to (*i*) the BCI empirical SAD plus three common SAD models; (*ii*) broken stick, (*iii*) log normal, and (*iv*) log series. All simulated SAD were based on the observed data (total species = 301, total abundance = 211 845). The three validation landscapes varying the SAD were created by simulating three abundance vectors based on the broken stick, log normal and log series species abundance distribution models using R package ‘sads’ (Prado et al., 2017). The three SAD represented a gradient of Pielou’s evenness (Pielou, 1975): broken stick (~0.93); lognormal (~0.87); log series (~0.70); with the empirical data similar in evenness to the log series (0.69). The spatial pattern used in the SAD validation was as described above for the simulated aggregated landscape. I used a value for sigma of 50 m, which had the closest sampling properties (alpha diversity, c-parameter estimates) to the empirical data of all spatial patterns.

After simulating each landscape, they were sub-sampled at different sampling grains and number of replicate samples to use as observed data. Sub-samples were square quadrats at 5-m increments from 5 x 5 to 50 x 50 yielding ten sampling grains (25, 100, 225, 400, 625, 900, 1225, 1600, 2025, and 2500-m^2) with shared species calculated for 5, 10, 15, 20, 25 and 30 samples at each grain.

At each sampling grain *a*, parameter *c* was estimated numerically as the value returning the smallest absolute difference between modelled and observed mean species richness (alpha diversity) at the relevant grain size (i.e., setting *m* = 1 in Eq. 4.4 and 4.5). The best-fit estimate for *c* was inserted into the relevant equation and used to calculate zeta diversity for m samples at that grain size. Zeta diversity was then used to calculate expected gamma diversity and single-patch endemics as described above. The predicted values for gamma diversity and single patch endemics were then compared with the mean of observed values from 100 replicate sets of samples for each combination of a and m in each validation landscape.

4.5.2 Scaling properties of the c-parameter in non-random models

As discussed under model development, parameter k_i in the non-random species area model represents the intraspecific spatial pattern for species i. For the negative and finite negative binomial spatial distributions, the parameter scales according to a power law and can be estimated at any scale once a base scale value is known (Plotkin and Muller-Landau, 2002, He and Hubbell, 2003):

$$c_a = c_0 \frac{a^{z}}{a_0} \tag{4.7}$$

where c_i is the value of the scaling parameter at the spatial grain to be estimated at scale a_i; c_0 is the value of the parameter as base scale a_0 and z is a parameter describing the scaling relationship. Using the community-level scaling factor *c* as a fitting parameter allows the exploration of scaling of this parameter with the area used to model alpha diversity. Here I fit separate estimates of the *c*-parameter at each scale to predict shared species. I also use 400 m^2 as the base scale (a_0) as an estimate of c_0 and test the predictive ability of the power function to estimate the scaling of the *c*-parameter with area in each of the different validation landscapes.

4.5.3 Patterns of shared species under different sampling and ecological constraints

Finally, I use the models to illustrate how the number of shared species is affected by three constraints: sampling grain; species abundance distribution; and, spatial patterns. In this analysis, I simulated landscapes with a total number of species, $S = 250$, distributed according to different species abundance distributions among $N = 250000$ individuals, over a total study area $A = 50$ ha. To illustrate the effects of sample area, I used a random placement of individuals and sampled 20 quadrats at six sampling grains; 0.05, 0.1, 0.25, 0.5, 0.75 and 1-ha. For the effects of the SAD, I simulated five different species abundance distributions varying in evenness. I bounded predictions using two extreme, though ecologically unrealistic, species abundance distributions; (*i*) where all species have an equal number of individuals ($N_i = N/S$) (hereafter 'most even' SAD), and, (*ii*) where all but one species are singletons, with the remaining species having abundance $N - (S - 1)$ ('least even' SAD). Between these two extreme cases, I used the three SAD models used in validation (broken stick, lognormal, log series), which differ in their relative evenness in species abundance.

Note that for all SAD used other than the lognormal SAD, the random placement species-area model has an analytical solution (He and Legendre, 2002), which can also be extended to predict shared species in multiple samples of area a. However, to remain consistent, here I used the random placement shared species model (Eq. 4.2) with simulated series species abundance distribution (SAD) models, generated using R package 'sads' (Prado et al., 2017). The five SAD represent a gradient of evenness according to Pielou's measure (Pielou, 1975); most even (Pielou's evenness = 1), broken stick (~0.93), lognormal (~0.85), log series (~0.70), and, least even (< 0.01). To examine the effect of spatial aggregation, I used the negative-binomial-based non-random model (Eq. 4.4), varying scaling factor c to represent regular ($1/c = -1.01$), random ($1/c = 10$), aggregated ($1/c = 0.1$) and highly aggregated ($1/c = 0.01$) spatial distributions (He and Legendre, 2002, Green and Ostling, 2003). For the species abundance vector in the non-random model, I used the log normal species abundance distribution described above. Sampling grain for the evenness and spatial scenarios was 0.25 ha and shared species were calculated for 20 samples. I normalized the predicted shared species to a proportion of total original landscape species number to provide a relative measure. All simulations and modelling were done in R 3.5.1 (R Core Team, 2019).

4.6 Results

4.6.1 Shared species model

At a 400-m^2 sampling grain, the number of species shared across multiple samples for random and non-random intraspecific spatial patterns were reliably predicted by the corresponding shared species models (Fig. 4.2). Predicted shared species for aggregated, random and empirical landscapes were all within 95% confidence limits for the observed data from repeated sampling of validation landscapes (Fig. 4.2). For regular intraspecific spatial patterns, the non-random model systematically under-predicted shared species, falling below the lower confidence interval (Fig. 4.2c). With increasing sampling grain, shared species model predictions in aggregated landscapes also tended to deviate from 95% confidence limits, although lying above and suggesting overprediction of shared species (the model predicted more shared species than were observed). For regular spatial patterns, increasing sampling grain led to the opposite pattern, increasingly under-predicting. However, even at the maximum sampling grain used in validation (2500 m^2), predicted shared species were close to empirical confidence limits (see Supporting information, Section 4.11, Fig. 4.7).

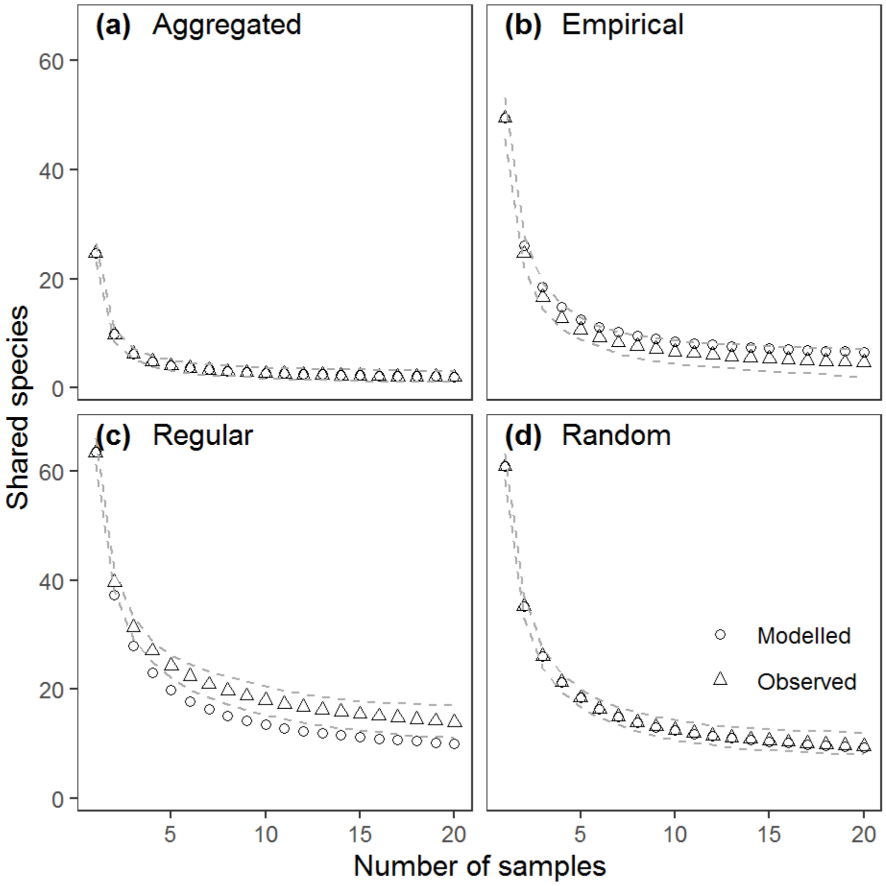


Figure 4.2 Predicted and observed shared species for 20 400-m^2 quadrat samples randomly located in simulated and observed 50-ha landscapes. All landscapes use the empirical Barro Colorado Island (BCI; 2005 census year) species abundance distribution but vary in spatial pattern; (a) high intraspecific aggregation, (b) empirical BCI data, (c) regular intraspecific pattern, and, (d) random placement. Each panel shows the mean (open triangles) and 95% confidence limits (grey dashed lines) in observed shared species from 100 repeat samples. Open circles in panels a-c are model predictions using the best fit estimate for the *c*-

parameter for Eq. 4.4 fit to mean alpha diversity. Panel (d) is the random placement model (Eq. 4.2).

For intraspecific spatial aggregation comparable to that observed in the empirical data, the non-random model predicted the number of shared species equally well for landscapes based on common species abundance distributions (broken stick, lognormal, log series; Fig. 4.8, Section 4.11). Although the model based on the finite negative binomial model tended to perform slightly better overall, there was little difference in performance of the two non-random models in terms of shared species (Table 4.1).

Table 4.1 Model validation for random (Eq. 2) and two non-random shared species models (Eq. 4.4 and 4.5; denoted 4 and 5 below), with estimated gamma diversity and single-patch endemics for each model under contrasting spatial distributions.

Validation landscape	**Measurement**	**Model**	***r*RMSE**	**R^2**
Empirical	Shared species	Eq. 4/5	0.371 / 0.366	0.999 / 0.999
	Gamma diversity	Eq. 4/5	0.031 / 0.027	0.999 / 0.999
	SPE	Eq. 4/5	0.029 / 0.028	0.963 / 0.948
Aggregated	Shared species	Eq. 4/5	0.271 / 0.078	0.998 / 0.999
(sigma=50)	Gamma diversity	Eq. 4/5	0.047 / 0.016	0.999 / 0.999
	SPE	Eq. 4/5	0.046 / 0.028	0.980 / 0.988
Aggregated	Shared species	Eq. 4/5	0.271 / 0.265	0.999 / 0.999
(sigma=25)	Gamma diversity	Eq. 4/5	0.046 / 0.044	0.999 / 0.999
	SPE	Eq. 4/5	0.047 / 0.030	0.980 / 0.987
Regular	Shared species	Eq. 4/5	0.289 / 0.295	0.999 / 0.998
	Gamma diversity	Eq. 4/5	0.029 / 0.026	0.999 / 0.999

	SPE	Eq. 4/5	0.047 / 0.068	0.962 / 0.966
Random	Shared species	Eq. 2	0.007	0.999
	Gamma diversity	Eq. 2	0.004	0.999
	SPE	Eq. 2	0.027	0.994

4.6.2 Validation of diversity predictions

Gamma diversity in sub-divided habitat was closely predicted (all $R^2 > 0.99$; rRMSE <0.047) for all models in all validation landscapes (Fig. 4.3, Table 4.1). The number of species found in a continuous area compared with that in sub-divided patches depended on spatial pattern; in aggregated and empirical landscapes, gamma diversity was lower in the single large patch (Fig. 4.3, 4.9). For regular landscapes, the model slightly over-predicted gamma diversity, although this estimate was nearly identical to the observed species in the continuous area, which lay above that of the sub-divided habitat, albeit within the 95% confidence limits in the observed sub-divided habitat (Fig 4.3c). Under random placement, shared species and gamma diversity were effectively in perfect agreement with mean observed data for all models ($R^2 > 0.999$; Table 4.1; Fig. 4.3d) and the number of species in continuous and sub-divided habitats at all grains was the same (Fig. 4.3d).

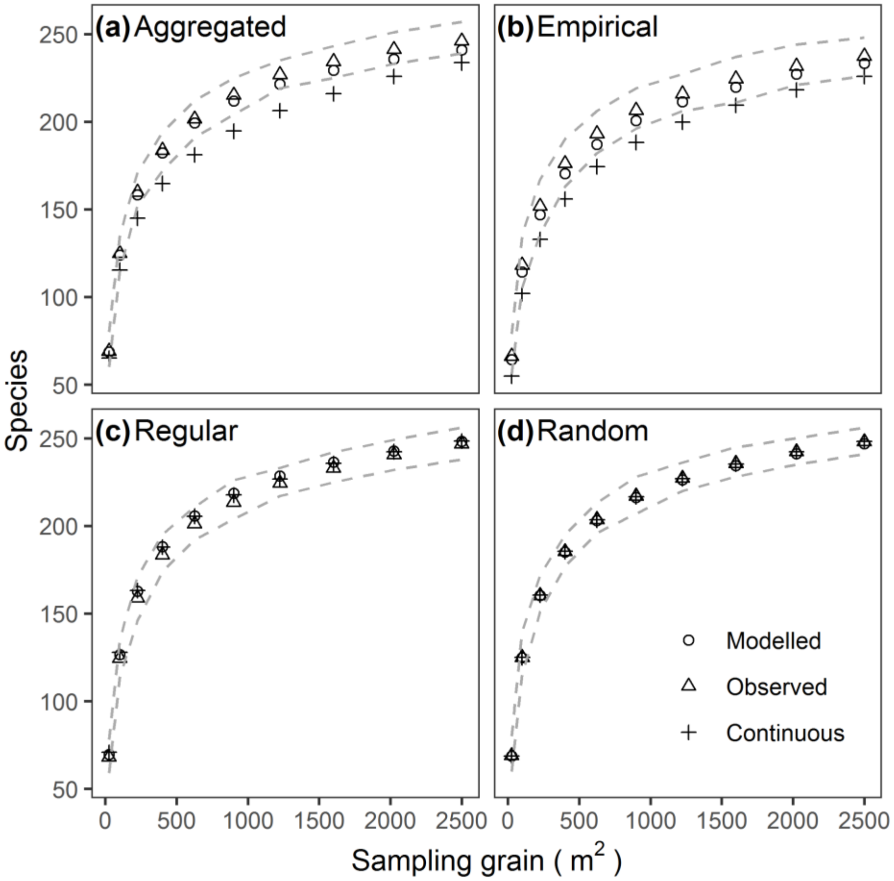


Figure 4.3 Observed and modelled gamma diversity for 20 samples from simulated and observed 50-ha landscapes varying sampling grain and spatial pattern. (a) highly aggregated intraspecific pattern; (b) empirical BCI data; (c) regular intraspecific pattern; and, (d) random placement. Each panel shows the mean (open triangles) and 95% confidence limits (grey dashed lines) in observed shared species from 100 repeat samples and the species richness for continuous areas of the same total size (+).

Single-patch endemics were closely predicted using the non-random shared species models, though not quite as well as gamma diversity ($R^2 > 0.94$; rRMSE < 0.068; Fig. 4.4). However, this component of diversity had considerable within-landscape variability relative to the variations in observed gamma diversity (Fig. 4.4). There was little difference in the predictive performance of the two non-random models for shared species, modelled gamma diversity or single-patch endemics (Table 4.1), although where differences were observed, the finite negative binomial model tended to be superior.

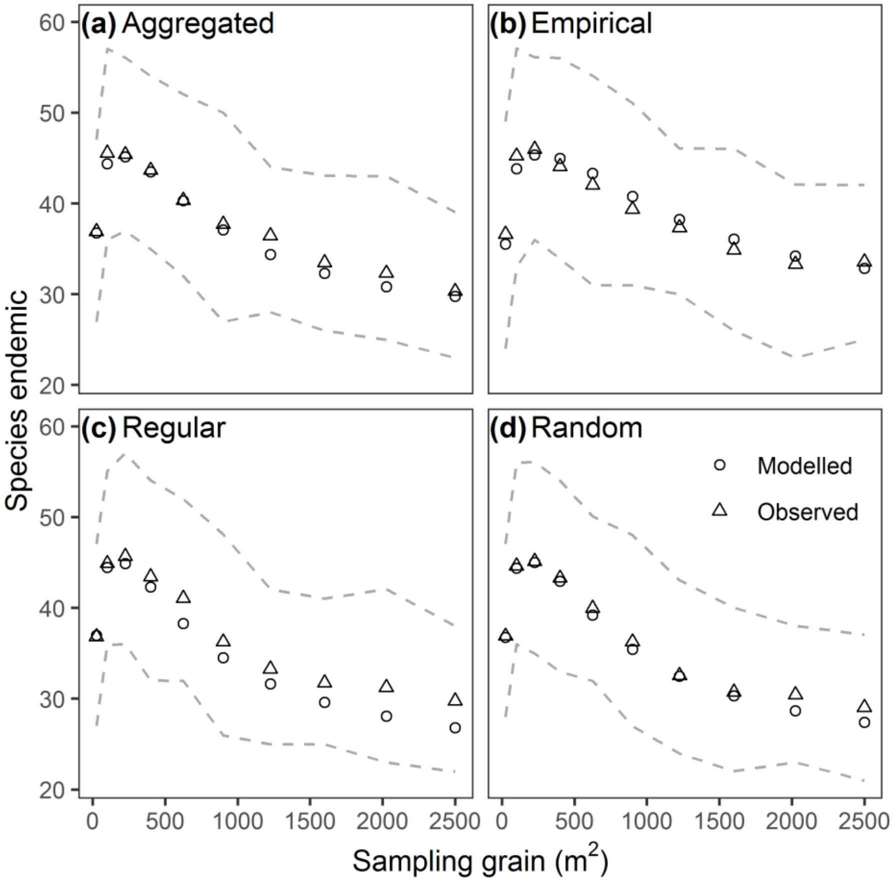


Figure 4.4 Observed (± 95% empirical confidence limits) and modelled single-patch endemic species from validation landscapes using the empirical BCI species abundance distribution but differing in spatial pattern. (a) highly aggregated intraspecific pattern; (b) empirical BCI data; (c) regular intraspecific pattern; and, (d) random placement. Each panel shows the mean (open triangles) and 95% confidence limits (grey dashed lines) in observed shared species from 100 repeat samples.

4.7 Scaling properties of non-random model *c*-parameter

The estimated *c*-parameter for aggregated spatial patterns scaled according to a power law over the range of spatial grains considered and was well predicted by Eq. 4.7 for both non-random shared species models (all $R^2 > 0.99$). Similarly, both the scaling exponent, z, and the estimated base scale value for c_0 were very similar in both non-random models, never differing by more than 3%. For a given modelled pattern of spatial aggregation, differences in species abundance distribution produced little change in base scale estimate (e.g., for landscapes with a sigma of 50 m, values for the different SAD differed by less than 9%; Table 4.2). However, the exponent value increased consistently with more even abundance distribution (e.g., log series = 0.63, broken stick = 0.84; Table 4.2). Although based on comparing only two values, changing spatial aggregation for a given SAD appeared to have the opposite effect, where increasing aggregation increased the estimated base-scale c-parameter, while having a limited affect on z (Table 4.2). Unlike the aggregated and empirical data, for random and regular landscapes the scaling relationship did not follow a power law and appeared not to scale consistently with spatial grain but rather adopted values close to zero as expected for random placement (Fig. 4.5).

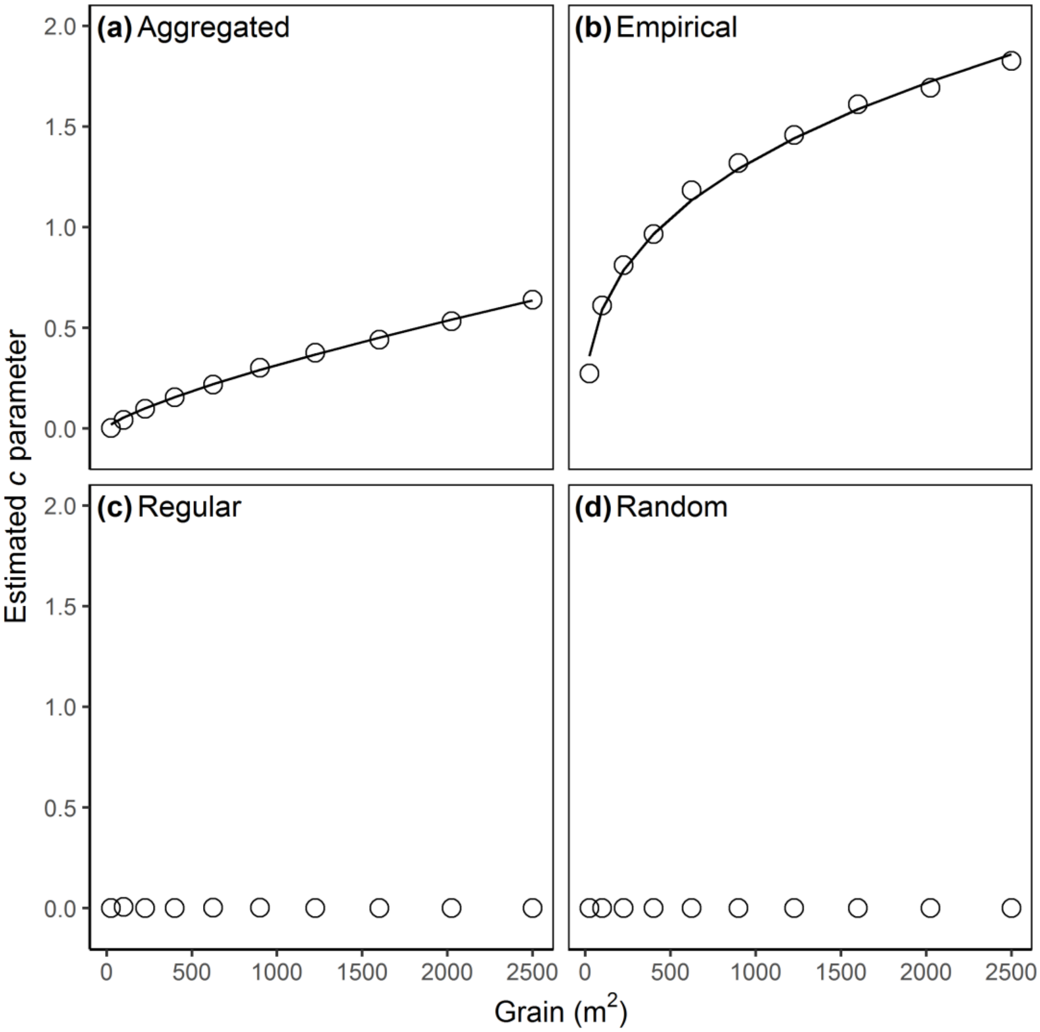


Figure 4.5 Scaling of the *c*-parameter for the non-random shared species model. Points show the fitted estimate for each grain and the curve is the best fit power function (Eq. 4.7). (a) simulated highly aggregated spatial pattern; (b) empirical data for BCI; (c) random placement; (d) simulated regular distribution. For each grain, the scaling factor was estimated numerically as the value providing the best fit of Eq. 4.4 to mean alpha diversity calculated from 200 randomly positioned quadrats in each landscape.

Table 4.2 Area scaling of fitting constant *c* in non-random shared species models in simulated and empirical validation landscapes. Shown are the coefficient of determination (R^2) and root-mean square error (RMSE) and estimated model parameters (α, β, γ) for the power exponential function model fit to estimated *c* at each spatial grain (see also Fig. 4.5). Each row shows the results for actual data (Empirical = Barro Colorado Island) or simulated 50-ha landscapes varying either spatial pattern (H. aggregated, L. Aggregated = high and low intraspecific aggregation, Regular) or species abundance distribution at low aggregation (Broken stick, Log normal, Log series).

Model	**Landscape**	z	c_0	R^2
Eq 4	Empirical	0.357	0.966	0.994
	H. Aggregated	0.75	0.718	0.998
	L. Aggregated	0.769	0.155	0.999
	Broken stick	0.842	0.168	0.999
	Lognormal	0.77	0.164	0.998
	Log series	0.633	0.19	0.999
Eq 5	Empirical	0.365	0.973	0.995
	H. aggregation	0.759	0.724	0.998
	L. aggregation	0.778	0.157	0.999
	Broken stick	0.845	0.167	0.999
	Lognormal	0.775	0.163	0.998
	Log series	0.648	0.188	0.998

4.8 The effects of ecological and sampling constraints on shared species

The expected proportion of total landscape diversity shared among samples is a (generally non-linear) decreasing function of sample number under any of the constraints analysed (Fig. 4.6). With decreasing sampling area and less even species abundance distributions, the number of shared species decreases (Fig. 4.6a, b). Spatial pattern has a strong influence on the expected number of shared species, with > 80% of all species predicted to be shared between 20 samples of 0.25-ha area under a regular spatial distribution and fewer than 10% in highly aggregated landscapes (Fig. 4.6c).

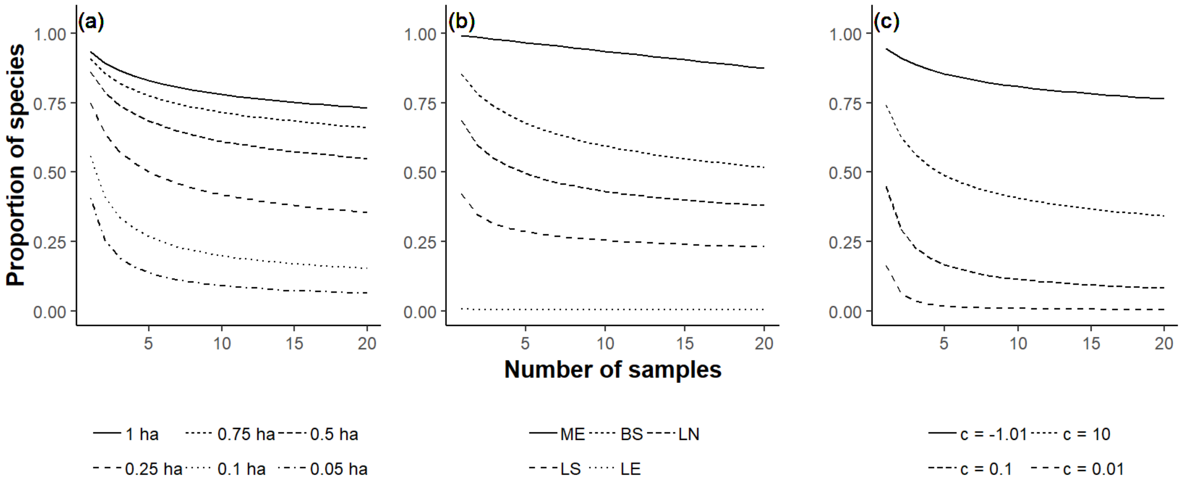


Figure 4.6 Change in expected species shared among 20 samples with variation in: (a) sampling area; (b) species abundance distribution; and, (c) intraspecific spatial distribution. Shared species in panels (b) and (c) were calculated using a 0.25-ha sampling grain. Proportional values on the *y*-axis represent shared species from a total species pool of 250, distributed among 250000 individuals according to the adopted SAD. In panel (b) individuals were randomly placed and the evenness of the SAD decreases in the order: most even (ME) > broken stick (BS) > lognormal (LN) > log series (LS) > least even (LE). In panel (c) a log normal species abundance distribution was used and the value of the scaling factor *c* simulates the effect of different intraspecific spatial patterns: -1.01 indicating a distribution more regular than random; 10, indicating approximately random placement; 0.1, indicating moderate intraspecific aggregation (clumping); and 0.01, indicating strong aggregation.

4.9 Discussion

Although methods exist to predict the number of species lost when a known proportion of total habitat is destroyed (Pereira and Daily, 2006, He and Hubbell, 2011, Hanski et al., 2013), no existing framework can model the expected pattern of species diversity across multiple patches of sub-divided habitat. Understanding of any future biotic relaxation in sub-divided habitat should be based on such an expectation. The proposed framework addresses this gap, by modelling the expected number of shared species (the zeta diversity) and thereby allowing multiple different diversity patterns to be calculated. I demonstrate the approach works well for gamma diversity and single-patch endemics under different species abundance and spatial distribution patterns, but the intermediate step of calculating shared species allows a range of metrics to be calculated (Hui and McGeoch, 2014). This supports analytical approaches to understand the effects of different fragmentation scenarios under various ecological constraints on species abundance and spatial distributions.

As one example of application, the framework accurately reproduces the higher gamma diversity of groups of small patches relative to that in an equivalent area of continuous habitat, but in so doing highlights a key point; this is only the case for spatially aggregated assemblages. Kobayashi (1985), demonstrated this same result analytically almost 40 years ago, but it seems not to be widely appreciated (Fahrig, 2017). Even sub-samples from continuous habitats (as used in model validation here) exhibit the ‘several small patches contain more species than a single large patch’ pattern under predominantly aggregated spatial patterns. This suggests the most parsimonious explanation for why higher diversity in sub-divided habitat is observed so frequently (e.g., Quinn and Harrison, 1988 and similar studies) is perhaps simply the prevalence of intraspecific spatial aggregation in nature (He et al., 1997, Condit et al., 2000). Although this does not preclude some independent positive effect of sub-division on species diversity (Fahrig, 2017), it is not necessary to invoke such a mechanism to explain it.

Similarly, while I used data sub-sampled from a continuous habitat to validate the models, results point to a largely statistical, or geometrical, explanation for some known patterns of compositional turnover in fragmented habitats. Assuming constant sample-level (alpha) diversity, the fewer species that are shared among a group of samples, the greater their overall (gamma) diversity (Whittaker, 1960, Jost et al., 2011). Fragmented landscapes often present just such an increase in dissimilarity (i.e., the complementary pattern to similarity), which helps explain how landscape species numbers can be maintained after fragmentation (reviewed in Tscharntke et al., 2012) or following invasion (Powell et al., 2013). The modelling framework has potential for further development to explore such questions.

The number of species found in only a single patch were also closely predicted by the framework. There were consistent patterns and limited variation in the number of single patch endemics across the different landscapes for a given abundance distribution. Relative to the observed gamma diversity though, there was a much wider scatter in confidence limits in the simulated and empirical landscapes. Both the similar numbers across spatial patterns and the wide scatter in observed data probably reflect the more random spatial patterns observed in less common species (He et al., 1997), which are, of course, the ones most likely to be found in only a single patch. This confirms the mathematical proof by He and Hubbell (2011) that endemics-area curves follow random placement irrespective of spatial aggregation. Further investigation is warranted into how the number of species confined to one, or a few, patches changes with ecological and geometric constraints.

Although model predictive performance was generally good, there was some systematic over prediction of shared species with increasing grain. A possible explanation for this is the distributional assumptions of the model, that species' spatial patterns follow a negative (or finite negative) binomial distribution. As sample grain increases, an increasing proportion of species will have a spatial distribution approaching saturation (i.e., presence in every sample). This could then result in over-estimation of the community level aggregation parameter c and, as a result, over-estimation of the shared species. This suggests the over-prediction could be a limitation of the data, rather than the models themselves. It was interesting to note that even despite the increasing over-prediction of shared species in aggregated spatial patterns (and under-prediction in regular landscapes) at larger grain sizes, the diversity values estimated from these remained within 95% confidence limits and it seems to not present a serious limitation on this aspect of model performance.

The generally poorer fit of regular spatial distributions might also reflect the nature of the data. I expected that regular spatial distributions would result in the opposite diversity pattern to that of aggregated landscapes (i.e., more species contained within a single large area than several small patches). However, the data from the simulated regularly distributed landscapes differed little from the random model, although numerically this difference could be important. This did not change even when individuals for each species were positioned as in a square lattice (result not shown) and appears to reflect the overlapping distribution of many species.

Similarly, the fitted parameter estimates for *c* in both the random and regular landscapes were both consistent with expected model behaviour for random placement, rather than favouring negative values for regular distributions (He and Legendre, 2002, Zillio and He, 2010). As the value for the *k* parameter in the negative binomial distribution increases, the probability of observing a species in area *a* converges to the random expectation under a Poisson distribution (Plotkin and Muller-Landau, 2002). In the non-random model, values of *c* near to zero result in large values for *k*. The reason the simulated regular landscapes appear like those under random placement might be because the number of species used in simulations meant that spatial patterns at the assemblage level were almost indistinguishable from random. Indeed, simulated regular distributions in He and Legendre (2002) showed much smaller variations from random than aggregated distributions. This is possibly because of physical limits to the range of variability; the strongest possible aggregation that can be simulated is where all individuals of a species occupy a single point in space, while distributions are limited to a maximum intraspecific interaction radius of $A/\sqrt{N}$ in a perfect lattice. For individual species, regular spatial distributions have been predicted to result in stronger, geometry-dependent impacts from fragmentation than species with random placement (May et al., 2019) and this warrants further investigation for multi-species assemblages.

It is known that patterns of spatial abundance change with the scale at which they are observed (Wright, 1991, Plotkin and Muller-Landau, 2002, He and Hubbell, 2003, Conlisk et al., 2012).

For use in simulation, it is important to understand the scaling behaviour of the *c* parameter as the spatial grain changes so that an appropriate value for each grain can be estimated. At small proportions of total study extent, the scaling parameter (*k*) in the negative binomial distribution (essentially replaced by fitting/scaling parameter *c*) tends to be self-similar, scaling according to a power-law, with an exponent in the range 0.2 - 0.6 (Wright, 1991, Plotkin and Muller-Landau, 2002, He and Hubbell, 2003). This relationship requires confirmation and better understanding if the modelling framework is to be used to model the effects of fragmentation. It is explored in Appendix C.

The main intended application for the framework is in simulations to help understand how different constraints such as species abundance distributions, spatial patterns and the number and size of fragments in a landscape affect the expected patterns of diversity. If used to simulate the effects of fragmentation in this way, this assumes habitat loss and sub-division is instantaneous and no biotic relaxation has taken place. Although this is unrealistic, its value is in providing a null expectation for the effects of sub-division of habitat on diversity as discussed above; it is the deviations from this expectation that then require biological interpretation. In addition to understanding the emergent patterns such as variation in the gamma diversity and number of single-patch endemic species, variations in expected shared species are also potentially useful. For example, as the models predict zeta diversity (Hui and McGeoch, 2014) they could potentially help elaborate the causal factors underlying its two main (power law and exponential) functional forms. They could also be used to explore the other elements of diversity that can be derived from zeta diversity including similarity indices, occupancy frequency distributions and species accumulation curves (Hui and McGeoch, 2014).

Although Eq. 4.4 and 4.5 were derived based on complete information being available for the abundance of all species across the total area *A*, these types of data are generally not available in empirical investigations. Plotkin and Muller-Landau (2002) found it was not necessary to have information on the complete species number for a landscape to predict the similarity of two samples. The interpretation of scaling factor *c* as a fitting parameter, allows the non-random models to be used to predict shared and endemic species with information available from a collection of samples. Thus, while model validation for Eq. 4.4 and 4.5 were done under the assumption of complete knowledge, they can also predict shared species in an empirical sample where the global SAD is replaced by the empirical abundance data and the global extent *A* is replaced by *m* x *a*. Applications of this nature will require further model development and validation on empirical data.

4.10 Conclusion

In this chapter I have developed a model that provides a statistical expectation for the effects of sub-division as distinct from area in sub-divided habitat. This expectation clarifies the role of sub-division alone in determining the resulting diversity and has clear implications for both the fragmentation *per se* and SLOSS debates.

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4.12 Supporting information for Chapter 4

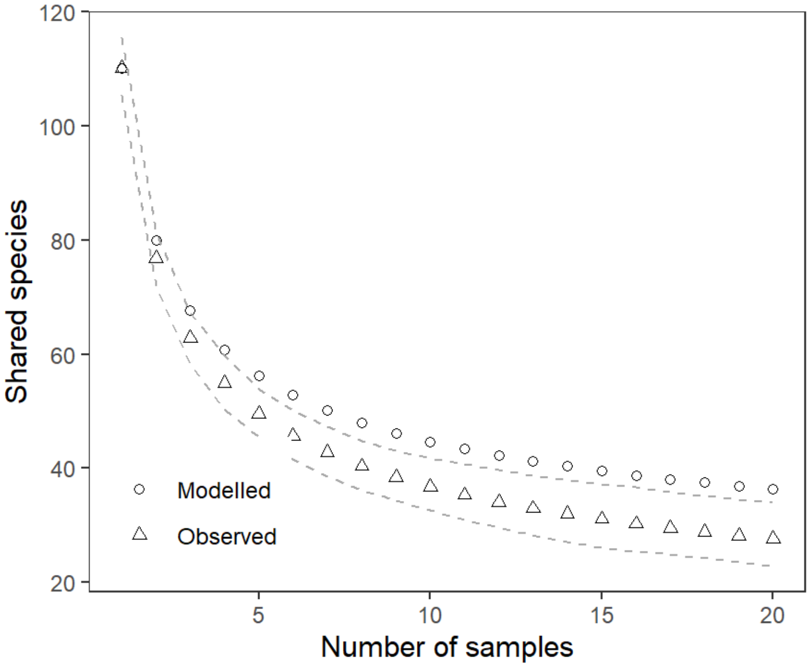

Figure 4.7 Observed and modelled shared species at 2500-m^2 sampling grain for BCI data. The model fit to alpha diversity systematically over-predicted shared species at sampling grains exceeding ~900 m^2. Points show observed and predicted shared species for increasing numbers of samples, with dashed lines showing 95% confidence limits in observed shared species from 100 replicate samples of the BCI landscape.

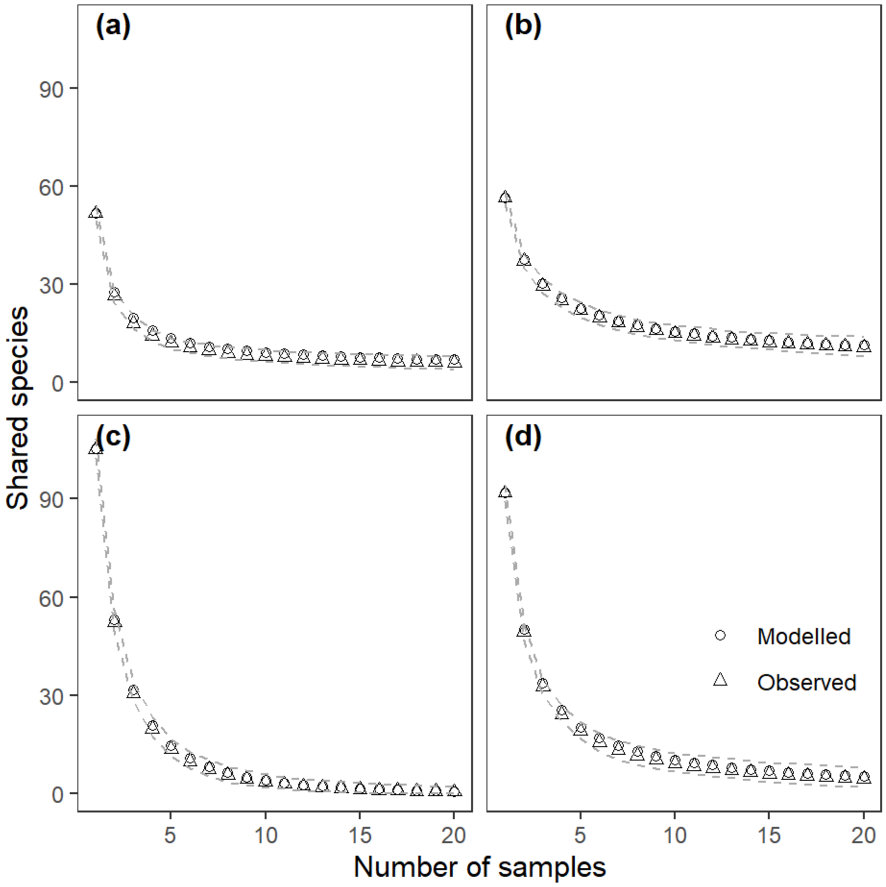

Figure 4.8 Shared species model validation under contrasting species abundance distributions and constant spatial aggregation at 400-m^2 sampling grain. Each panel shows the observed (± 95% confidence limits) and modelled shared species using Eq. 4 for a simulated validation landscape. In each landscape intraspecific aggregation was held constant (sigma = 50 m) but the observed BCI total species (S = 301) and number of individuals (N = 211845) distributed according to different abundance distributions: (a) log series (b) empirical (c) broken stick (d) log normal.

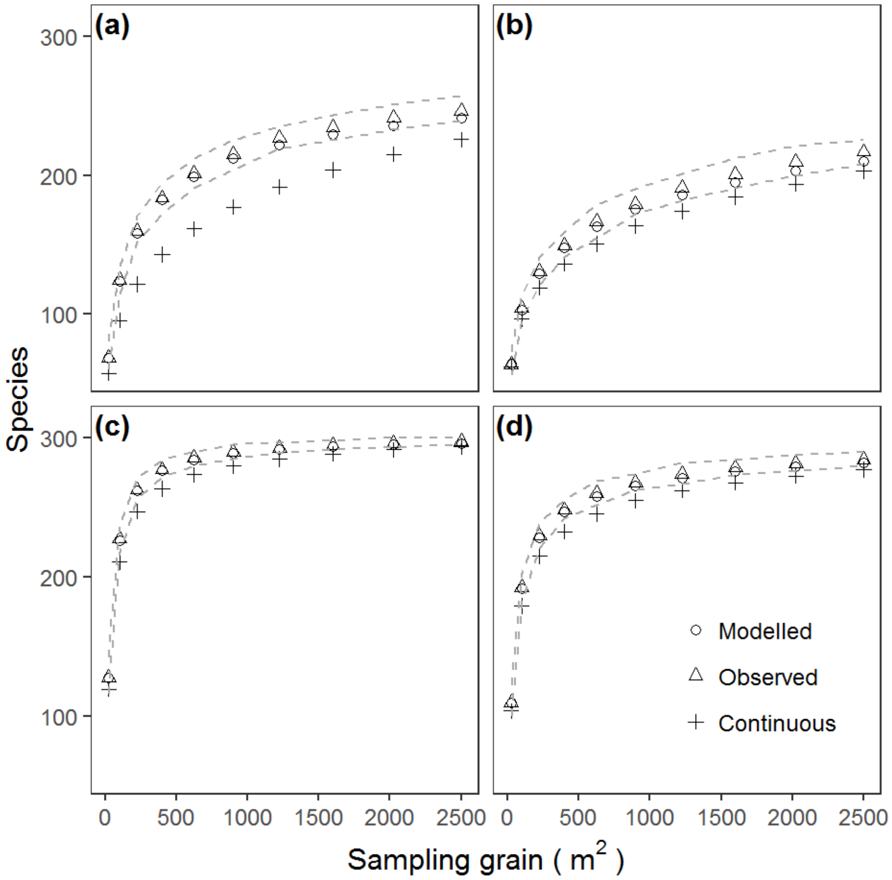

Figure 4.9 Observed and modelled gamma diversity for 20 samples from simulated 50-ha landscapes varying sampling grain and species abundance distribution. (a) BCI empirical SAD; (b) log series; (c) broken stick; and, (d) log normal. Each panel shows the mean (open triangles) and 95% confidence limits (grey dashed lines) in observed shared species from 100 repeat samples and the species richness for continuous areas of the same total size (+). Landscapes simulated aggregated spatial patterns for each species using the Thomas point pattern process, with the dispersal parameter (sigma) set to 50 m.

Chapter Five: Expected patterns of species loss under habitat destruction and sub-division depend on species' abundances and spatial distributions

5.1 Abstract

The effects of habitat sub-division on diversity are highly controversial. Here, I simulate the effects of both habitat loss and sub-division on species diversity using an analytical modelling framework. I model changes in proportional species loss and the number of remaining species confined to a single patch (single-patch endemics) for destruction of 20-90% of total habitat area. I compare these effects over gradients of species evenness and spatial aggregation at 6 different levels of sub-division. Only under random placement was loss of species unaffected by sub-division; under any level of intraspecific aggregation, more species were retained in the sub-divided habitat. For ecologically realistic evenness and aggregation, increasing the number of habitat patches from 1 to 32 preserved an additional 2-5% of original species richness and reduced the number of surviving species confined to a single patch. Both the magnitude of species losses and the moderating effects of sub-division were more sensitive to changes in relative abundance than the strength of intraspecific aggregation. Highly even abundance distributions resulted in <3% of original species being lost at 80% reduction of area while at low evenness, this value approached 40%. I suggest some apparently positive effects of sub-division on species diversity can be attributed to intraspecific aggregation, with clear relevance for the fragmentation *per se* debate. Findings underline the importance of understanding macroecological patterns in predicting the impacts of habitat loss; as evenness of the pre-clearance assemblage increases, the risk of species loss likely shifts from imminent to delayed extinction.

5.2 Introduction

It has been estimated that by the end of the 20th century more than half of the global terrestrial land surface was dominated by human land use (Ellis et al., 2010). It is increasingly apparent that the future of biodiversity will depend not only on formal conservation reserve networks, but also on how well it can be integrated within the mixed-land-use ‘countryside’ landscapes that result from ever-expanding human activity (Pereira and Daily, 2006, Proença and Pereira, 2013, Mendenhall et al., 2014). A confusing obstacle policy makers currently face in fostering positive countryside biodiversity outcomes is conflicting ecological opinion on how habitat sub-division (fragmentation *per se*) affects species diversity (e.g., Fahrig, 2017, Haddad et al., 2017, Fletcher et al., 2018, Fahrig et al., 2019). Ecologists currently disagree not only on how sub-division affects diversity (Fletcher et al., 2018, Fahrig et al., 2019), but also on whether the conceptually separate processes of habitat loss and sub-division can be considered independently at all (Didham et al., 2012, Fahrig, 2017, Fahrig, 2019). Part of the problem lies in the practical difficulty of distinguishing these effects experimentally (Haila and Hanski, 1984, McGarigal and Cushman, 2002); here I avoid these potential pitfalls by using an analytical model to predict the expected effects of sub-division on patterns of diversity at different levels of habitat loss.

Land clearance results in two distinct processes (Wilcox, 1980); reduction in total habitat area, and, its breaking apart into discrete habitat patches ('fragmentation *per se*'; Fahrig, 2003). Habitat loss is unequivocally counted among the leading anthropogenic causes of extinction (Brooks et al., 2002, Butchart et al., 2010), but the effects of habitat sub-division are highly controversial. The key point of disagreement relates to whether the effects of fragmentation *per se* (i.e., controlling for the negative impacts of habitat loss) are typically positive or negative for diversity (Fahrig, 2017, Haddad et al., 2017, Fletcher et al., 2018, Fahrig et al., 2019). Here I will show that the truth is probably that it is neither; rather that (at least some of) the observed patterns interpreted as being positive are a probable consequence of the prevailing macroecological patterns.

To some extent, the fragmentation *per se* controversy can be viewed as a continuation of the single-large-or-several-small debate over conservation reserve design originating in the 1970s (Diamond, 1975b, Simberloff and Abele, 1976, Higgs and Usher, 1980). This debate was largely fueled by the observation that groups of small patches typically contain more species than a single large patch of equivalent area – an observation with considerable empirical support (reviewed in Quinn and Harrison, 1988, Fahrig, 2017). The explanation offered for greater species numbers in sub-divided habitat is usually increased environmental heterogeneity and higher beta diversity (Kitchener et al., 1980, Simberloff and Gotelli, 1984, Tscharntke et al., 2002b, Fahrig, 2017). However, theoretical justification for this pattern has also been proposed, particularly for aggregated spatial distributions (Simberloff and Abele, 1976, Higgs and Usher, 1980; Chapter 4, Kobayashi, 1983, Kobayashi, 1985). If a greater number of species being present within sub-divided habitat is the expected pattern for assemblages where intraspecific aggregation dominates (Kobayashi, 1985), then it should probably be viewed as a null expectation.

There are two distinct species-loss processes recognized to result from habitat destruction. Imminent (also ‘immediate’ or ‘instantaneous’) extinctions are ‘cookie cutter’ losses where a species is lost from a landscape during clearance because all individuals of the species were found in the destroyed habitat (Harte and Kinzig, 1997). Delayed extinction (also biotic relaxation, extinction debt) occurs over some unspecified period of time after initial habitat destruction as a result of the demographic impacts of habitat loss and fragmentation such as reduced population size or isolation of sub-populations (Diamond, 1972, Tilman et al., 1994, Mouquet et al., 2011). These two stages of extinction map broadly onto the two elements of systematic conservation planning; species representation and persistence (Margules and Pressey, 2000). Imminent extinctions represent a reduction in landscape species representation due to clearance, while delayed extinctions threaten persistence of the species that remain in the isolated fragments.

Understanding how fragmentation of habitat affects imminent and delayed extinction are both the subject of considerable current research effort (Claudino et al., 2015, Hanski, 2015, Arnillas et al., 2017, Deane et al., 2017a, Chisholm et al., 2018, MacDonald et al., 2018a, Rybicki et al., 2018, May et al., 2019). Here my main interest is in determining whether fragmentation could moderate loss of species from the landscape by preserving more species in undestroyed habitat, which relates only to imminent extinctions. However, to have some understanding of the effects of fragmentation on persistence over the longer term, I adopt a metapopulation view of the problem. I assume that, after fragmentation, species confined to a single sub-population (i.e., within a single fragment – hereafter single-patch endemics) will have the highest risk of extinction (Hanski, 1999). It is reasonable to expect that, as the number of remaining patches increases (albeit of smaller area), the number of species confined to a single patch should decrease. Empirical data suggests that this can indeed be the case and, moreover, that this occurs concurrently with increasing gamma diversity (Fig. 5.1). These phenomena are important to understand as they suggest fragmented landscapes could perhaps exhibit patterns that are interpretable as arising from some positive effect of fragmentation (hereafter, ‘sub-division’ to distinguish the breaking apart of habitat from its loss), whereas they are attributable to the way a sub-divided geometry samples the landscape under intraspecific aggregation.

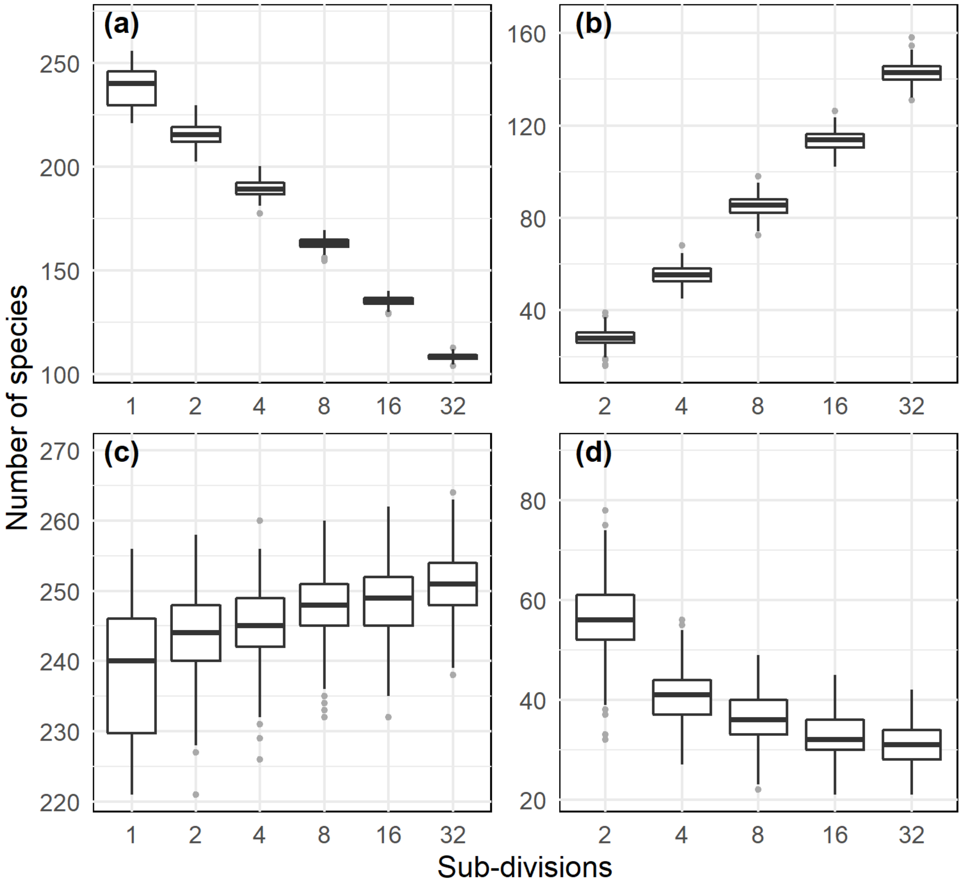

Figure 5.1 Variations in empirical diversity patterns from sub-division of sampling area. (a) species richness; (b) additive beta diversity; (c) total observed species (gamma diversity); (d) number of species confined to a single patch (single-patch endemics). Data are from 200 randomly positioned sets of samples taken from the Barro Colorado Island

stem-mapped forest plot data (2005 census). Each panel shows how diversity changes as a sampling area representing 15% of the 50-ha plot is sub-divided among the number of plots shown on the *x*-axis.

5.3 Methods

5.3.1 Modelling framework

The modelling framework developed in Chapter 4 provides a means to analyse the effects of different sub-division and habitat loss scenarios on species diversity. The framework consists of first calculating the number of shared species, which is a function of fragment area (*a*), the number of fragments (*m*), the species abundance distribution over the study extent (*S* species, with abundance N_i) and the intraspecific spatial pattern for individuals. When individuals are randomly positioned with respect to one another, the number of shared species is obtained from (Chapter 4):

$$E\left(SS_{m|a}\right) = \sum\left[1-\left(1-\frac{a}{A}\right)^{N_i}\right]^{m} \tag{5.1}$$

For non-random placement of individuals, the equivalent model is:

$$E\left(SS_{m|a}\right) = \sum_{i=1}^{S}\left(1-(1+c)^{-k_i}\right)^{m} \tag{5.2}$$

where $k_i = aN_i/Ac$. Non-random models thus require specification of a single parameter, community-level scaling factor, *c*, the value of which depends on spatial scale and intraspecific spatial pattern (Appendix C). However, as c scales consistently with area (Plotkin and Muller-Landau, 2002, Chapter 4, He and Hubbell, 2003), it is only necessary to know its value at some base spatial scale ($0 < a_0 < A$), to calculate its value at any fraction of the total area of interest from the scaling relationship (Chapter 4; Appendix C):

$$c_a = c_0 \left(\frac{a}{a_o}\right)^z \tag{5.3}$$

Once shared species have been calculated, zeta diversity theory (Hui and McGeoch, 2014) can be used to quantify the emergent properties of diversity resulting in the landscape (Chapter 4).

By varying evenness of species abundance distributions and strength of intraspecific aggregation independently, a ‘crossed’ experimental design can be implemented. By then sub-dividing the amount of remaining habitat among different numbers of equal-sized patches, the effects of these geometrical constraints on the expected diversity patterns under the different ecological constraints can be analysed. The modelling framework provides a statistical expectation for the species richness within and among samples if sub-division into patches were to occur instantaneously. It is most likely to reflect reality in a relatively homogeneous pre-clearance landscape (at least one lacking strong directional environmental gradients).

5.3.2 Specifying species abundance and spatial distributions

To be of practical use, the range of ecological conditions represented in simulations should ideally fall along a gradient that spans the set of conditions likely to be observed in nature, requiring some reference to observed data. The most detailed enumeration of species and spatial distributions for complete assemblages has been for forest trees (e.g., Condit et al., 1996, He et al., 1997, Condit et al., 2000, He and Hubbell, 2003). Here, I used values for the total number of species (S) and individuals (N) for to the 2005 census data from the 50-ha Barro Colorado Island (BCI) stem-mapped plot (Hubbell et al., 2005), comprising 301 species and 211845 living stems. Provided the underlying model assumptions of stationarity and isotropy in spatial processes hold, the shared species model will scale to any area, suggesting these values could be used directly. However, more severe impacts of habitat loss might not emerge until at least 70-90% of the area is cleared (Andrén, 1994, Swift and Hannon, 2010). To sub-divide the remaining habitat into 32 patches would result in habitat fragments of only 40 m^2. Therefore, to ensure the minimum habitat area of interest includes an adequate number of individuals to characterise the underlying species abundance distribution, I adopted a study extent of 10 x 10-km.

To characterise the species abundance distribution when area was extrapolated from 50-ha to 100 km^2, I first scaled the number of individuals linearly, assuming a similar individual density as BCI ($\approx$0.4 individuals/m^2) giving 40 million individuals in the larger landscape. I then used a species-individual model based on the logistic function (He and Legendre, 1996) for the BCI plot (2005 census) to estimate the number of species this would be expected to represent. I fit 200 realizations of the logistic model using 100 repeated random samples of 2000 individuals and extrapolated each model to estimate the number of species at 40 million individuals. This yielded 333.9 [318.2, 353.4] species (mean ± [95% confidence limits]) and I adopted 330 as a base number of species for simulations.

The base values of $S = 330$ species and $N = 40$ million individuals were then used as the dimensions from which to estimate species abundance distributions that differed in evenness. To vary evenness in species abundance, I used the zero-truncated negative binomial distribution (TNBD), a commonly-used distribution in applications where a systematic variation in evenness is desired without changing the underlying distribution model (e.g., He and Legendre, 2002, Wilber et al., 2015). I systematically varied the shape parameter, gamma, which determines the evenness of the resulting SAD, using values from 0.1 to 1.0 in increments of 0.1. As values for gamma exceeding 0.5 showed little difference in species loss, I present results for 0.1, 0.2, 0.3 and 0.5 which had values for Pielou's evenness (PE) of 0.68, 0.77, 0.82 and 0.88, respectively.

As discussed above, the shared species model incorporates non-random spatial patterns by changing the value of c_0 and z in Equation 5.3. Thus, the effects of aggregation can be incorporated in model predictions by varying their values (Chapter 4; Appendix C). I use three pairs of values (Table 5.1), simulating landscapes with low, moderate and high levels of intraspecific clustering (Appendix C). I created landscapes using every combination of each spatial and species abundance distribution (i.e., a crossed design), yielding 16 scenarios; four levels of evenness in abundance by four spatial patterns (random plus three strengths of aggregation). It is theoretically possible to simulate regular distributions, but this is of little practical relevance as few species follow such a spatial distribution and, to my knowledge, it has never been demonstrated in any multi-species assemblage. Moreover, simulations showed the effects of this on diversity differed little from that of random placement (Chapter 4), so I consider random placement simulations to adequately represent non-aggregated patterns. Based on comparative species richness with simulated communities (Appendix C), the strength of aggregation (at the community-level) in the empirical data for BCI is comparable to that produced in the moderate aggregation scenario. Thus, of the 16 scenarios, I consider the moderate aggregation and with evenness of 0.77 or 0.82 present the most typical ecological scenarios, at least in terms of similarity with ecosystems with properties comparable to the BCI data.

Table 5.1 Parameter values used to incorporate different levels of intraspecific aggregation in model predictions.

Spatial scenario	Base value c_0	Exponent (z)
Weak aggregation	0.2	0.8
Moderate aggregation	1	0.7
Strong aggregation	4	0.6

To extend the simulations to consider a broader range of ecosystem types, I also investigated the effects of varying individual density and overall species number. The intent behind this analysis was to identify any systematic variation from the base conditions as individual density increased or decreased, which can help to infer whether the results would change for non-tree organisms that differed greatly in their relative density. I therefore created communities where both the base richness (330 species) and individual density (0.4 m^{-2}) were each doubled and halved. While this resulted in 9 different combinations, only five of these provide unique combinations of individual density and species number (because doubling or halving both species richness and abundance results in the same model prediction). In addition to the three base conditions (330 species with 0.2, 0.4 and 0.8 individuals/m^2), I modelled landscapes with 165 species and individual density of 0.8 m^2 and 660 species with 0.2 m^2. I identify these scenarios by using the ratio of the mean number of individuals per species relative to the base scenario (330 species at 0.4 m^2). Thus, $N/S = 0.25$ (660 species with individual density of 0.2 ind/m^2) refers to a scenario with 25% of the mean number of individuals per species relative to the base scenario, $N/S = 0.5$ (330 species at 0.2 ind/m^2) represents half the individual density, $N/S = 2$ (330 species at 0.8 ind/m^2) a factor of 2, and, $N/S = 4$ (165 species at 0.8 ind/m^2) four times the base scenario density. As with the base scenario, I calculated these for each of the 16 spatial and abundance distributions. As results differed consistently from the base scenario within each combination of spatial and abundance distributions, I present only the results for moderate aggregation and Pielou's evenness = 0.77.

5.3.3 Analyzing the effects of sub-division

Using the above four species abundance distributions and patterns of spatial aggregation (hereafter, scenario), I calculated the number of species remaining in the landscape after simulating the destruction of habitat from 20 to 90% of the original area in 10% increments. For each incremental loss of area, I divided the remaining habitat among five levels of sub-division determined from 2^n (where $n = 1, 2, 3, 4, 5$), yielding 2-32 patches. Thus, for each 10% loss of habitat area, I divided the remaining habitat area, x (where $x = 80, 70, 60, \dots, 10\%$), into five sub-divisions of n patches (where $n = 2, 4, 8, \dots, 32$), each of area x/n. I also calculated the equivalent number of species contained in a single contiguous patch (i.e., of area *x*) as an additional point of comparison yielding 6 levels of sub-division from 1 - 32 patches. For each scenario, I calculated gamma diversity and single-patch endemics from expected shared species as described in Section 5.3.1 (see also Chapter 4) under each sub-division (excluding single-patch endemics for the single patch scenario as this must include all remaining species). To facilitate comparison among scenarios, I report the proportional loss of species relative to the original gamma diversity and the proportion of single patch endemics relative to the predicted number of surviving species. Proportional species loss can be compared directly among scenarios, but for single-patch endemics, the proportion of remaining species will not be independent of the geometry (i.e., as patch number increases, the number of species confined to only one patch is likely to decline). Thus, the effects of sub-division on single-patch endemics are interpreted relative to that observed for random placement for a given species abundance distribution. All modelling was done in R 3.5.1 (R Core Team, 2019) with species abundance distributions modelled using R package ‘sads’ (Prado et al., 2017).

5.4 Results

General effect of habitat reduction

Across all sub-division, spatial and abundance distribution scenarios, proportional species loss increased with decreasing evenness in abundance and with increasing strength of aggregation (Fig. 5.2). However, the magnitude of species loss was more sensitive to relative abundance, increasing 20-fold over the evenness gradient considered compared with a doubling over the spatial gradient (from random placement to strong aggregation; Fig 5.2). Broadly, a decrease in

Pielou's evenness of ~ 0.05 resulted in more than a doubling of proportional species loss for a given spatial pattern.

Loss of species as a function of habitat reduction was slightly curvilinear, with the slope of the species-loss curve increasing as more area was removed, particularly as habitat loss increased from 80-90% (Fig. 5.2, 5.3). Non-linearity was more apparent in the most evenly distributed abundance scenarios and the most highly aggregated spatial distributions, although these scenarios also resulted in the lowest proportional species loss (Fig. 5.2). For example, even under moderate levels of aggregation, the most even SAD resulted in fewer than 3% of species being lost at 80% of habitat loss.

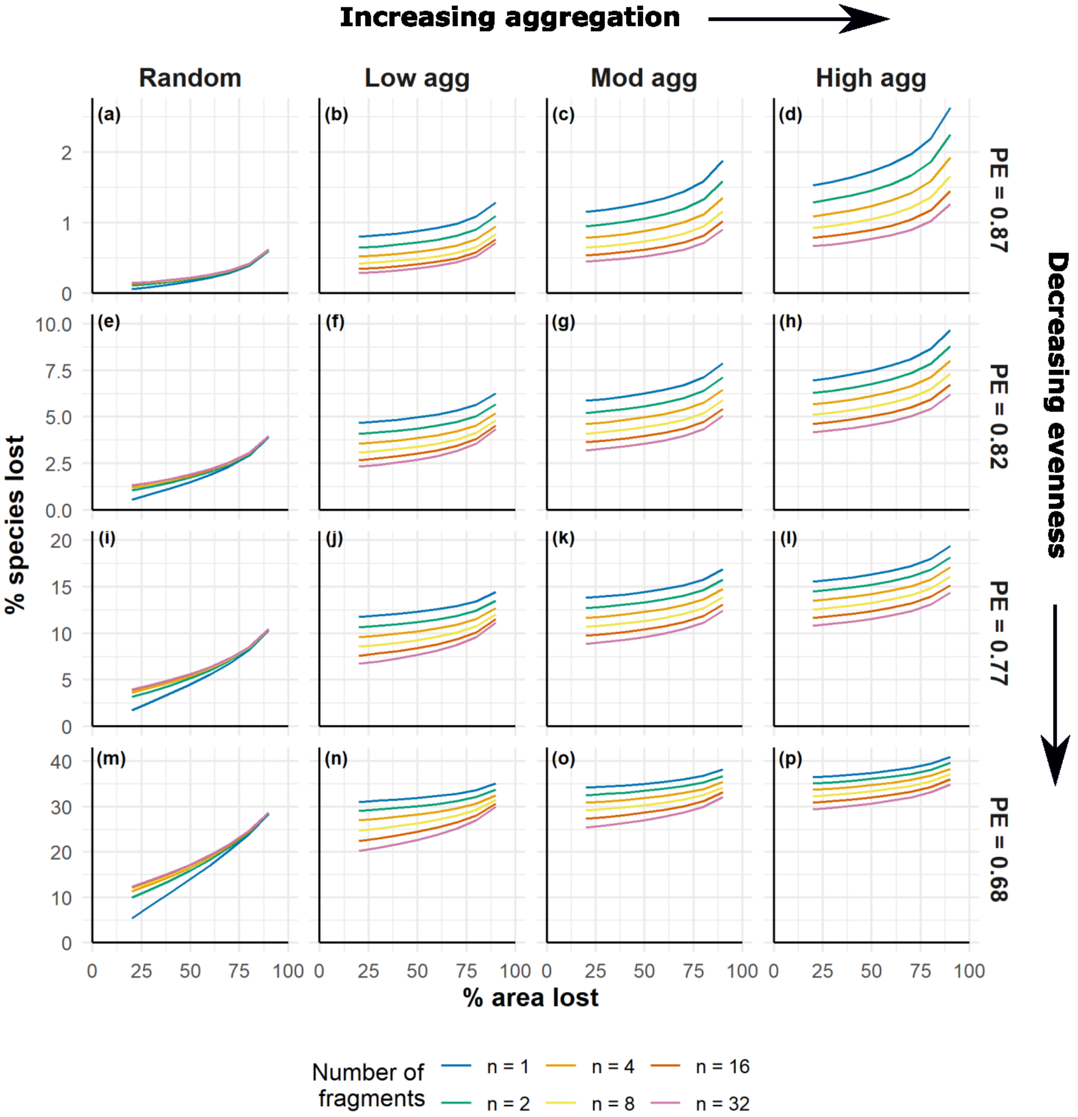

Figure 5.2 Predicted effects of sub-division and habitat reduction on species loss under different spatial and abundance distributions. Each panel represents simulated assemblages with a different combination of spatial pattern (organised into rows, increasing in aggregation from left to right) and evenness (columns; decreasing in evenness from top to bottom). Within each panel, the proportion of species lost (*y*-axes) are given for increasing proportions of habitat loss (*x*-axes), where the remaining habitat is divided into different numbers of equal-sized fragments (indicated by line colour). Note *y*-axis values differ for each row to make patterns clearer.

For a given spatial and abundance distribution, the mean number of individuals per species also affected proportional loss of species, which increased with higher mean abundance per species (Fig. 5.3). At moderate spatial aggregation and evenness (PE= 0.77), an eight-fold change in mean abundance per species increased the proportion of species lost for an 80% loss of habitat area by 6-8% depending on the amount of sub-division considered (Fig. 5.3).

Effects of sub-division

With any level of intraspecific aggregation, more species were predicted for sub-divided habitat, decreasing proportional species loss (Fig. 5.2, 5.3; Table 5.2). For an 80% reduction in total habitat area, sub-division from a single contiguous area to 32 separate patches was predicted to reduce proportional species loss by between 0.6 and 7% (Table 5.2). As for proportional species loss, evenness of species abundance distribution largely determined the strength of this effect of sub-division; for base-level diversity (330 species), the mean additional number of species at minimum and maximum evenness (PE = 0.68, PE = 87) were 2.9 and 21.7 species respectively.

Also consistent with proportional species loss, this moderating effect of sub-division on species loss increased in effect size with increasing mean abundance per species (Fig. 5.3). At 80% habitat reduction of habitat, the minimum mean abundance per species (N/S = 0.25 x base scenario) sub-division into 32 patches preserved 3.5% more species than that of a single patch; at maximum mean abundance per species (N/S = 4 x base scenario) 6.1% more species were predicted in the sub-divided habitat.

For all scenarios, as the number of patches into which the habitat was sub-divided increased, the number of extra species found decreased proportionally. So, taking the non-random base-diversity scenarios (*S* = 330 species) at 80% habitat loss as an example, a doubling in the number of patches from 1-2 on average increased the number of species present by 2.9, while doubling from 16-32 patches increased the number of species on average by 1.9. This suggests the increase in species number under increasing sub-division will attain some maximum value above which the total number of species contained within the sub-divided habitat will no longer increase; that is, sub-division results in diminishing returns in terms of the number of species that are contained in the total area.

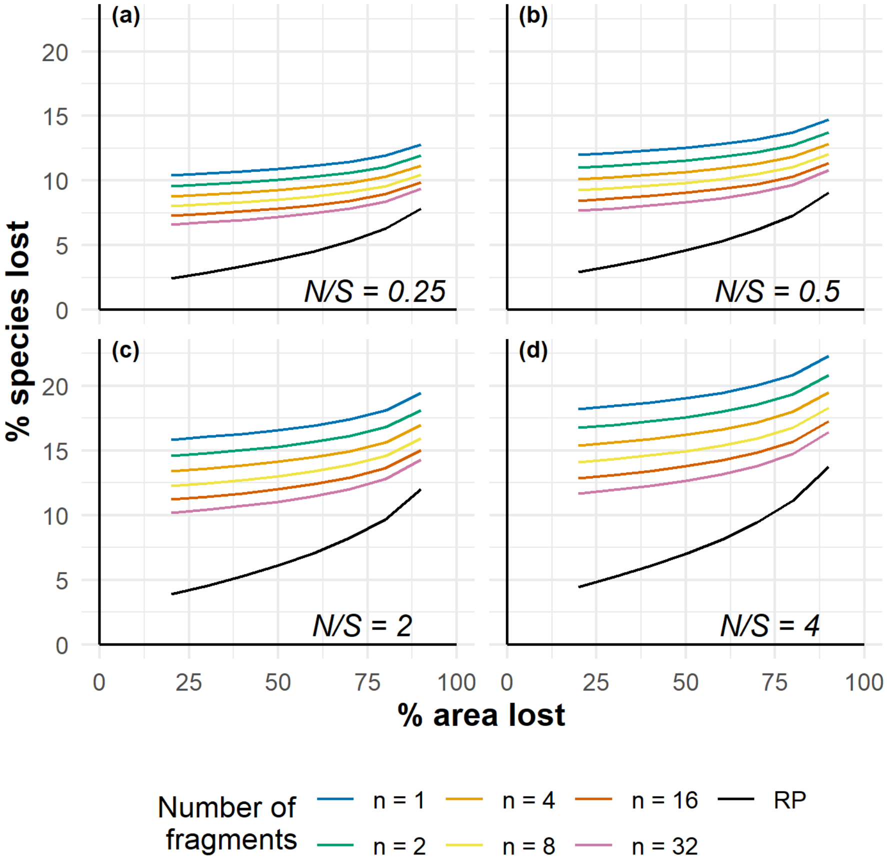

Figure 5.3 Predicted effects of differences in relative abundance on species loss. Each panel represents a different relative abundance to the base scenarios presented in Fig. 5.2, with the difference in the ratio of mean abundance per species relative to that of the base scenario shown in each panel. (a) *N/S* = 0.25 (S_0 = 660, mean individual density = 0.2/m^2), (b) *N/S* = 0.5 (330, 0.2/m^2); (c) *N/S* = 2 (330, 0.8/m2); (d) *N/S* = 4 (165, 0.8/m^2). The scenarios shown are as per Fig. 5.2, showing the percentage of species lost for 10-80% of habitat clearance under 6 sub-division scenarios from *n* = 1 - 32 under aggregation (coloured lines) and the corresponding random placement values in black. The species abundance distribution used was PE = 0.77, with moderate spatial aggregation.

Table 5.2 Effect of sub-division on proportion of original species lost for different species abundance distribution (Evenness) and strength of intraspecific aggregation (Aggregation). % change is the difference in the proportion of original species diversity predicted at an 80% habitat reduction, when remaining habitat is contained in a single contiguous patch vs. being sub-divided into 32 patches of equal total area. Random placement scenarios did not differ under sub-division (other than rounding errors).

Aggregation	**Evenness**	**% change**
Low	PE = 0.68	6.6
	PE = 0.77	3.9
	PE = 0.82	2.1
	PE = 0.87	0.6
Moderate	PE = 0.68	6.8
	PE = 0.77	4.6
	PE = 0.82	2.8
	PE = 0.87	0.9
High	PE = 0.68	6.3
	PE = 0.77	4.9
	PE = 0.82	3.2
	PE = 0.87	1.2

The predicted proportion of single-patch-endemic species depended mainly on species abundance distributions, increasing with decreasing evenness, ranging from < 2% to 7-10% of remaining species as evenness decreased (Fig. 5.4). However, the direction of change with increasing habitat loss was complex (Fig. 5.4). Considering the results for random placement (which shows the expected change in single-patch endemics that arises purely because the number of remaining patches changes, thus providing a baseline), the number of single patch endemic species always increased as habitat loss proceeded at high evenness, but decreased at low evenness (compare Fig. 5.4a and 5.4m). There was a similar non-linear response to habitat loss with evenness in the aggregated spatial patterns, but this was less obvious (e.g. compare Fig. 5.4c and 5.4o).

The effects of sub-division on the number of single patch endemic species also changed with both evenness and spatial pattern. Sub-division had the greatest relative difference in more even and highly aggregated communities (e.g., Fig. 5.4d, 5.4h). In general, increasing sub-division decreased the number of single-patch endemics while habitat loss increased it (Fig 5.4, panels b-d, f-h). However, for the least even abundance distribution, the proportion of remaining species confined to a single patch remained almost constant at around 7-10% under any level of aggregation (Fig. 5.4, panels n - p).

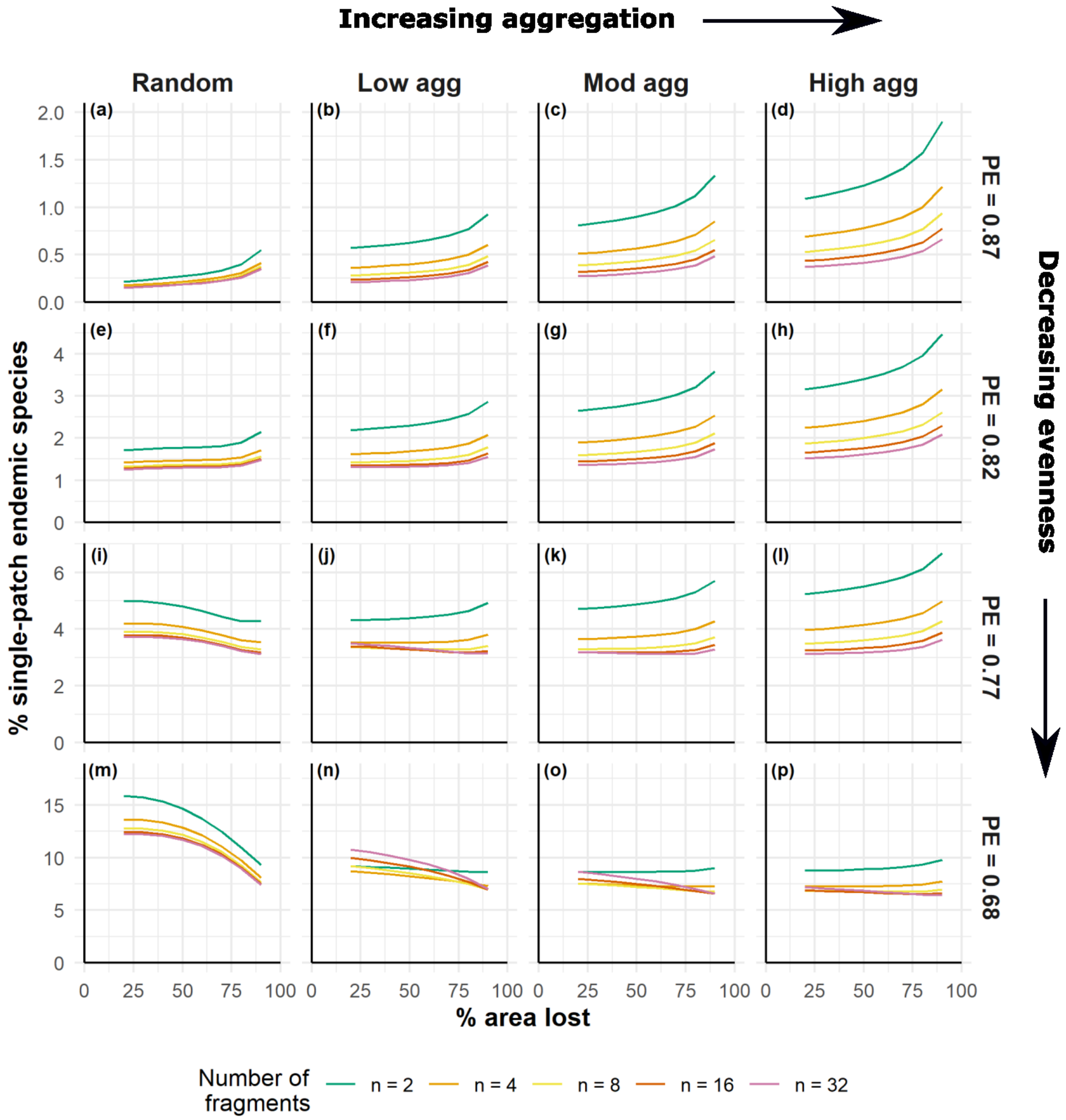

Figure 5.4 Predicted effects of sub-division and habitat reduction on the proportion of single-patch endemic species under different spatial and abundance distributions. Each panel represents simulated assemblages with a different combination of spatial pattern (columns, increasing in aggregation from left to right) and evenness (rows; decreasing in evenness from top to bottom). Within each panel, the proportion of species found in only a single patch (single-patch endemic species; *y*-axes) are given for increasing proportions of habitat loss (*x*-axes), where the remaining habitat is divided into different numbers of equal-sized fragments (indicated by line colour).

5.5 Discussion

Ecologists have predicted the effects of habitat loss on diversity using species-area-based models for over 40 years (e.g., Simberloff, 1974, Pimm and Askins, 1995, Brooks et al., 1999, Brook et al., 2003, Lewis, 2006, He and Hubbell, 2011, Halley et al., 2013). Recent research seeks to build on this understanding by developing methods that can explicitly account for the effects of sub-division of the remaining habitat (Hanski et al., 2013, Claudino et al., 2015, Arnillas et al., 2017, Deane et al., 2017a, Chisholm et al., 2018, Deane and He, 2018), of ecological processes (Matias et al., 2014), for delayed extinction (Halley et al., 2014, Claudino et al., 2015, Kitzes and Harte, 2015), and for the species-level effects of the geometry of habitat loss (May et al., 2019). This study contributes to this growing body of knowledge by showing how sub-division moderates the expected diversity patterns, simulating the effects of fragmentation *per se* following habitat destruction. The results help explain a body of empirical evidence suggesting a group of small patches often contain more species than a single large patch of equivalent area, and re-affirm this as a predictable consequence of intraspecific aggregation (Kobayashi, 1983, Kobayashi, 1985). Models also provide the first estimates for the expected magnitude of this sub-division 'richness subsidy', showing it could be expected to preserve an additional 3-5% of original species diversity over that expected for a single patch under ecological conditions consistent with those assumed for the base scenario.

Of those studies that have examined the effect of fragmentation or the geometry of habitat loss on species diversity, most have used some extension of species area relationships (Hanski et al., 2013, Rybicki and Hanski, 2013, Halley et al., 2014, Keil et al., 2015), or derived bounding estimates for the range of species loss for differing amounts of species overlap among patches and patterns of fragmentation (Arnillas et al., 2017, Chisholm et al., 2018). In contrast, I use species abundance and spatial patterns to predict the expected overlap in species (Plotkin and Muller-Landau, 2002), and calculate the exact number of species expected to be found in sub-divided habitat. Where most prior studies agree, is that sub-division of habitat tends to ameliorate the conservation of species to some extent.

The typical explanation offered for elevated species richness among sub-divided habitat patches is a promotion of beta diversity in the fragmented habitat explained by differences in dispersal or environmental heterogeneity (Kitchener et al., 1980, Tscharntke et al., 2002b, Fahrig, 2017). Based on this analysis, and prior evidence, I suggest that the simplest hypothesis is that these patterns arise as a probable consequence of intraspecific aggregation of individuals (Kobayashi, 1983, Kobayashi, 1985, He and Legendre, 2002, Plotkin and Muller-Landau, 2002, Green and Ostling, 2003). Given the prevalence of intraspecific aggregation in nature (Wright, 1991, Kretzschmar and Adler, 1993, He et al., 1997), perhaps this view should form the basic expectation for how diversity initially assembles in newly sub-divided habitat. Following habitat reduction and isolation, species richness within and among patches will almost certainly change as the new habitat structure matures. The number of species in patches of sub-divided habitat could be enhanced further by increased beta diversity due to drift or sorting along environmental axes (Chase, 2003, Liu et al., 2018) and promoted, or eroded, due to changes in competitive or extinction and colonization processes among the newly isolated patches (MacArthur and Wilson, 1967, Patterson and Atmar, 1986, Leibold and Loeuille, 2015, Lu et al., 2019). Interpretation of the observed diversity of fragmented landscapes should probably commence with an expectation that species diversity was higher than a contiguous area of the original habitat would have contained.

In terms of the overall impact of habitat destruction on species richness predicted, there was a much stronger effect of evenness in abundance distributions than the strength of spatial aggregation. It seems any amount of aggregation results in some elevated species richness under sub-division, but its magnitude depends more on evenness. Under a highly uneven pre-clearance distribution of abundance, my results suggest many species will be lost to imminent extinctions. More even communities lose few species initially, suggesting a higher potential for delayed extinctions should exist in such communities as they relax to the new habitat configuration. This general result is consistent with Kitzes and Harte (2015) who modelled imminent and delayed extinction in global biodiversity hotspots using a related sampling-theory-based approach. In their study, more even abundance distributions assumed for bird communities resulted in no imminent extinction and high extinction debt, while less evenly distributed plant communities were predicted to have imminent extinction of 5-14% of species for 70-95% habitat reduction but no extinction debt (Kitzes and Harte, 2015). The imminent extinction estimates accord well with my results under maximum sub-division: for even distributions I predict fewer than 1.5% species loss at 90% habitat reduction; for less even distributions, 80-90% of habitat loss predicted 3.5-12.5% imminent extinctions. While I did not explicitly predict extinction debt, at intermediate evenness approximately 3-5% of species remaining after habitat loss were single-patch endemics. This proportion was consistent for a range of aggregation strengths, varying little from the null expectation under random placement. If species confined to a single remaining sub-population in a landscape are viewed as vulnerable to future extinction, this might represent a baseline expectation for minimum extinction debt in low-moderately even assemblages in fragmented landscapes.

Some of my other results are consistent with established patterns for the assembly of diversity in discrete habitat networks. For example, diminishing returns in the total number of species found from sub-dividing habitat over a greater number of patches has been shown empirically through negative area-to-patch number interaction terms in regressions of re-sampled habitat 'archipelagos' (Simberloff and Gotelli, 1984, McCoy and Mushinsky, 1994). Similarly, the increasing effect of sub-division with increasing mean abundance per species is consistent with the higher sub-division differential in richness relative to that of a single large patch found in more abundant taxa such as invertebrates often reported for empirical data (Tscharntke et al., 2002b, Rosch et al., 2015, Deane and He, 2018; Chapter 3). It also aligns with the general expectation of elevated beta diversity in fragmented landscapes (reviewed in Tscharntke et al., 2012).

As in any modelling study, simplification is necessary to achieve generality. Some key simplifying assumptions here were that (*i*) no specific pattern of sub-division is proposed, rather the models predict a statistical expectation, and, (*ii*) models predict an initial configuration of diversity that would be present were all the habitat loss and sub-division to occur instantaneously. There are important caveats associated with both assumptions. The precise geometry of clearance and the shape of the remaining habitat will affect the remaining species

(Harte and Kinzig, 1997, Ney-Nifle and Mangel, 2000, Pereira et al., 2012, Keil et al., 2015) and the impact on individual populations (May et al., 2019). It will also affect delayed extinctions (Tilman et al., 1997, Claudino et al., 2015). The assumption of instantaneous habitat loss, while not uncommon for studies of this nature (e.g., Kitzes and Harte, 2015), is obviously unlikely to occur in reality. The biological implication is, as discussed, that results assume that no biotic relaxation of the remaining populations has occurred. Despite these limitations, I suggest the results are useful as a null model for the expected effects of sub-division, particularly given the extent to which they accord with some commonly observed patterns of diversity in discrete habitat networks.

5.6 Conclusion

In this chapter I have further elaborated on the independent effects of sub-division in ameliorating species conservation under habitat loss. More, smaller patches will sample more species from the original landscape, but the effect typically constitutes only a few percent of the original diversity (3-5%). Moreover, as the remaining area is divided up among ever more numerous, but smaller patches, the increase in sampled species decreases. In a conservation reserve design context, this could be interpreted as supporting a small number of large reserves; such a design this would compromise between sampling more species from the original landscape while maintaining larger, more viable populations within each reserve.

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Chapter Six: Conclusions

In this thesis I have focused on studying discrete habitat networks by addressing three questions critical for conservation; (*i*) whether small patches typically comprise only common generalist species, (*ii*) whether beta diversity alone can adequately explain the more rapid accumulation of species typically observed among small patches relative to a single larger patch, and, (*iii*) how one should *expect* diversity to change at varying levels of sub-division under different spatial and abundance distributions. Several common themes emerged, some confirmatory or explanatory of previously proposed patterns, others identifying new hypotheses to explore.

Chapter 2 shows that removing all the smallest patches in most discrete habitat networks (whether naturally occurring or created as a result of land clearance) would remove at least some species from that network. The proportional loss of species would be high, relative to that expected for only a reduction in area, particularly for plants and invertebrate groups. However, even mammals, which lost the smallest proportion of species, still lost at least one species in 50% of datasets; the risk for vertebrate groups under loss of small patches is lower, but not zero. Given the greater propensity for destruction of small habitat patches under various global change processes, the potential for rapid loss of species is concerning.

Chapter 3 introduces two new competing hypotheses for the more rapid accumulation of species with area than the standard explanation; that it is due to increased species sorting along more spatially extensive environmental gradients. Increased evenness in the distribution of abundance in smaller patches could explain around the same amount of variation, while size-dependent disproportionate sampling efficiency that decreases with patch size, also accounted for a similar amount of explained variation. It is arguable that evenness is of questionable predictive value, as it is not in itself a mechanism. However, having confirmed increased evenness directly increases differences in richness between small and large patches, while decreases in evenness increase the impact of beta diversity, evenness offers scope as a unifying metric to investigate the effects of habitat sub-division on diversity. Clearly any question of sampling efficiency raises uncertainties over the inference that can be drawn using Quinn-Harrison curves. It also suggests that the strength of the findings of Chapter 2 could be overstated via the same sampling bias, where rare species are systematically under-recorded in large patches. This is somewhat ironic, because it was my lingering concern over this source of uncertainty around the findings of Chapter 2 that inspired this test in Chapter 3.

Chapters 4 and 5 are more theoretical and deductive than the inductive meta-studies of chapters 2 and 3. Together, I hope the main result of publishing chapters 4 and 5 will be recognition that there is no need to invoke some unspecified positive effect of sub-division to explain modest increases in diversity. It is a probable outcome for assemblages with uneven distribution of abundance and the prevalence of intraspecific aggregation in most taxa. Other useful findings from the study were the diminishing returns in the increase of species richness due to sub-division and quantifying effect sizes for the ‘species richness subsidy’ from sub-division. The small effect sizes involved also offers an explanation as to why purported positive effects of fragmentation *per se*, when detected, tend to be weak. A final contribution was a base line estimate of extinction debt under log series type species abundance distributions of 3-5%.

6.1 Synthesis and major contributions

The main contribution of my thesis has been to apply sampling theory to demonstrate how the expected species richness in sub-divided habitat depends on underlying spatial and abundance distributions of species. From this, I calculated the expected number of shared species, which others identified as being critical to resolving the SLOSS debate very early on (Simberloff and Abele, 1976, Higgs and Usher, 1980). To date however, it has only been possible to do this using the power law species-area relationship (Simberloff and Abele, 1976, Harte and Kinzig, 1997, Tjørve and Tjørve, 2008), which requires an unrealistic assumption of self similarity. The analytical shared species models I derived in Chapter 4 addressed this, providing the ability to calculate the expected number of shared species under different species abundance and spatial patterns. Moreover, by leveraging the recently derived zeta diversity partition (Hui and McGeoch, 2014), the probable consequences of sub-division for species richness can be shown to depend on spatial and abundance distributions - something which has been previously suggested (Kobayashi, 1985), but remains poorly understood.

Having an expectation for patterns of species richness in sub-divided habitat can help to resolve both the 'SLOSS', and 'fragmentation *per se*' debates, which - I argue herein - essentially arise from the same misunderstanding of the consequences of intraspecific aggregation for the expected number of species sub-divided habitat will contain. If the individuals of all species are randomly positioned, the number of species depends only on total habitat area; in any other situation, the statistical expectation can be predicted if relative abundance and spatial patterns are known. Unequal abundance and intraspecific aggregation results in a statistical expectation that sub-division of habitat means more species will be present in a group of small patches than a single large patch. Because intraspecific aggregation pre-dominates in nature, this should be the *a priori* expectation, but whether that should be interpreted as a positive effect on diversity is questionable.

The models in Chapter 4 can be used to develop an expectation for the effects of sub-division and are useful for theoretical applications, such as I demonstrated in Chapter 5. This type of analysis could be done in any terrestrial, marine or freshwater system where spatial and relative abundance information are available. I discuss some other potential uses for the models in Section 6.2.

In the meta-studies of chapters 2 and 3, I have challenged common, but largely untested, assumptions used to explain the relative diversity of several small vs. single large patches and found both are, at best, over-simplifications. I show the distributions of some species in spatially discrete habitat types, natural and artificial, are confined to small patches and their loss would remove species. The results of these chapters can be interpreted in the light of the two theoretical paradigms posited in Chapter 1. For example, three of the four different species-loss-curve models presented in Fig. 2.2 can be directly assigned to one or other of the paradigms, so by comparing the proportion of datasets falling within each category, an informal test of the strength of support for each can be made. The threshold and random models (Fig. 2.2 a and b, respectively) are both in accord with the predictions of the extinction/colonization paradigm. Together these accounted for around 29% of datasets. In comparison, the linear model - which directly follows from the spatial coexistence paradigm - was supported in 27% of datasets. The step model is not as easily assigned to either of the two paradigms, as it will depend on the specific mechanism generating the pattern. As a result, I conclude there is a similar amount of support for both theoretical paradigms, illustrating why debate around the importance of small patches has been so difficult to resolve.

While I remain somewhat guarded as to whether chapters 2 and 3 suggest that small patches are critical for biodiversity conservation (Wintle et al., 2019), available data indicate (uncertainties raised in Chapter 3 notwithstanding) that they are often critical for species representation and I propose some reasons why this is the case in Chapter 2. Improving our understanding of why some species are localized to small patches is important as it also holds relevance for both the SLOSS and fragmentation *per se* debates in terms of the role of small patches. For fragmented biomes, the ubiquity of this finding suggests that the initial expectation of sub-division under intraspecific aggregation (i.e., higher richness among groups of smaller patches) probably persists and possibly even strengthens over time, rather than eroding into nested subsets by patch area (Patterson and Atmar, 1986). Chapter 3 suggests this is as likely to be due to changes in evenness from priority effects and/or shifts in competitive hierarchies as increased beta diversity driven by habitat heterogeneity. Either (or indeed, both) of these mechanisms would explain why diversity of isolated patches might retain or increase their compositional differences through time. Both findings warrant more attention.

6.2 Limitations and future work

Throughout this thesis I have adopted a predominantly binary view of the landscape, where a patch either represents viable habitat or it does not. This approach implicitly assumes that (*i*) either all patches are of suitable quality for all species, or there is adequate dispersal among patches for species to reach optimal patches, and, (*ii*) that non-patch areas of a landscape (i.e., the matrix) are of no habitat value. Both assumptions are over-simplifications, with habitat suitability or quality (Soule and Simberloff, 1986, Mortelliti et al., 2010), landscape connectivity (Taylor et al., 1993, Kindlmann and Burel, 2008) and matrix composition (Andrén, 1994, Ricketts, 2001) known to affect the observed diversity within and among patches. However, despite the ecological limitations of such a binary view of landscapes, it nonetheless represents a null model from which we can infer statistical expectations. Moreover, in a practical sense, the legislative frameworks within which natural habitats are managed are typically categorical in their treatment of landscape units, so having appropriate null expectations is important.

Similarly, I have adopted a predominantly neutral view of the ecological processes that produce the observed variations in spatial and abundance distributions. To thoroughly summarise theoretical and empirical evidence relating these patterns to their generating processes is beyond the scope of this thesis, but it is an important direction for future research of this nature. Thus, for completeness, some consideration of this topic is appropriate. Essentially, both spatial and abundance patterns reflect the mechanisms determining coexistence, albeit at different scales. The species abundance distribution in one sense expresses the outomce of coexistence mechanisms at a landscape scale, while the spatial pattern can tell us how this scales with area.

Chesson (2000), suggests conceptualizing the differences among species that allow for coexistence as a niche space comprising four axes; resources, natural enemies, space and time.

For discrete habitat networks, we can integrate Chesson's coexistence-niche space within a metacommunity framework, considering axes of species equivalence, environmental heterogeneity and dispersal (Logue et al., 2011). Overlain on this conceptual metacommunity space, disturbance intensity and frequency also play a role in the observed diversity patterns over time (Levin and Paine, 1974, Sousa, 1984). Following Chesson's coexistence-niche concept, the greater the number of dimensions involved in each axis, and/or the more finely that this niche space is partitioned, the more species can coexist. Smaller overlap in preferred conditions (i.e., a narrower per-species niche width indicating greater specialization), should promote a more even distribution of abundance.

The scale at which coexistence is determined among species will vary according to trophic rank and body size, which largely determines minimum area and energy requirements (Brown and Maurer, 1989). Indeed, differences in body size accounted for much of the variation in response among taxonomic groups found in chapters 2 and 3. In discrete habitat networks, an interaction between patch-scale environmental heterogeneity and among-patch dispersal rates can, in theory, determine regional species abundance distributions (Mouquet and Loreau, 2003). At high levels of dispersal, regionally dominant species occur at all sites, leading to a less even distribution of abundance – a pattern I have previously observed in highly connected wetland plant communities (Deane et al., 2017b). Conversely, at low levels of dispersal, regional species abundance distributions are predicted to be more even, as dominant competitors are restricted to fewer patches (Mouquet and Loreau, 2003). Disturbance will reset successional trajectories, with effects on abundance distributions. For example, evenness tends to be lower in early successional communities, increasing with time since disturbance (Bazzaz, 1975, Hill et al., 1995).

For spatial distributions, the local-scale processes that determine coexistence are of most interest, as the strength of intraspecific aggregation decreases with increasing sampling area (Plotkin and Muller-Landau, 2002, Conlisk et al., 2012). Indeed, in Chapter 4, I confirm this theoretical expectation of decreasing aggregation follows a power-law scaling relationship with area at the community level (Plotkin and Muller-Landau, 2002, He and Hubbell, 2003). As aggregation decreases with area, the observed spatial pattern will depend on an interaction between fine-scale heterogeneity in environmental conditions and biological competition. Generally, any mechanism generating negative density dependence in recruitment success in the vicinity of adult conspecifics would tend to result in more regular distributions, with the Janzen-Connell effect one example (reviewed in Wright, 2002). On the other hand, if heterogeneity in environmental conditions occurs at scales over which competition operates (i.e., among near neighbours), then it is likely the species most suited to local conditions will dominate, promoting aggregated spatial patterns. An example of such a situation is the strong zonation along depth gradients observed among aquatic macrophytes. Interestingly though, random processes can also produce non- random spatial patterns. For example, the negative binomial, and finite negative binomial distributions can be generated by a range of stochastic processes influencing demographic rates (Boswell and Patil, 1970, Zillio and He, 2010).

Future work that follows from this thesis include testing of some of the implied patterns in the meta-studies and further validation and development of the shared species models. Most importantly, I believe the work demonstrates the value of obtaining additional detail on spatial and abundance distributions in nature. My personal feeling is that research has focussed heavily on finding ever more statistical models to fit species abundances to, while syntheses of systematic variation in the influential *properties* of relative abundance, particularly evenness, among taxa and biomes would provide more value in being able to predict the consequences of global change. A global synthesis of variations in Pielou's evenness (rather than the best fitting species abundance model) among taxonomic groups and habitat types, in contiguous and sub-divided habitats could be very informative; I note that a recently compiled database makes such an analysis possible (Chase et al., 2019).

Among the more interesting, if speculative, hypotheses that arose during the work for future consideration was the trade-off between imminent and delayed extinction implied by the results of Chapter 5. Kitzes and Harte (2015) reached a similar conclusion. There would seem to be an opportunity to use sampling theory, perhaps by integrating it with metapopulation theory (Hanski et al., 2013), to directly predict the relaxation of cleared landscapes. Similarly, the four different species loss categories I identified in Chapter 2 offer broad scope to investigate the hypothesised link between these patterns and the mechanisms I proposed in that chapter (e.g., the random-placement of species among patches in highly disturbed biomes and the interaction between body size and habitat heterogeneity in producing the linear pattern). Another hypothesis worthy of further exploration was the possible latitudinal gradient in the SLOSS effect due to the general decline in evenness (Chapter 3). Representing both an uncertainty in my own conclusions and a direction for future work, Chapters 2 and 3 also highlighted the need to investigate the role of size-dependent sampling efficiency in producing SLOSS-type patterns. The taxonomic bias in published Quinn-Harrison curves could also be addressed to provide a valid test of the generality of this pattern in vertebrates.

Perhaps the most useful future development for the shared species models is their application to empirical, rather than simulated, abundance data. In preliminary testing, the non-random models can provide a reliable fit to observed species overlap from empirical samples (i.e., with no knowledge of the underlying abundance or spatial distributions of the sampled assemblage). In such a case, scaling factor *c* then has use not only as a fitting parameter, but potentially as a measure of expected overlap among patches (particularly if the variance for expect shared species was derived to statistically differentiate among groups of samples).

Other model developments would include addressing uncertainty in the scaling of the model parameters; additional validation with landscapes other than stem-mapped forests to test model predictions is warranted. Other modifications could be incorporated to allow more complex spatial phenomena, such as environmental gradients to be simulated and are necessary if the model is to provide reliable predictions over larger extents where the assumptions of stationarity and isotropy are unlikely to be met. Incorporating distance decay of similarity in model structure would also provide a valuable improvement.

Despite the promise of these new hypotheses, and work that could be based on them, I stress this type of theoretical development must be supported by improved and targeted empirical data collection. Model validation and scenarios herein relied heavily on spatial and diversity patterns consistent with stem-mapped forest plots. We have no information on the assemblage structure of similar forests when they occur as isolated patches. It is not even clear if the assumption of constant values for individual density – the cornerstone of many ecological theories – is valid in sub-divided habitat. Perhaps this is unlikely. More information on the species abundance distribution of entire assemblages other than trees, while undoubtedly costly, would almost certainly prove equally useful for improving our ability to provide practical tools and ecologically realistic predictions. This is especially important for trophic levels other than primary producers. Were such detailed species abundance and spatial data available at a single location at multiple trophic levels, it would provide the data necessary to begin the work of incorporating sampling theory based (and other) approaches for modelling diversity at the ecological network level. Such detailed understanding would be invaluable for informing our baseline understanding of the expected human impacts on biodiversity.

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APPENDIX A: DATA SOURCES AND SPECIES LOSS CURVES

A.1. Data sources

Table A.1 Data sources used in Chapter 2 and 3

Dataset	Chatpers used	Source	Citation
brdFAcWTw_Azeria	2	(Azeria, 2004)	Azeria ET (2004) Terrestrial bird community patterns on the coralline islands of the Dahlak Archipelago, Red Sea, Eritrea. Global Ecology and Biogeography, 13, 177-187.
brdFAcWTw_Bourne	2	(Bourne & Harris, 1979)	Bourne WRP, Harris MP (1979) Birds of the Hebrides - seabirds. Proceedings of the Royal Society of Edinburgh Section B-Biological Sciences, 77, 445-475.
brdFAcWTw_Haila83	2, 3	(Haila, 1983; Haila et al., 1983)	Haila Y (1983) Land birds on northern islands - a sampling metaphor for insular colonization. Oikos, 41, 334-351.
brdFAcWTw_Martin	2	(Martin, 1983)	Martin JL (1983) Impoverishment of island bird communities in a Finnish archipelago. Ornis Scandinavica, 14, 66-77.
brdFAcWTw_Martin95	2	(Martin et al., 1995)	Martin JL, Gaston AJ, Hitier S (1995) The effect of island size and isolation on old-growth forest habitat and bird diversity in Gwaii Haanas (Queen Charlotte Islands, Canada). Oikos, 72, 115-131.
brdFAcWTw_Power	2	(Power, 1972)	Power DM (1972) Numbers of bird species on California islands. Evolution, 26, 451-&.
brdFAcWTw_Thibault	2	(Thibault et al., 1990)	Thibault JC, Martin JL, Guyot I (1990) The breeding land birds of the small islands in the Strait of Bonifacio population analysis
brdFAmWTw_Bengston	2	(Bengtson & Bloch, 1983)	Bengtson SA, Bloch D (1983) Island land bird population densities in relation to island size and habitat quality on the Faroe Islands. Oikos, 41, 507-522.

brdFAmWTw_ConnorBis	2	(Connor et al., 2013)	Connor, E.F., Collins, M.D. & Simberloff, D. (2013) The checkered history of checkerboard distributions. Ecology, 94, 2403-2414.
brdFAmWTw_ConnorSol	2	(Connor et al., 2013)	Connor, E.F., Collins, M.D. & Simberloff, D. (2013) The checkered history of checkerboard distributions. Ecology, 94, 2403-2414.
brdFAmWTw_ConnorVan	2	(Connor et al., 2013)	Connor, E.F., Collins, M.D. & Simberloff, D. (2013) The checkered history of checkerboard distributions. Ecology, 94, 2403-2414.
brdFAmWTw_Donozar	2	(Donazar et al., 2005)	Donazar JA, Gangoso L, Forero MG, Juste J (2005) Presence, richness and extinction of birds of prey in the Mediterranean and Macaronesian islands. Journal of Biogeography, 32, 1701-1713.
brdFAmWTw_Gotelli	2	(Gotelli & Abele, 1982)	Gotelli NJ, Abele LG (1982) Statistical distributions of West Indian land bird families. Journal of Biogeography, 9, 421-435.
brdFAmWTw_Harris	2	(Harris, 1973)	Harris MP (1973) Galapogos avifauna. Condor, 75, 265-278.
brdFArWTw_Feeley	2	(Feeley, 2003)	Feeley K (2003) Analysis of avian communities in Lake Guri, Venezuela, using multiple assembly rule models. Oecologia, 137, 104-113.
brdFArWTw_Wang	2	(Wang et al., 2010)	Wang YP, Ding P, Chen SH, Zheng GM (2013) Nestedness of bird assemblages on urban woodlots: Implications for conservation. Landscape and Urban Planning, 111, 59-67.
brdFArWTw_Wright	2	(Wright, 1985)	Wright SJ (1985) How isolation affects rates of turnover of species on islands. Oikos, 44, 331-340.
brdFFfPTt_Anciaes	2	(Anciaes & Marini, 2000)	Anciaes M, Marini MA (2000) The effects of fragmentation on fluctuating asymmetry in passerine birds of Brazilian tropical forests. Journal of Applied Ecology, 37, 1013-1028.
brdFFfPTt_Blake2	2	(Blake, 1991)	Blake JG (1991) Nested subsets and the distribution of birds on isolated woodlots. Conservation Biology, 5, 58-66.
brdFFfPTt_Capizzi1	2, 3	(Capizzi et al., 2015)	Capizzi D, Luiselli L, Papi R (2015) Temporal changes in Mediterranean bird communities across fragmented and continuous forests. Ecological Research, 30, 615-624.

brdFFfPTt_Capizzi2	2, 3	(Capizzi et al., 2015)	Capizzi D, Luiselli L, Papi R (2015) Temporal changes in Mediterranean bird communities across fragmented and continuous forests. Ecological Research, 30, 615-624.
brdFFfPTt_Castellata	2	(Castelletta et al., 2005)	Castelletta M, Thiollay JM, Sodhi NS (2005) The effects of extreme forest fragmentation on the bird community of Singapore Island. Biological Conservation, 121, 135-155.
brdFFfPTt_Daily	2, 3	(Daily et al., 2001)	Daily, G.C., Ehrlich, P.R. & Sanchez-Azofeifa, G.A. (2001) Countryside biogeography: Use of human-dominated habitats by the avifauna of southern Costa Rica. Ecological Applications, 11, 1-13
brdFFfPTt_Flaspoler	2	(Flaspohler et al., 2010)	Flaspohler DJ, Giardina CP, Asner GP, Hart P, Price J, Lyons CK, Castaneda X (2010) Long-term effects of fragmentation and fragment properties on bird species richness in Hawaiian forests. Biological Conservation, 143, 280-288.
brdFFfPTt_Ford	2	(Ford, 1987)	Ford HA (1987) Bird communities on habitat islands in England. Bird Study, 34, 205-218.
brdFFfPTt_Haila	2, 3	(Haila et al., 1993)	Haila Y, Hanski IK, Raivio S (1993) Turnover of breeding birds in small forest fragments - the sampling colonization hypothesis corroborated. Ecology, 74, 714-725.
brdFFfPTt_Haila1987	2	(Haila et al., 1987)	Haila Y, Hanski IK, Raivio S (1987) Breeding bird distribution in fragmented coniferous taiga in southern Finland. Ornis Fennica, 64, 90-106.
brdFFfPTt_Holbech	2, 3	(Holbech, 2005)	Holbech LH (2005) The implications of selective logging and forest fragmentation for the conservation of avian diversity in evergreen forests of south-west Ghana. Bird Conservation International, 15, 27-52.
brdFFfPTt_Howe	2	(Howe & Jones, 1977)	Howe RW, Jones G (1977) Avian utilization of small woodlots in Dane County, Wisconsin. Passenger Pigeon, 39, 313-319,illust.
brdFFfPTt_Marini	2	(Marini, 2001)	Marini MA (2001) Effects of forest fragmentation on birds of the cerrado region, Brazil. Bird Conservation International, 11, 13-25.

brdFFfPTt_McCollin	2	(McCollin, 1993)	Mccollin D (1993) Avian distribution patterns in a fragmented wooded landscape (North Humberside, UK) - the role of between-patch and within-patch structure. Global Ecology and Biogeography Letters, 3, 48-62.
brdFFfPTt_Meynard	2	(Meynard & Quinn, 2008)	Meynard CN, Quinn JF (2008) Bird metacommunities in temperate South American forest: Vegetation structure, area, and climate effects. Ecology, 89, 981-990
brdFFfPTt_Newmark	2	(Newmark, 1991)	Newmark WD (1991) Tropical forest fragmentation and the local extinction of understory birds in the eastern Usambara Mountains, Tanzania. Conservation Biology, 5, 67-78.
brdFFfPTt_Wang	2, 3	(Wang et al., 2013)	Wang YP, Ding P, Chen SH, Zheng GM (2013) Nestedness of bird assemblages on urban woodlots: Implications for conservation. Landscape and Urban Planning, 111, 59-67.
brdFFfPTt_Watson	2	(Watson, 2003)	Watson DM (2003) Long-term consequences of habitat fragmentation - highland birds in Oaxaca, Mexico. Biological Conservation, 111, 283-303.
brdFFfUTt_MohdAzlan	2, 3	(Mohd-Azlan & Lawes, 2011)	Mohd-Azlan J, Lawes MJ (2011) The effect of the surrounding landscape matrix on mangrove bird community assembly in north Australia. Biological Conservation, 144, 2134-2141.
brdFFvUTt_Crooks	2	(Crooks et al., 2001)	Crooks KR, Suarez AV, Bolger DT, Soule ME (2001) Extinction and colonization of birds on habitat islands. Conservation Biology, 15, 159-172.
brdFFvUTt_Fernandez	2	(Fernandez-Juricic, 2000)	Fernandez-Juricic E (2000) Bird community composition patterns in urban parks of Madrid: The role of age, size and isolation. Ecological Research, 15, 373-383.
brdFFvUTt_Soule	2	(Soule et al., 1988)	Soule ME, Bolger DT, Alberts AC, Wright J, Sorice M, Hill S (1988) Reconstructed dynamics of rapid extinctions of chaparral-requiring birds in urban habitat islands. Conservation Biology, 2, 75-92.
brdFHmMTt_Behle	2	(Behle, 1978)	Behle WH (1978) Avian biogeography of the Great Basin and inter mountain region. Great Basin Naturalist Memoirs, 55-80.

brdFHmMTt_Brown	2	(Brown, 1978)	Brown JH (1978) The theory of insular biogeography and the distribution of boreal birds and mammals. Great Basin Naturalist Memoirs, 209-227.
brdFHmMTt_Dorst	2	(Dorst et al., 1986)	Dorst J, Vuilleumier F, Vuilleumier F, Monasterio M (1986) Convergences in bird communities at high altitudes in the Tropics (especially the Andes and Africa) and at high temperate latitudes (Tibet).
brdFHmMTt_Dowsett	2	(Dowsett et al., 1986)	Dowsett RJ, Vuilleumier F, Monasterio M (1986) Origins of the high-altitude avifaunas of tropical Africa.
brdFHmMTt_Johnson	2	(Johnson, 1975)	Johnson NK (1975) Controls of number of bird species on montane islands in Great-Basin. Evolution, 29, 545-567.
brdFHmMTt_Kratter	2	(Kratter, 1992)	Kratter AW (1992) Montane avian biogeography in southern California and Baja California. Journal of Biogeography, 19, 269-283.
brdFHmMTt_Nores	2	(Nores, 1995)	Nores M (1995) Insular biogeography of birds on mountain-tops in north-western Argentina. Journal of Biogeography, 22, 61-70.
brdFHvGTt_Anjos	2	(Dos Anjos & Bocon, 1999)	Dos Anjos L, Bocon R (1999) Bird communities in natural forest patches in southern Brazil. Wilson Bulletin, 111, 397-414.
brdFHvNTt_Andrade	2	(Andrade & Marini, 2002)	Andrade RD, Marini MA (2002) Bird species richness in natural forest patches in southeast Brazil. Lundiana, 3, 141-149.
brdFHvNTt_Edenius	2, 3	(Edenius & Sjoberg, 1997)	Edenius L, Sjoberg K (1997) Distribution of birds in natural landscape mosaics of old-growth forests in northern Sweden: relations to habitat area and landscape context. Ecography, 20, 425-431.
brdFHwNWt_Gotmark	2, 3	(Gotmark et al., 1986)	Gotmark F, Ahlund M, Eriksson MOG (1986) Are indexes reliable for assessing conservation value of natural areas - an avian case study. Biological Conservation, 38, 55-73.
brdFHwPWt_RM03_07	2	(Waanders, 2007)	Waanders, P. (2007) River Murray wetland bird surveys. In: Draft report on the Bird survey component of the 2006 SA River Murray Wetlands Baseline Survey

fshAHwPWt_DingS3	2	(Ding et al., 2017)	Ding CZ, Jiang XM, Xie ZC, Brosse S (2017) Seventy-five years of biodiversity decline of fish assemblages in Chinese isolated plateau lakes: widespread introductions and extirpations of narrow endemics lead to regional loss of dissimilarity. Diversity and Distributions, 23, 171-184.
fshAHwPWt_Graham	2	(Graham, 1993)	Graham JH (1993) Species diversity of fishes in naturally acidic lakes in New Jersey. Transactions of the American Fisheries Society, 122, 1043-1057.
fshAHwPWt_Granado	2	(Granado-Lorencio et al., 2012)	Granado-Lorencio C, Serna AH, Carvajal JD, Jimenez-Segura LF, Gulfo A, Alvarez F (2012) Regionally nested patterns of fish assemblages in floodplain lakes of the Magdalena river (Colombia). Ecology and Evolution, 2, 1296-1303.
fshAHwPWt_Mitsuo	2	(Mitsuo et al., 2011)	Mitsuo Y, Tsunoda H, Ohira M, Doi M, Senga Y (2011) Nested subset patterns of species composition in a pond-dwelling fish fauna. Ecological Research, 26, 311-316.
fshAHwPWt_Tonn	2	(Tonn & Magnuson, 1982)	Tonn WM, Magnuson JJ (1982) Patterns in the species composition and richness of fish assemblages in northern Wisconsin lakes. Ecology, 63, 1149-1166.
hrpWAcWTw_Bittencourt	2	(Bittencourt-Silva & Silva, 2014)	Bittencourt-Silva GB, Silva HR (2014) Effects of Fragmentation and Sea-Level Changes upon Frog Communities of Land-Bridge Islands off the Southeastern Coast of Brazil. Plos One, 9.
hrpWAcWTw_Burbrink	2	(Burbrink et al., 2015)	Burbrink FT, Mckelvy AD, Pyron RA, Myers EA (2015) Predicting community structure in snakes on Eastern Nearctic islands using ecological neutral theory and phylogenetic methods. Proceedings of the Royal Society B-Biological Sciences, 282.
hrpWAcWTw_Corti	2	(Corti et al., 1999)	Corti C, Masseti M, Delfino M, Perez-Mellado V (1999) Man and herpetofauna of the Mediterranean islands. Revista Espanola de Herpetologia, 13, 83-100.

hrpWAcWTw_Hausdorf	2	(Hausdorf & Hennig, 2005)	Hausdorf B, Hennig C (2005) The influence of recent geography, palaeogeography and climate on the composition of the fauna of the central Aegean Islands. Biological Journal of the Linnean Society, 84, 785-795.
hrpWAcWTw_Krystufek	2	(Krystufek & Kletecki, 2007)	Krystufek B, Kletecki E (2007) Biogeography of small terrestrial vertebrates on the Adriatic landbridge islands. Folia Zoologica, 56, 225-234.
hrpWAcWTw_Soule1966	2	(Soule & Sloan, 1966)	Soule M, Sloan AJ (1966) Biogeography and distribution of the reptiles and amphibians on islands in the Gulf of California, Mexico. Trans San Diego Soc Natur Hist, 14, 137-156.
hrpWFfNTt_Vallan	2, 3	(Vallan, 2000)	Vallan D (2000) Influence of forest fragmentation on amphibian diversity in the nature reserve of Ambohitantely, highland Madagascar. Biological Conservation, 96, 31-43.
hrpWFfPTt_Cabrera	2	(Cabrera-Guzman & Reynoso, 2012)	Cabrera-Guzman E, Reynoso VH (2012) Amphibian and reptile communities of rainforest fragments: minimum patch size to support high richness and abundance. Biodiversity and Conservation, 21, 3243-3265.
hrpWFfPTt_Pineda	2, 3	(Pineda & Halffter, 2004)	Pineda E, Halffter G (2004) Species diversity and habitat fragmentation: frogs in a tropical montane landscape in Mexico. Biological Conservation, 117, 499-508.
hrpWFvPTt_Kitchener	2	(Kitchener et al., 1980a)	Kitchener DJ, Chapman A, Dell J, Muir BG (1980a) Lizard assemblage and reserve size and structure in the western Australian wheatbelt - some implications for conservation. Biological Conservation, 17, 25-62.
hrpWFvPTt_Smith	2	(Smith et al., 1996)	Smith GT, Arnold GW, Sarre S, Abenspergtraun M, Steven DE (1996) The effects of habitat fragmentation and livestock-grazing on animal communities in remnants of gimlet Eucalyptus salubris woodland in the Western Australian wheatbelt .2. Lizards. Journal of Applied Ecology, 33, 1302-1310.
hrpWHvPTt_Gouveia	2	(Gouveia & Faria, 2015)	Gouveia SF, Faria RG (2015) Effects of Habitat Size and Heterogeneity on Anuran Breeding Assemblages in the Brazilian Dry Forest. Journal of Herpetology, 49, 442-446.

hrpWHwPWt_Almeida	2, 3	(Almeida-Gomes et al., 2016)	Almeida-Gomes M, Rocha CFD, Vieira MV (2016) Local and Landscape Factors Driving the Structure of Tropical Anuran Communities: Do Ephemeral Ponds have a Nested Pattern? Biotropica, 48, 365-372.
hrpWHwPWt_Peltzer	2	(Peltzer et al., 2003)	Peltzer PM, Lajmanovich RC, Beltzer A (2003) The effect of habitat fragmentation on amphibian species richness in the floodplain of the Middle Parana River, Argentina. Herpetological Journal, 13, 95-98.
invAHwNWt_AndersonBanff	2	(Anderson, 1974)	Anderson RS (1974) Crustacean plankton communities of 340 lakes and ponds in and near national parks of Canadian Rocky Mountains. Journal of the Fisheries Research Board of Canada, 31, 855-&.
invAHwNWt_AndersonJasper	2	(Anderson, 1974)	Anderson RS (1974) Crustacean plankton communities of 340 lakes and ponds in and near national parks of Canadian Rocky Mountains. Journal of the Fisheries Research Board of Canada, 31, 855-&.
invAHwNWt_Urban	2	(Urban, 2004)	Urban MC (2004) Disturbance heterogeneity determines freshwater metacommunity structure. Ecology, 85, 2971-2978.
invAHwPWt_Ball	2, 3	(Ball et al., 2015)	Ball OJP, Pohe SR, Winterbourn MJ (2015) Littoral macroinvertebrate communities of dune lakes in the far north of New Zealand. New Zealand Journal of Marine and Freshwater Research, 49, 192-204.
invAHwPWt_Deane	2, 3	(Deane & Walters, 2008)	Deane DC, Walters AC (2008) Baseline survey of refugia pools in the north-eastern Willochra Creek and Western Lake Frome Catchments, DWLBC Report 2008/15, Adelaide, Government of South Australia.
invAHwPWt_King	2	(King et al., 1996)	King JL, Simovich MA, Brusca RC (1996) Species richness, endemism and ecology of crustacean assemblages in northern California vernal pools. Hydrobiologia, 328, 85-116.
invAHwPWt_Markwell	2	(Markwell & Fellows, 2008)	Markwell KA, Fellows CS (2008) Habitat and biodiversity of on-farm water storages: A case study in Southeast Queensland, Australia. Environmental Management, 41, 234-249.

invAHwPWt_Stamou	2	(Stamou et al., 2017)	Stamou G, Polyzou C, Karagianni A, Michaloudi E (2017) Taxonomic distinctness indices for discriminating patterns in freshwater rotifer assemblages. Hydrobiologia, 796, 319-331.
invFAcWTw_Dapporto	2	(Dapporto & Cini, 2007)	Dapporto L, Cini A (2007) Faunal patterns in Tuscan archipelago butterflies: The dominant influence is recent geography not paleogeography. European Journal of Entomology, 104, 497-503.
invFAcWTw_Dapporto2	2	(Dapporto & Dennis, 2008)	Dapporto L, Dennis RLH (2008) Species richness, rarity and endemicity on Italian offshore islands: complementary signals from island-focused and species-focused analyses. Journal of Biogeography, 35, 664-674.
invFAcWTw_Dennis	2	(Dennis et al., 2000)	Dennis RLH, Shreeve TG, Olivier A, Coutsis JG (2000) Contemporary geography dominates butterfly diversity gradients within the Aegean archipelago (Lepidoptera : Papilionoidea, Hesperioidea). Journal of Biogeography, 27, 1365-1383.
invFAcWTw_HausButterfly	2	(Hausdorf & Hennig, 2005)	Hausdorf B, Hennig C (2005) The influence of recent geography, palaeogeography and climate on the composition of the fauna of the central Aegean Islands. Biological Journal of the Linnean Society, 84, 785-795.
invFAcWTw_Simberloff	2	(Simberloff, 1976)	Simberloff D (1976) Experimental zoogeography of islands - effects of island size. Ecology, 57, 629-648.
invFAcWTw_Spengler	2	(Spengler et al., 2011)	Spengler A, Hartmann P, Buchori D, Schulze CH (2011) How island size and isolation affect bee and wasp ensembles on small tropical islands: a case study from Kepulauan Seribu, Indonesia. Journal of Biogeography, 38, 247-258.
invFAcWTw_Tennant	2	(Tennent & Russell, 2014)	Tennent WJ, Russell PJC (2014) Butterflies of the Cape Verde Islands (Insecta, Lepidoptera). Zoologia Caboverdiana, 5, 64-104.
invFAcWTw_Zhang	2	(Zhang et al., 2016)	Zhang X, Han X, Liu L, Xu A (2016) Influencing factors of the nested distribution of butterfly assemblages in the Zhoushan Archipelago, China. Biodiversity Science, 24, 321-331.

invFAmWTw_Hirao	2	(Hirao et al., 2015)	Hirao T, Kubota Y, Murakami M (2015) Geographical patterns of butterfly species diversity in the subtropical Ryukyu Islands: the importance of a unidirectional filter between two source islands. Journal of Biogeography, 42, 1418-1430.
invFAmWTw_Xu	2, 3	(Xu et al., 2017)	Xu AC, Han XF, Zhang XM, Millien V, Wang YP (2017) Nestedness of butterfly assemblages in the Zhoushan Archipelago, China: area effects, life-history traits and conservation implications. Biodiversity and Conservation, 26, 1375-1392.
invFFfPTt_Baz	2, 3	(Baz & GarciaBoyero, 1996)	Baz A, Garciaboyero A (1996) The SLOSS dilemma: A butterfly case study. Biodiversity and Conservation, 5, 493-502.
invFFfPTt_Bennedick	2, 3	(Benedick et al., 2006)	Benedick S, Hill JK, Mustaffa N et al. (2006) Impacts of rain forest fragmentation on butterflies in northern Borneo: species richness, turnover and the value of small fragments. Journal of Applied Ecology, 43, 967-977.
invFFfPTt_Daily	2	(Daily & Ehrlich, 1995)	Daily GC, Ehrlich PR, Sanchez-Azofeifa GA (2001) Countryside biogeography: Use of human-dominated habitats by the avifauna of southern Costa Rica. Ecological Applications, 11, 1-13.
invFFfPTt_Filguerias	2, 3	(Filgueiras et al., 2011)	Filgueiras BKC, Iannuzzi L, Leal IR (2011) Habitat fragmentation alters the structure of dung beetle communities in the Atlantic Forest. Biological Conservation, 144, 362-369.
invFFfPTt_Nyeko	2, 3	(Nyeko, 2009)	Nyeko P (2009) Dung Beetle Assemblages and Seasonality in Primary Forest and Forest Fragments on Agricultural Landscapes in Budongo, Uganda. Biotropica, 41, 476-484.
invFFfPTt_Pavuk	2	(Pavuk & Wadsworth, 2012)	Pavuk DM, Wadsworth AM (2012) Longhorned beetle (Coleoptera: Cerambycidae) diversity in a fragmented temperate forest landscape. F1000Research, 1, 25.
invFFfPTt_Shreeve	2	(Shreeve & Mason, 1980)	Shreeve TG, Mason CF (1980) The number of butterfly species in woodlands. Oecologia, 45, 414-418.

invFFfPTt_Usher	2, 3	(Usher & Keiller, 1998)	Usher MB, Keiller SWJ (1998) The macrolepidoptera of farm woodlands: determinants of diversity and community structure. Biodiversity and Conservation, 7, 725-748.
invFFvPTt_Baldi	2, 3	(Baldi & Kisbenedek, 1997, 1999)	Báldi A, Kisbenedek T (1997) Orthopteran assemblages as indicators of grassland naturalness in Hungary. Agriculture Ecosystems & Environment, 66, 121-129.
invFFvPTt_Essl	2	(Essl & Dirnbock, 2012)	Essl F, Dirnbock T (2012) What determines Orthoptera species distribution and richness in temperate semi-natural dry grassland remnants? Biodiversity and Conservation, 21, 2525-2537.
invFFvUTt_Nufio	2, 3	(Nufio et al., 2011)	Nufio CR, Mcclenahan JL, Bowers MD (2011) Grasshopper response to reductions in habitat area as mediated by subfamily classification and life history traits. Journal of Insect Conservation, 15, 409-419.
invFHvNTt_Aranda	2	(Aranda & Olivier, 2017)	Aranda R, Olivier RD (2017) Preliminary study of species-area, isolation and impact of environmental heterogeneity on insect communities in natural patches in the Brazilian Pantanal. Entomological News, 126, 312-327.
invWAcWTw_Clark	2	(Clark et al., 2011)	Clark AT, Rykken JJ, Farrell BD (2011) The Effects of Biogeography on Ant Diversity and Activity on the Boston Harbor Islands, Massachusetts, USA. Plos One, 6.
invWAcWTw_Davidson	2	(Davidson et al., 2011)	Davidson RL, Rykken J, Farrell B (2011) Carabid beetle diversity and distribution in Boston Harbor Islands national park area (Coleoptera, Carabidae). Zookeys, 497-526.
invWAcWTw_Fattorini	2	(Fattorini, 2002)	Fattorini S (2002) Biogeography of the tenebrionid beetles (Coleoptera, Tenebrionidae) on the Aegean Islands (Greece). Journal of Biogeography, 29, 49-67.
invWAcWTw_HausBeetles	2	(Hausdorf & Hennig, 2005)	Hausdorf B, Hennig C (2005) The influence of recent geography, palaeogeography and climate on the composition of the fauna of the central Aegean Islands. Biological Journal of the Linnean Society, 84, 785-795.

invWAcWTw_HausIsopods	2	(Hausdorf & Hennig, 2005)	Hausdorf B, Hennig C (2005) The influence of recent geography, palaeogeography and climate on the composition of the fauna of the central Aegean Islands. Biological Journal of the Linnean Society, 84, 785-795.
invWAcWTw_HausMoll	2	(Hausdorf & Hennig, 2005)	Hausdorf B, Hennig C (2005) The influence of recent geography, palaeogeography and climate on the composition of the fauna of the central Aegean Islands. Biological Journal of the Linnean Society, 84, 785-795.
invWAcWTw_Macias	2	(Macias-Hernandez et al., 2016)	Macias-Hernandez N, Lopez SD, Roca-Cusachs M, Oromi P, Arnedo MA (2016) A geographical distribution database of the genus Dysdera in the Canary Islands (Araneae, Dysderidae). Zookeys, 11-23.
invWAcWTw_Rizali	2	(Rizali et al., 2010)	Rizali A, Lohman DJ, Buchori D et al. (2010) Ant communities on small tropical islands: effects of island size and isolation are obscured by habitat disturbance and 'tramp' ant species. Journal of Biogeography, 37, 229-236.
invWArWTw_Davis	2, 3	(Davies et al., 2003)	Davies RG, Hernandez LM, Eggleton P, Didham RK, Fagan LL, Winchester NN (2003) Environmental and spatial influences upon species composition of a termite assemblage across neotropical forest islands. Journal of Tropical Ecology, 19, 509-524.
invWFfPTt_Galle	2, 3	(Galle, 2008)	Galle R (2008) The effect of a naturally fragmented landscape on the spider assemblages. North-Western Journal of Zoology, 4, 61-71.
invWFfPTt_Ribas	2	(Ribas et al., 2005)	Ribas CR, Sobrinho TG, Schoereder JH, Sperber CF, Lopes-Andrade C, Soares SM (2005) How large is large enough for insects? Forest fragmentation effects at three spatial scales. Acta Oecologica-International Journal of Ecology, 27, 31-41.
invWFfUTt_Gaublomme	2, 3	(Gaublomme et al., 2008)	Gaublomme E, Hendrickx F, Dhuyvetter H, Desender K (2008) The effects of forest patch size and matrix type on changes in carabid beetle assemblages in an urbanized landscape. Biological Conservation, 141, 2585-2596.

invWFfUTt_Miyashita	2	(Miyashita et al., 1998)	Miyashita T, Shinkai A, Chida T (1998) The effects of forest fragmentation on web spider communities in urban areas. Biological Conservation, 86, 357-364.
invWFfUTt_Weller	2	(Weller & Ganzhorn, 2004)	Weller B, Ganzhorn JU (2004) Carabid beetle community composition, body size, and fluctuating asymmetry along an urban-rural gradient. Basic and Applied Ecology, 5, 193-201.
invWFvPTt_Gavish	2	(Gavish et al., 2012)	Gavish Y, Ziv Y, Rosenzweig ML (2012) Decoupling Fragmentation from Habitat Loss for Spiders in Patchy Agricultural Landscapes. Conservation Biology, 26, 150-159.
invWFvPTt_Suarez	2	(Suarez et al., 1998)	Suarez AV, Bolger DT, Case TJ (1998) Effects of fragmentation and invasion on native ant communities in coastal southern California. Ecology, 79, 2041-2056.
invWHwNWt_Friday	2	(Friday, 1987)	Friday LE (1987) The diversity of macroinvertebrate and macrophytes communities in ponds. Freshwater Biology, 18, 87-104.
mamFAmWTw_Baker	2	(Baker & Genoways, 1978)	Baker RJ, Genoways HH (1978) Zoogeography of Antillean bats. Special Publication Academy of Natural Sciences Philadelphia, 53-97.
mamFAmWTw_PresleyBA	2	(Presley & Willig, 2010)	Presley SJ, Willig MR (2010) Bat metacommunity structure on Caribbean islands and the role of endemics. Global Ecology and Biogeography, 19, 185-199.
mamFAmWTw_PresleyGA	2	(Presley & Willig, 2010)	Presley SJ, Willig MR (2010) Bat metacommunity structure on Caribbean islands and the role of endemics. Global Ecology and Biogeography, 19, 185-199.
mamFAmWTw_PresleyLA	2	(Presley & Willig, 2010)	Presley SJ, Willig MR (2010) Bat metacommunity structure on Caribbean islands and the role of endemics. Global Ecology and Biogeography, 19, 185-199.
mamWAcWTw_Conroy	2	(Conroy et al., 1999)	Conroy CJ, Demboski JR, Cook JA (1999) Mammalian biogeography of the Alexander Archipelago of Alaska: a north temperate nested fauna. Journal of Biogeography, 26, 343-352.

mamWAcWTw_Crowell	2	(Crowell, 1986)	Crowell KL (1986) A comparison of relict versus equilibrium models for insular mammals of the Gulf of Maine. Biological Journal of the Linnean Society, 28, 37-64.
mamWAcWTw_Dueser	2	(Dueser & Brown, 1980)	Dueser RD, Brown WC (1980) Ecological correlates of insular rodent diversity. Ecology, 61, 50-56.
mamWAcWTw_Krystofek	2	(Krystufek & Kletecki, 2007)	Krystufek B, Kletecki E (2007) Biogeography of small terrestrial vertebrates on the Adriatic landbridge islands. Folia Zoologica, 56, 225-234.
mamWAfWTw_Cramer	2	(Cramer, 1994)	Cramer KL (1994) New mammal record for Fremont Island with an updated checklist of mammals on islands in the Great Salt Lake Great Basin Naturalist, 54, 287-289.
mamWAfWTw_Lomolino	2	(Lomolino, 1986)	Lomolino MV (1986) Mammalian community structure on islands - the importance of immigration, extinction and interactive effects. Biological Journal of the Linnean Society, 28, 1-21.
mamWAmWTw_Heaney	2	(Heaney, 1986)	Heaney LR (1986) Biogeography of mammals in SE Asia - estimates of rates of colonization, extinction and speciation. Biological Journal of the Linnean Society, 28, 127-165.
mamWArPTw_Dalecky	2	(Dalecky et al., 2002)	Dalecky A, Chauvet S, Ringuet S, Claessens O, Judas J, Larue M, Cosson JF (2002) Large mammals on small islands: Short term effects of forest fragmentation on the large mammal fauna in French Guiana. Revue D Ecologie-La Terre Et La Vie, 145-164.
mamWArWTw_Wang	2	(Wang et al., 2010)	Wang YP, Bao YX, Yu MJ, Xu GF, Ding P (2010) Nestedness for different reasons: the distributions of birds, lizards and small mammals on islands of an inundated lake. Diversity and Distributions, 16, 862-873.
mamWFfPTt_deCastro	2	(de Castro & Fernandez, 2004)	De Castro EBV, Fernandez FaS (2004) Determinants of differential extinction vulnerabilities of small mammals in Atlantic forest fragments in Brazil. Biological Conservation, 119, 73-80.

mamWFfPTt_Dinesan	2	(Dinesen et al., 2001)	Dinesen L, Lehmberg T, Rahner MC, Fjeldsa J (2001) Conservation priorities for the forests of the Udzungwa Mountains, Tanzania, based on primates, duikers and birds. Biological Conservation, 99, 223-236.
mamWFfPTt_Kelt	2	(Kelt, 2000)	Kelt DA (2000) Small mammal communities in rainforest fragments in Central Southern Chile. Biological Conservation, 92, 345-358.
mamWFfPTt_Lomolino	2	(Lomolino & Perault, 2001)	Lomolino MV, Perault DR (2001) Island biogeography and landscape ecology of mammals inhabiting fragmented, temperate rain forests. Global Ecology and Biogeography, 10, 113-132.
mamWFfPTt_marshall	2	(Marshall et al., 2010)	Marshall AR, Jorgensbye HIO, Rovero F, Platts PJ, White PCL, Lovett JC (2010) The Species Area Relationship and Confounding Variables in a Threatened Monkey Community. American Journal of Primatology, 72, 325-336.
mamWFfPTt_Matthiae	2, 3	(Matthiae & Stearns, 1981)	Matthiae PE, Stearns F (1981) Mammals in forest islands in southeastern Wisconsin. Ecological Studies, 41, 55-66.
mamWFfPTt_Rosenblatt	2	(Rosenblatt et al., 1999)	Rosenblatt DL, Heske EJ, Nelson SL, Barber DH, Miller MA, Macallister B (1999) Forest fragments in east-central Illinois: Islands or habitat patches for mammals? American Midland Naturalist, 141, 115-123.
mamWFfPTt_Silva	2, 3	(Silva, 2001)	Silva M (2001) Abundance, diversity, and community structure of small mammals in forest fragments in Prince Edward Island National Park, Canada. Canadian Journal of Zoology-Revue Canadienne De Zoologie, 79, 2063-2071.
mamWFfUTt_Charles	2	(Charles & Ang, 2010)	Charles JK, Ang BB (2010) Non-volant small mammal community responses to fragmentation of kerangas forests in Brunei Darussalam. Biodiversity and Conservation, 19, 543-561.

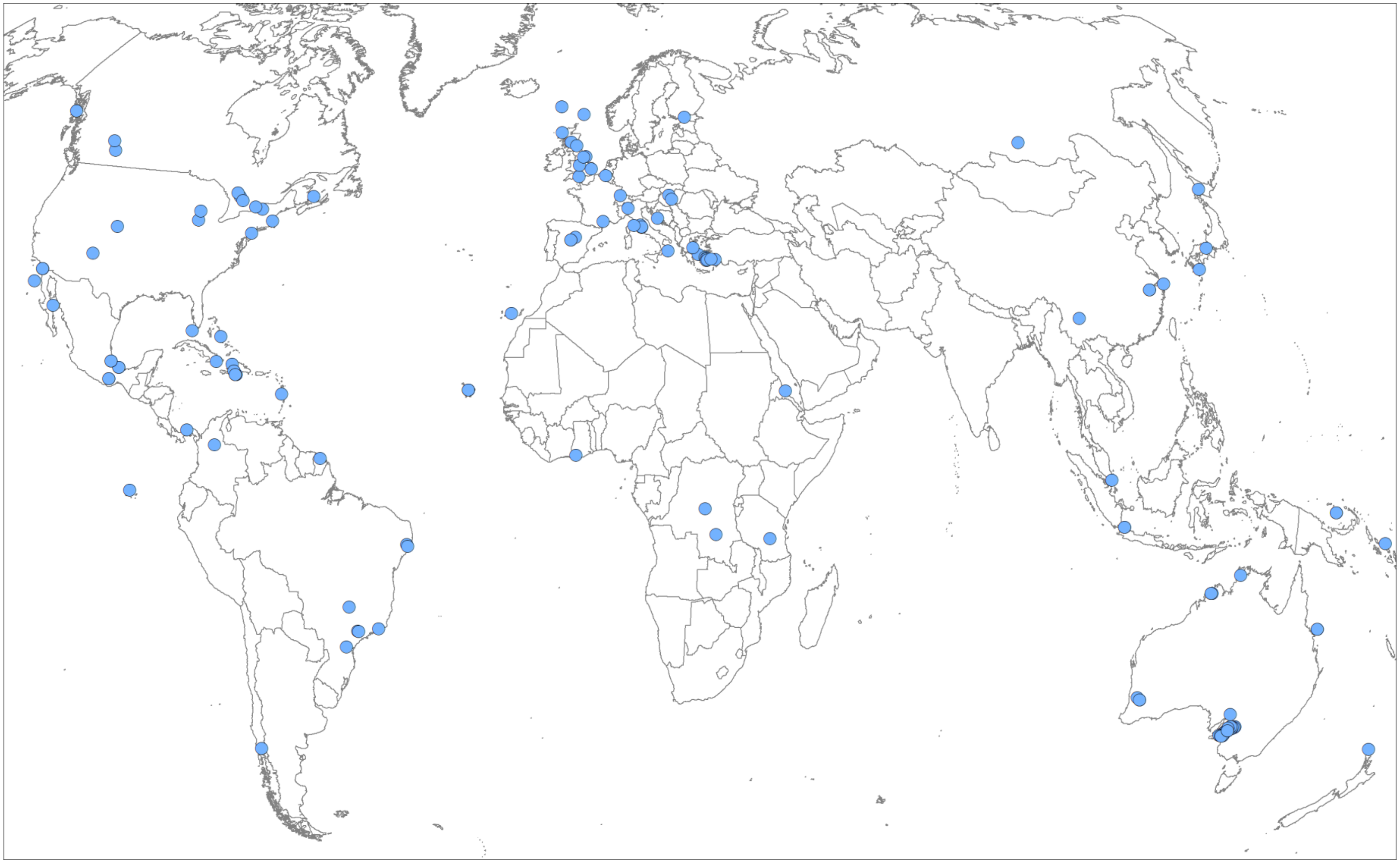
mamWFvMTt_Kitchener	2	(Kitchener et al., 1980b)	Kitchener DJ, Chapman A, Muir BG, Palmer M (1980b) The conservation value for mammals of reserves in the western Australian wheatbelt. Biological Conservation, 18, 179-207.
mamWFvUTt_Bolger	2, 3	(Bolger et al., 1997)	Bolger DT, Alberts AC, Sauvajot RM et al. (1997) Response of rodents to habitat fragmentation in coastal southern California. Ecological Applications, 7, 552-563.
mamWFvUTt_Crooks	2	(Crooks, 2002)	Crooks KR (2002) Relative sensitivities of mammalian carnivores to habitat fragmentation. Conservation Biology, 16, 488-502.
mamWFvUTt_Dickman	2	(Dickman, 1987)	Dickman CR (1987) Habitat fragmentation and vertebrate species richness in an urban environment. Journal of Applied Ecology, 24, 337-351.
mamWHmMTt_Brown71	2	(Brown, 1971)	Brown JH (1971) Mammals on mountaintops - nonequilibrium insular biogeography. American Naturalist, 105, 467-478.
mamWHmMTt_Brown78	2	(Brown, 1978)	Brown JH (1978) The theory of insular biogeography and the distribution of boreal birds and mammals. Great Basin Naturalist Memoirs, 209-227.
mamWHmMTt_Davis	2	(Davis et al., 1988)	Davis R, Dunford C, Lomolino MV (1988) Montane mammals of the American Southwest - the possible influence of post-Pleistocene colonization. Journal of Biogeography, 15, 841-848.
mamWHmMTt_Lomolino	2	(Lomolino et al., 1989)	Lomolino MV, Brown JH, Davis R (1989) Island biogeography of montane forest mammals in the American southwest. Ecology, 70, 180-194.
mamWHmMTt_Lomolino97	2	(Lomolino & Davis, 1997)	Lomolino MV, Davis R (1997) Biogeographic scale and biodiversity of mountain forest mammals of western North America. Global Ecology and Biogeography Letters, 6, 57-76.
pltAHwNWt_Friday	2	(Friday, 1987)	Friday LE (1987) The diversity of macroinvertebrate and macrophytes communities in ponds. Freshwater Biology, 18, 87-104.

pltAHwNWt_Jackson	2	(Jackson & Charles, 1988)	Jackson ST, Charles DF (1988) Aquatic macrophytes in Adirondack (New York) USA: lakes patterns of species composition in relation to environment. Canadian Journal of Botany, 66, 1449-1460.
pltAHwPWt_Deane	2	(Deane et al., 2016)	Deane D (2016) Fleurieu Peninsula wetlands collated plant survey data Version 2, DOI: 10.4227/05/57450480691AA, University of Adelaide, Available via ÆKOS Data Portal (Persistent hyperlink: http://www.aekos.org.au/dataset/239810).
pltAHwPWt_Hitchin	2	(Hitchin et al., 1984)	Hitchin, G.G., Wile, I., Miller, G.E. & Yan, N.D. (1984) Macrophyte data from 46 southern Ontario soft-water lakes of varying pH. In. Report DR 84/2, Ont. Min. Environ. Data, Ontario, Canada.
pltAHwPWt_Sebastien	2	(Sebastian-Gonzalez et al., 2012)	Sebastian-Gonzalez E, Molina JA, Paracuellos M (2012) Distribution patterns of a marsh vegetation metacommunity in relation to habitat configuration. Aquatic Biology, 16, 277-285.
pltAHwPWt_Soga	2	(Soga et al., 2014)	Soga M, Ishiyama N, Sueyoshi M, Yamaura Y, Hayashida K, Koizumi I, Negishi JN (2014) Interaction between patch area and shape: lakes with different formation processes have contrasting area and shape effects on macrophyte diversity. Landscape and Ecological Engineering, 10, 55-64.
pltAHwPWt_SWdbHP	2	Scottish Standing Waters database	Standing Waters Database, Scottish Natural Heritage, accessed 13 September 2017, URL: http://gateway.snh.gov.uk/pls/apex_cagdb2/f?p=111:1000:::NO:::
pltSAcWTw_Panitsa	2	(Panitsa & Tzanoudakis, 2010)	Panitsa M, Tzanoudakis D (2010) Floristic diversity on small islands and islets: Leros islets' group (East Aegean area, Greece). Phytologia Balcanica, 16, 271-284.

pltSAfWTw_Chepinoga	2	(Chepinoga et al., 2012)	Chepinoga VV, Zverev VE, Zvereva EL, Kozlov MV (2012) Vascular plants on the islands and peninsulas of Maloe More (Lake Baikal): patterns of diversity and species turnover. Boreal Environment Research, 17, 219-236.
pltSAmWTw_CapeVerde	2	(Arechavaleta et al., 2005)	Arechavaleta, M., Zurita, N., Marrero, M.C. & Martin, J.L. (2005) Lista preliminary de especies silvestres de Cabo Verde (hongos plantas y animals terrestres). In: (ed. M.O.E.a.S. Planning). Government of the Canaries, Santa Cruz de Tenerife.
pltSAmWTw_Chiarucci	2	(Chiarucci et al., 2017)	Chiarucci A, Fattorini S, Foggi B, Landi S, Lazzaro L, Podani J, Simberloff D (2017) Plant recording across two centuries reveals dramatic changes in species diversity of a Mediterranean archipelago. Scientific Reports, 7.
pltSAmWTw_fernsCVerde	2	(Arechavaleta et al., 2005)	Arechavaleta, M., Zurita, N., Marrero, M.C. & Martin, J.L. (2005) Lista preliminary de especies silvestres de Cabo Verde (hongos plantas y animals terrestres). In: (ed. M.O.E.a.S. Planning). Government of the Canaries, Santa Cruz de Tenerife.
pltSAmWTw_fungiCVerde	2	(Arechavaleta et al., 2005)	Arechavaleta, M., Zurita, N., Marrero, M.C. & Martin, J.L. (2005) Lista preliminary de especies silvestres de Cabo Verde (hongos plantas y animals terrestres). In: (ed. M.O.E.a.S. Planning). Government of the Canaries, Santa Cruz de Tenerife.
pltSAmWTw_lichenCVerde	2	(Arechavaleta et al., 2005)	Arechavaleta, M., Zurita, N., Marrero, M.C. & Martin, J.L. (2005) Lista preliminary de especies silvestres de Cabo Verde (hongos plantas y animals terrestres). In: (ed. M.O.E.a.S. Planning). Government of the Canaries, Santa Cruz de Tenerife.
pltSArWTw_Hu	2	(Hu et al., 2012)	Hu G, Wu JG, Feeley KJ, Xu GF, Yu MJ (2012) The Effects of Landscape Variables on the Species-Area Relationship during Late-Stage Habitat Fragmentation. Plos One, 7.
pltSFfPTt_Berglund	2	(Berglund & Jonsson, 2003)	Berglund H, Jonsson BG (2003) Nested plant and fungal communities; the importance of area and habitat quality in maximizing species capture in boreal old-growth forests. Biological Conservation, 112, 319-328.

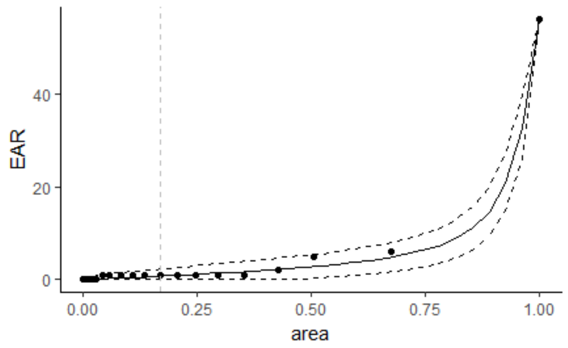
pltSFfPTt_dosSantos	2	(dos Santos et al., 2007)	Dos Santos K, Kinoshita LS, Dos Santos FaM (2007) Tree species composition and similarity in semideciduous forest fragments of southeastern Brazil. Biological Conservation, 135, 268-277.
pltSFfPTt_Hattori	2	(Hattori & Ishida, 2000)	Hattori T, Ishida H (2000) Relationship between species diversity, species composition and forest area of fragmented lucidophyllous forests in central Miyazaki Prefecture. Japanese Journal of Ecology (Otsu), 50, 221-234.
pltSFfPTt_Ishida	2	(Ishida et al., 1998)	Ishida H, Hattori T, Takeda Y, Kodate S (1998) Relationship between species richness or species composition and area of fragmented lucidophyllous forests in southeastern Hyogo Prefecture. Japanese Journal of Ecology (Tokyo), 48, 1-16.
pltSFfPTt_Silva	2	(Silva & Porto, 2009)	Silva MPP, Porto KC (2009) Effect of fragmentation on the community structure of epixylic bryophytes in Atlantic Forest remnants in the Northeast of Brazil. Biodiversity and Conservation, 18, 317-337.
pltSFfPTt_Weaver	2	(Weaver & Kellman, 1981)	Weaver M, Kellman M (1981) The effects of forest fragmentation on woodlot tree biotas in southern Ontario. Journal of Biogeography, 8, 199-210.
pltSFvMTt_Aldosoro	2	(Aldasoro et al., 2004)	Aldasoro JJ, Cabezas F, Aedo C (2004) Diversity and distribution of ferns in sub-Saharan Africa, Madagascar and some islands of the South Atlantic. Journal of Biogeography, 31, 1579-1604.
pltSFvPTt_Lumaret	2	(Lumaret et al., 1997)	Lumaret R, Guillerm JL, Maillet J, Verlaque R (1997) Plant species diversity and polyploidy in islands of natural vegetation isolated in extensive cultivated lands. Biodiversity and Conservation, 6, 591-613.
pltSFvUTt_Crowe	2	(Crowe, 1979)	Crowe TM (1979) Lots of weeds - insular phytogeography of vacant urban lots. Journal of Biogeography, 6, 169-181.

Fig. A.1 Global distribution of datasets used in Chapters 2 and 3



A.2. Species-loss curves

This section presents the species-loss curves for every dataset. Each panel represents a different dataset and can be referenced against the data sources in Section A.1. The solid dark line is the random placement endemics-area curve, with dashed lines indicating an approximate 95% confidence limit (see Equations 2.3 and 2.4). Points show the cumulative loss of species associated with the removal of each patch and the patches smaller than it. The vertical dashed line indicates the point where species loss for the notional 20% loss of area was quantified.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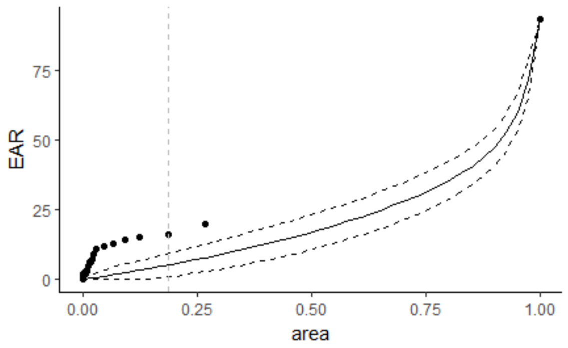
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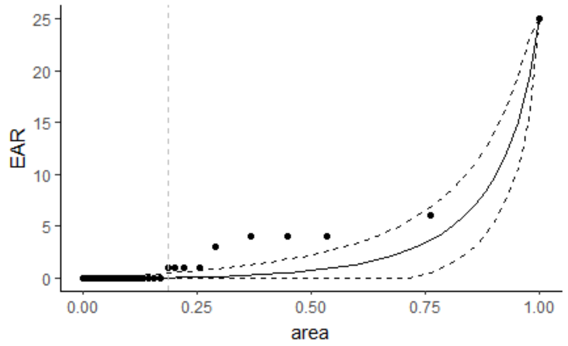
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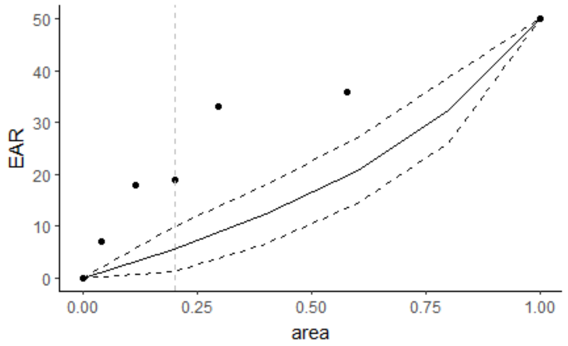
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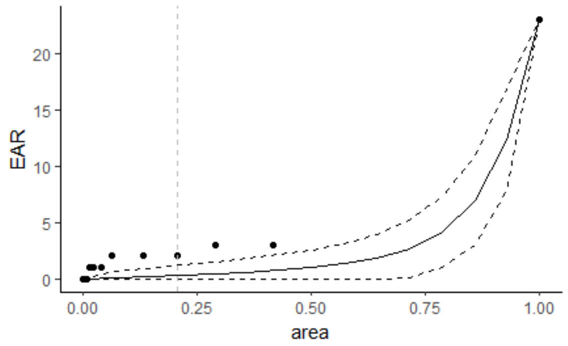
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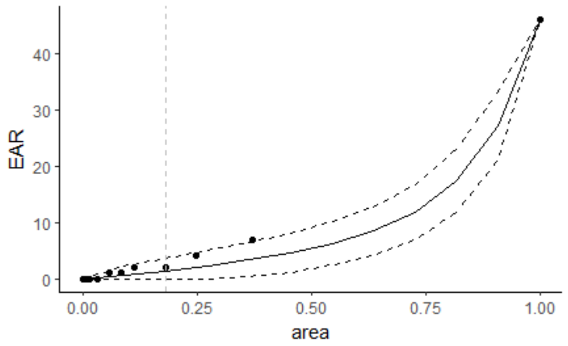
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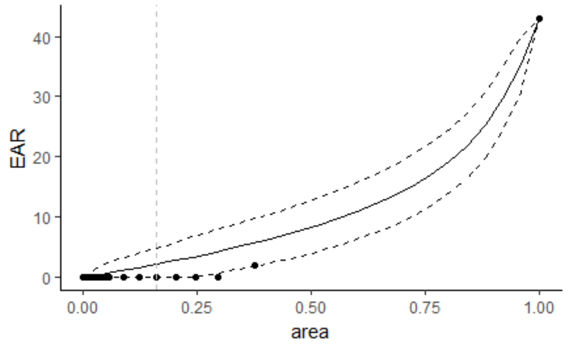
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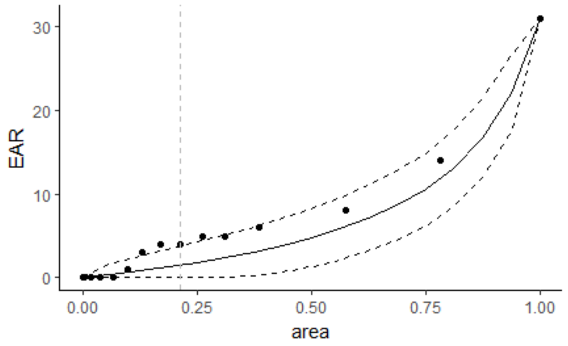
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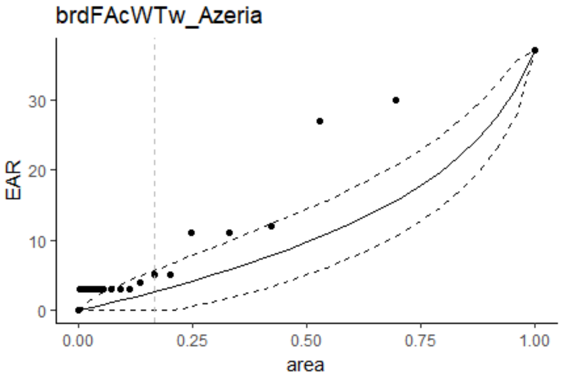
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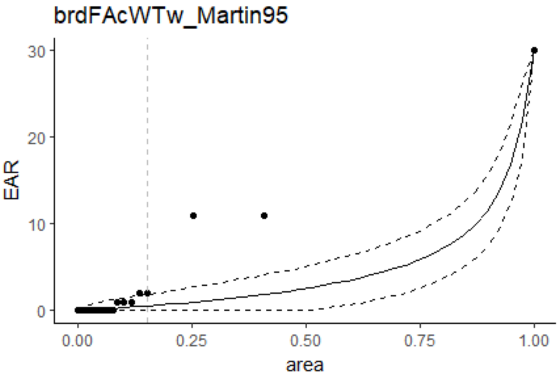
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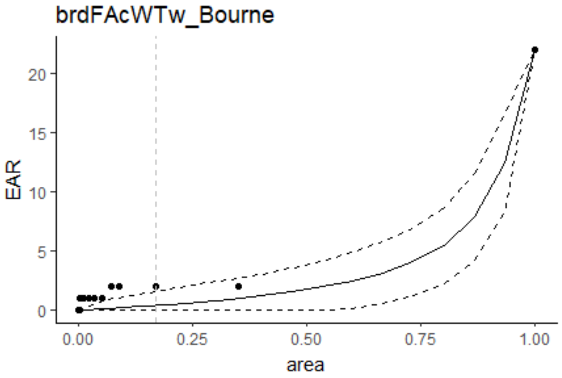
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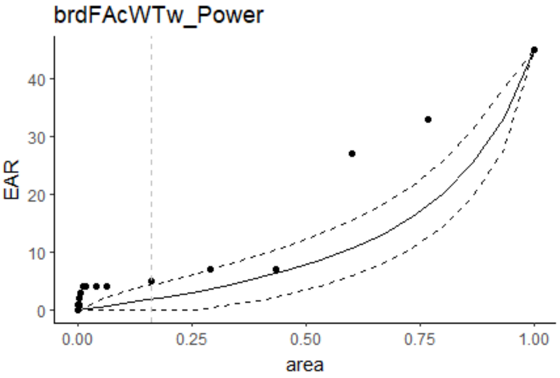
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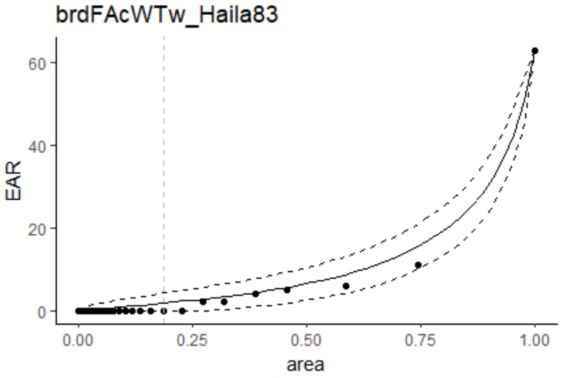
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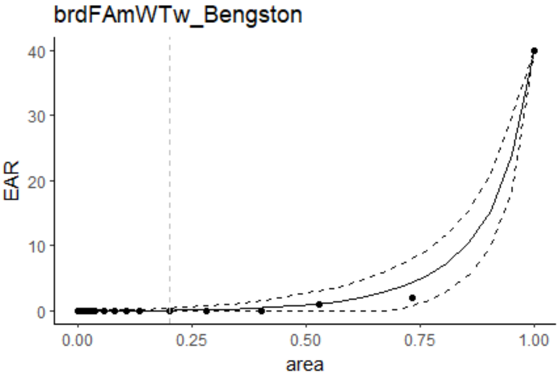
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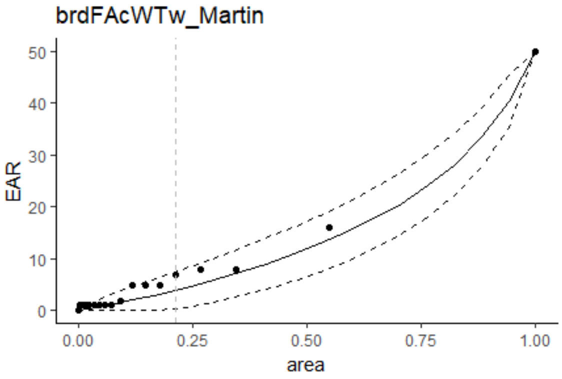
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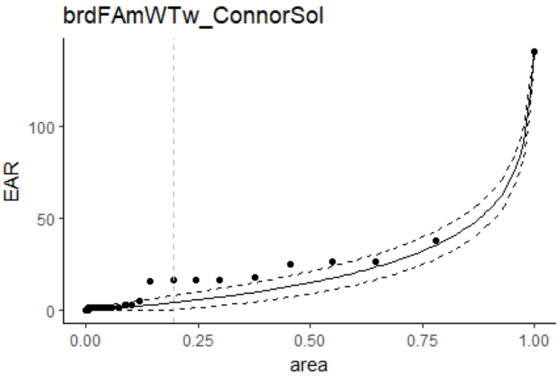
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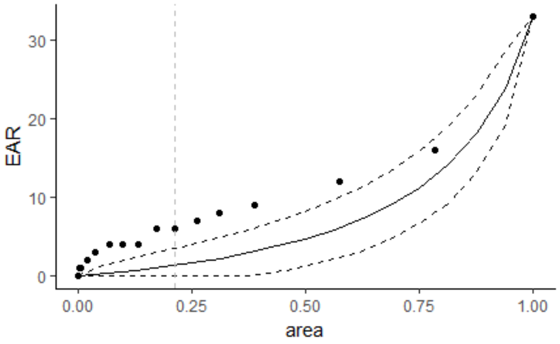

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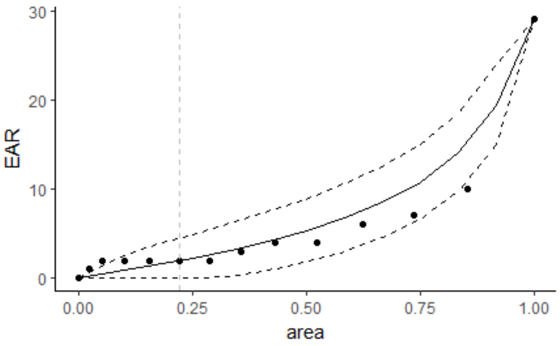

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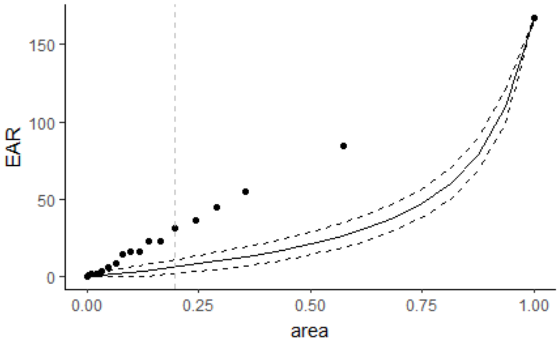

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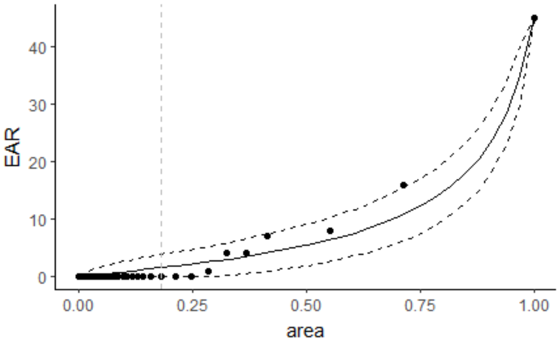

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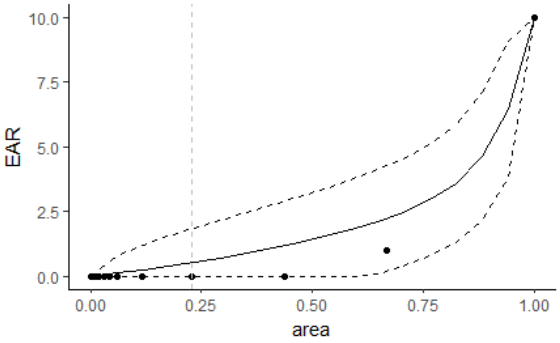

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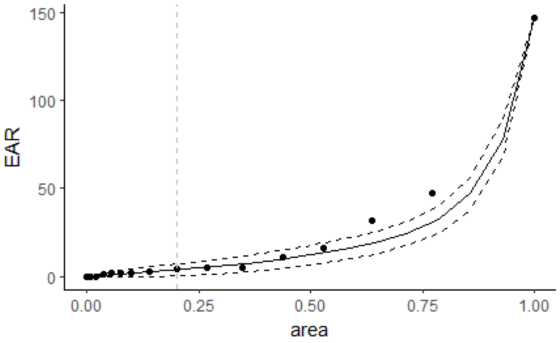

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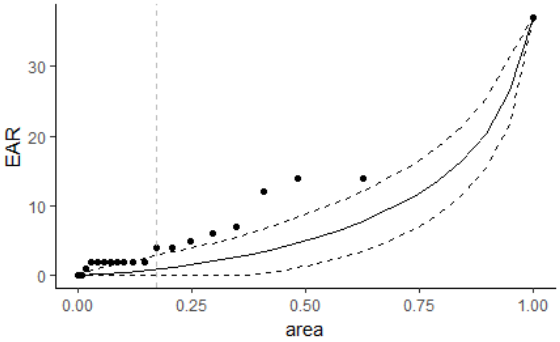

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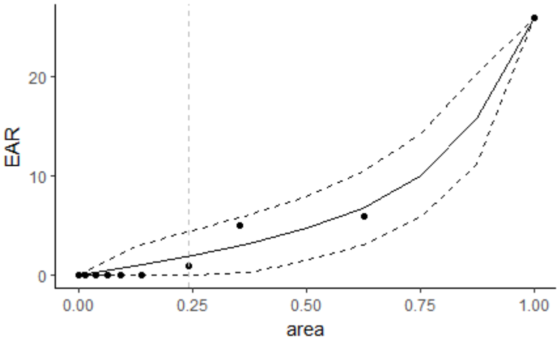

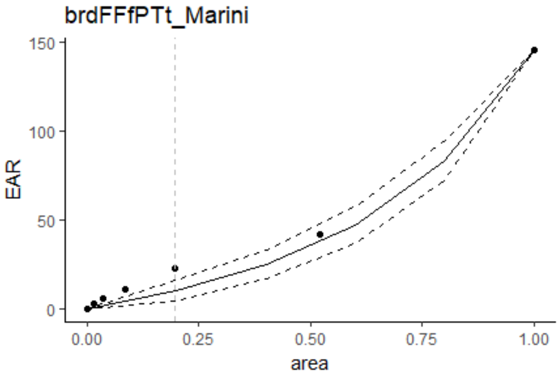
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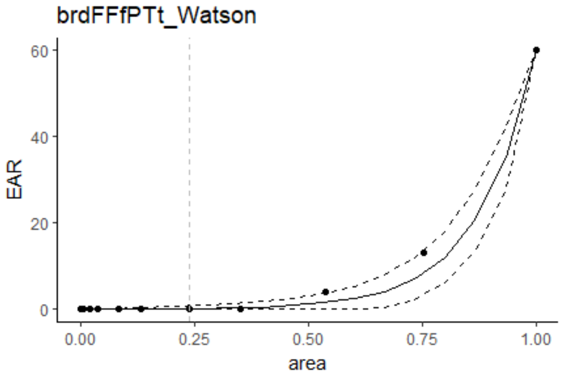
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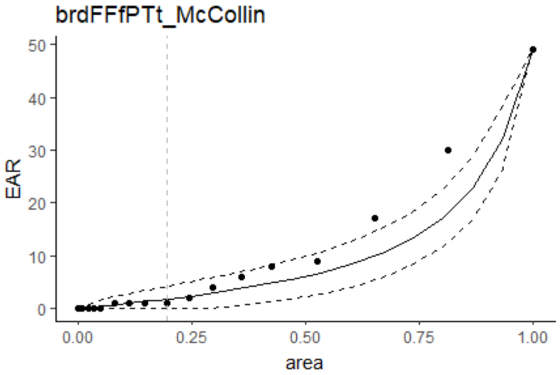
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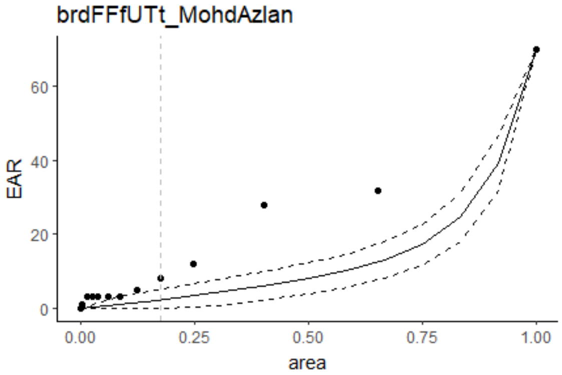
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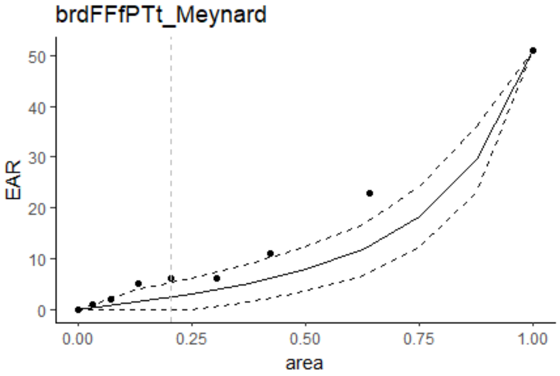
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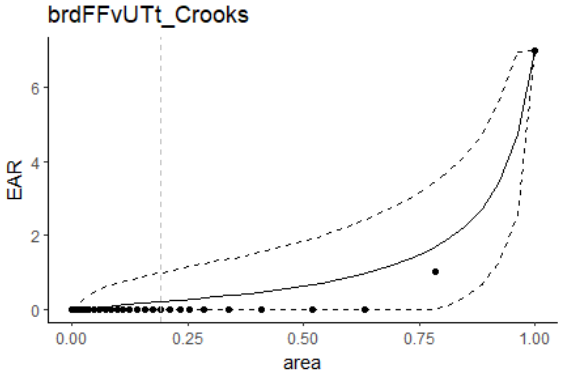
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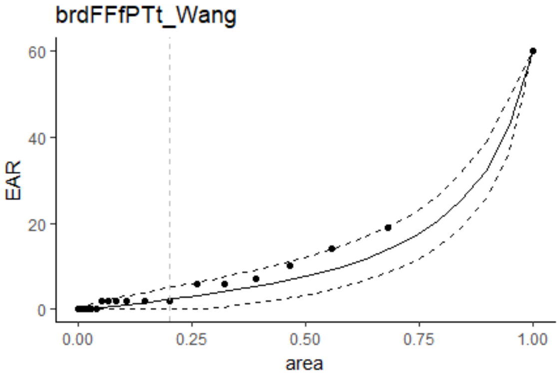
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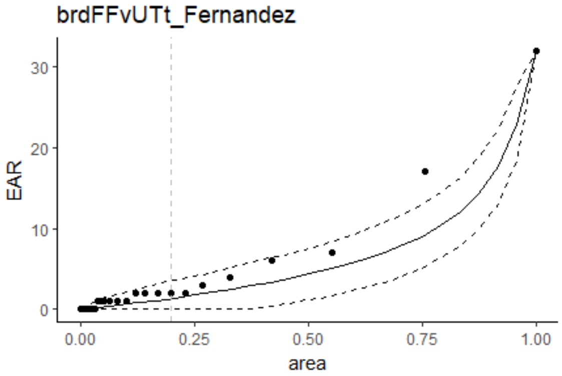
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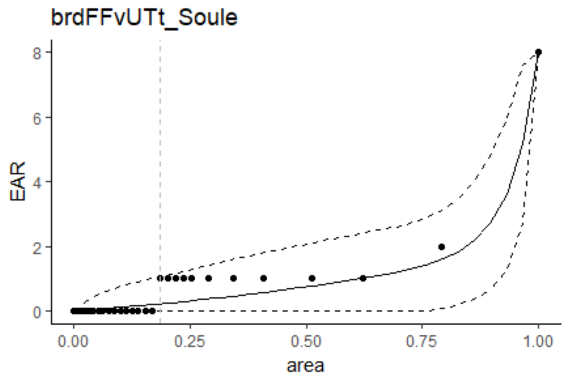
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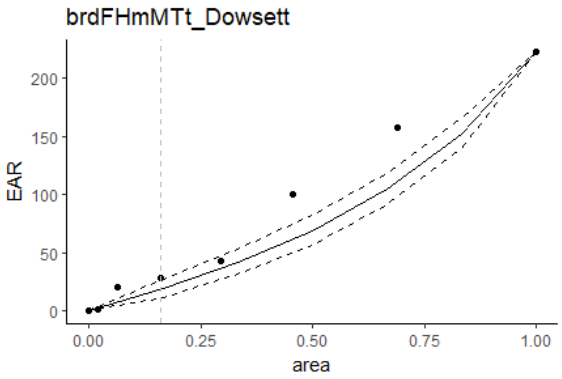
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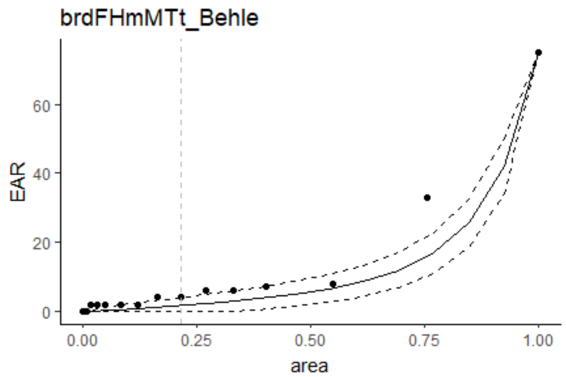
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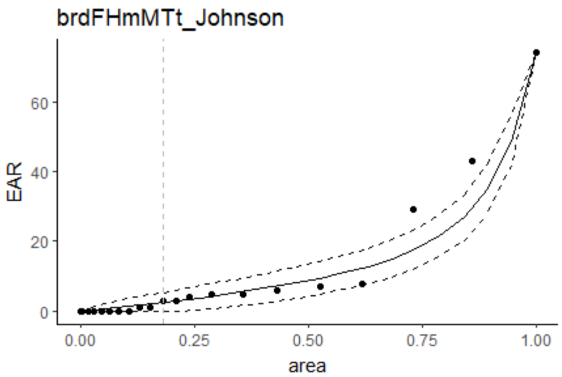
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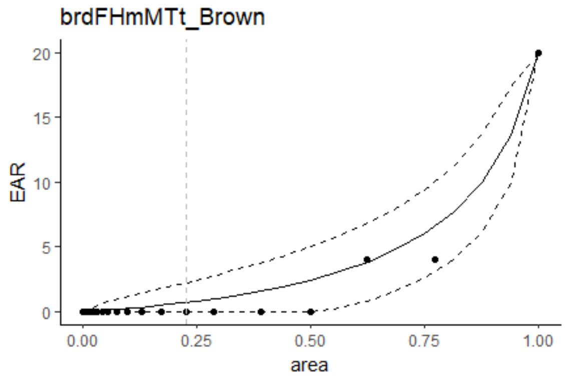
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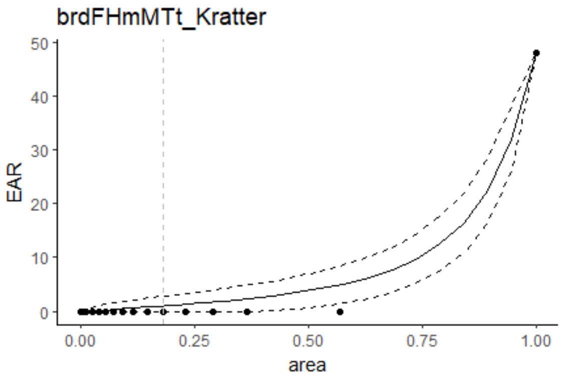
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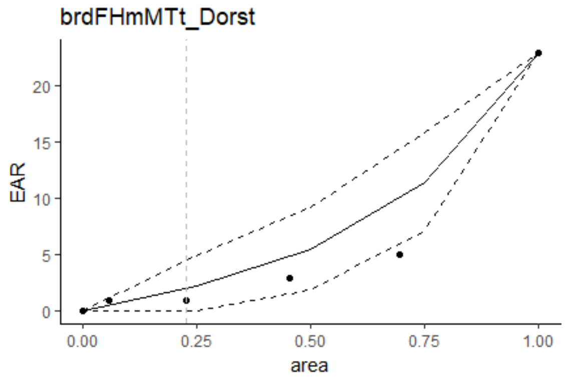
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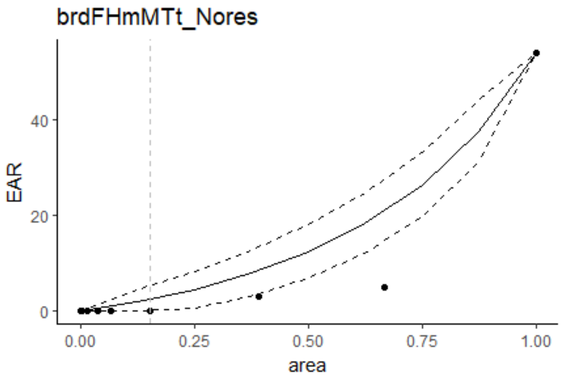
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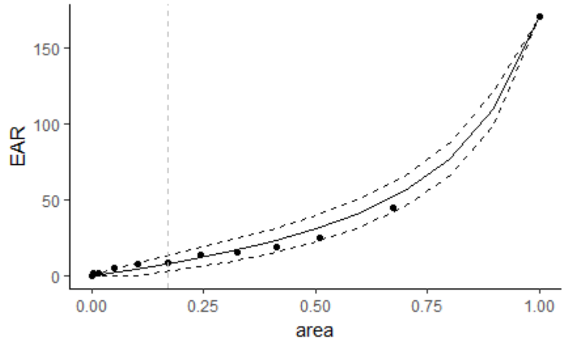

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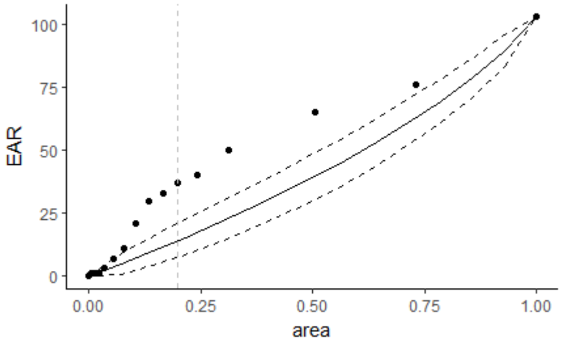

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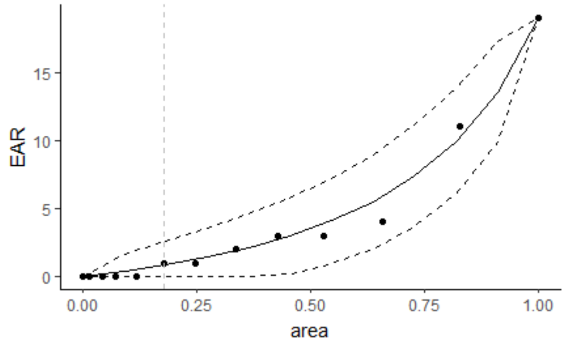

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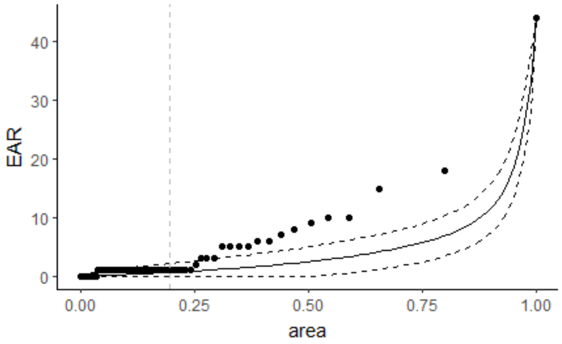

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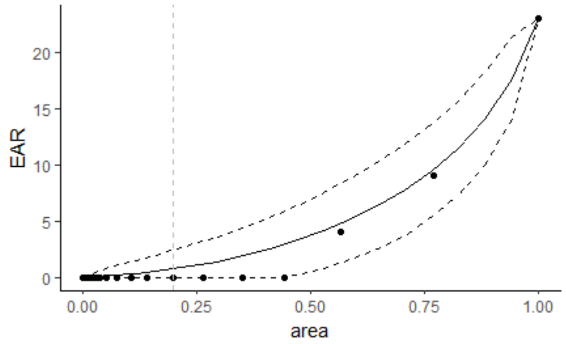

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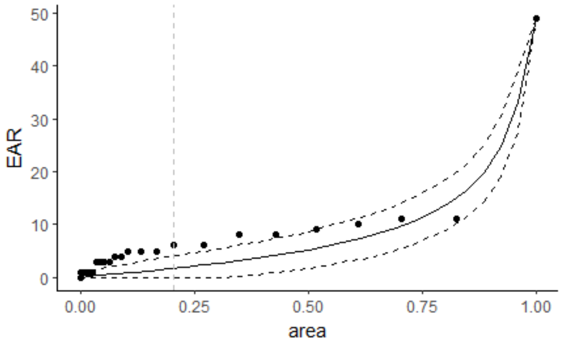

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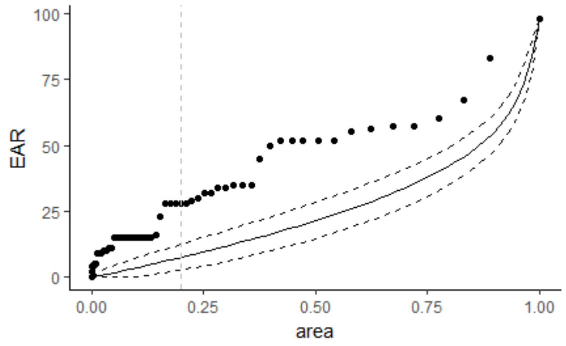

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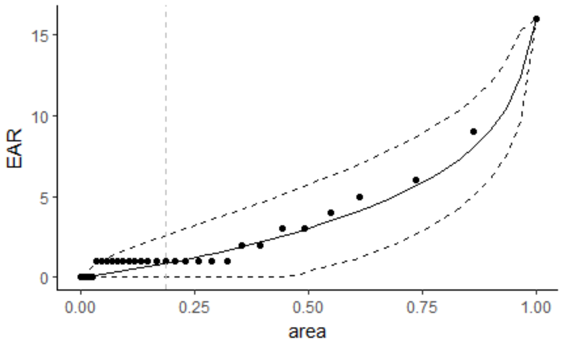

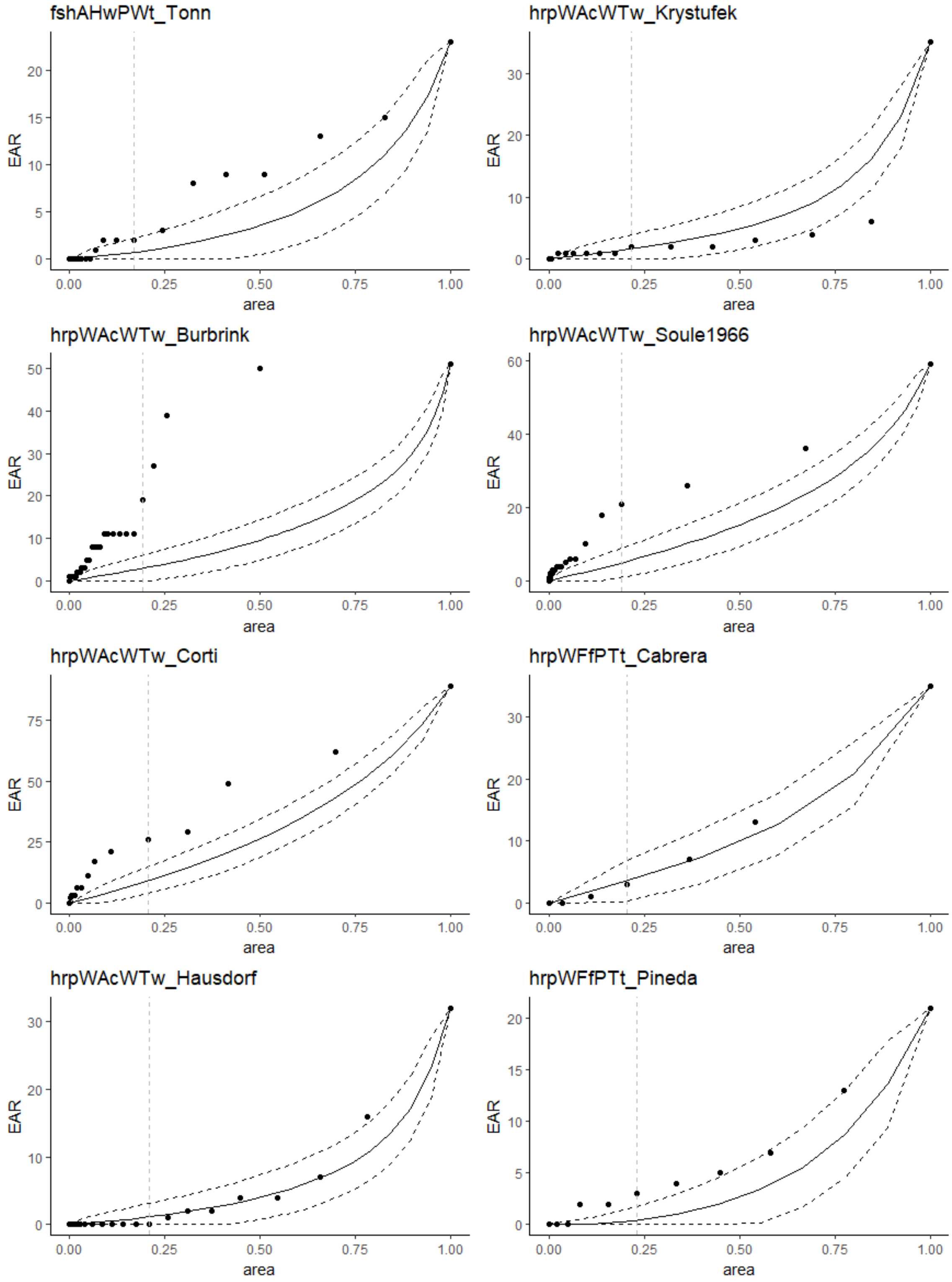
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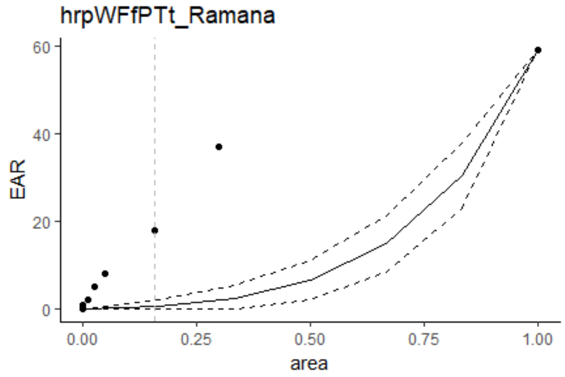
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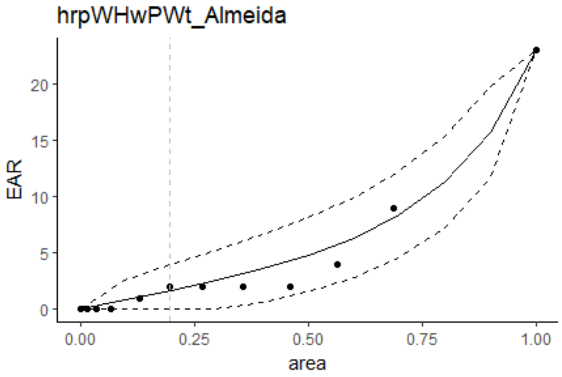
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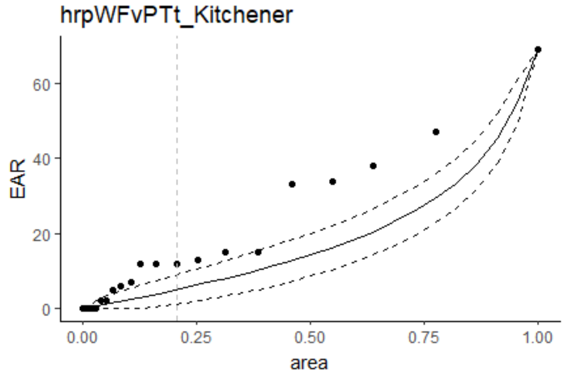
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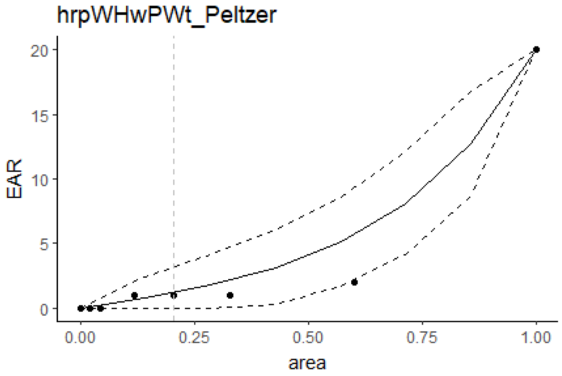
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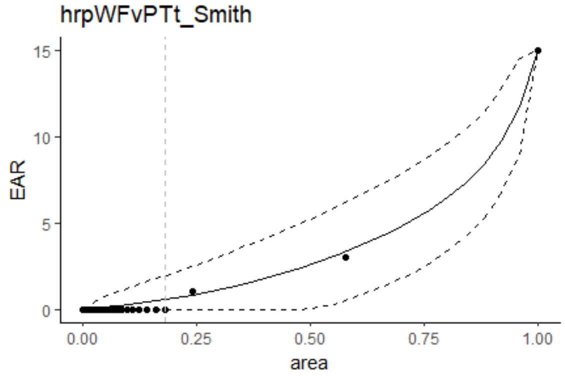
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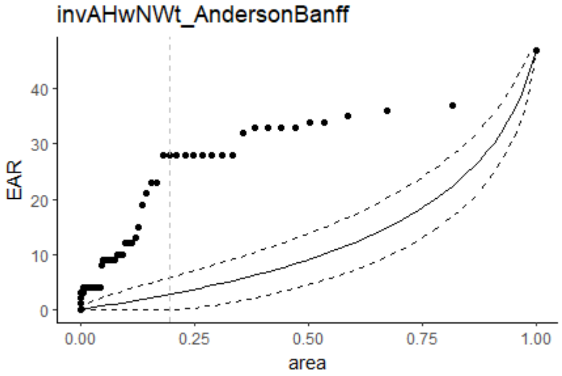
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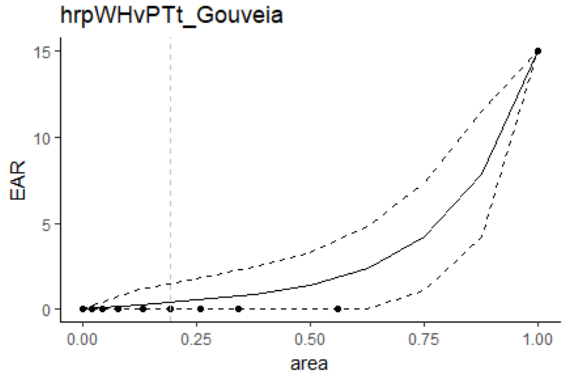
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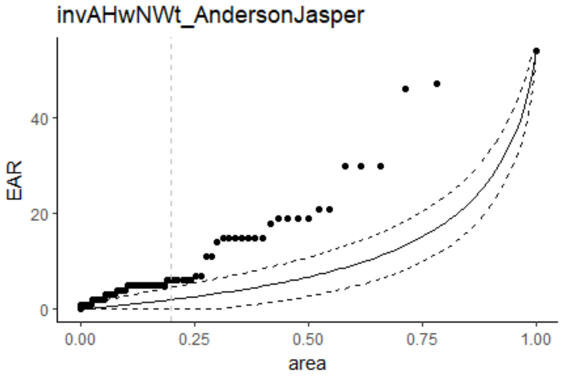
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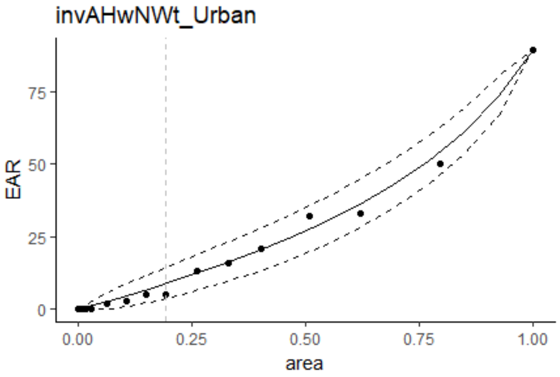
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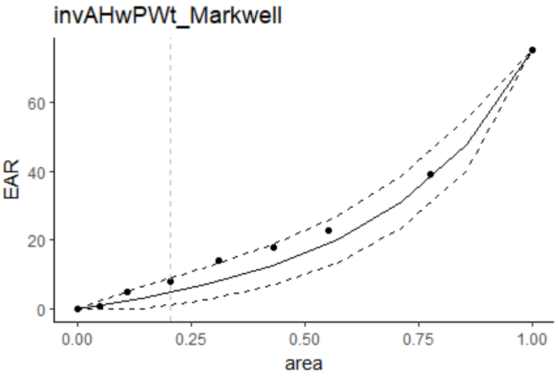
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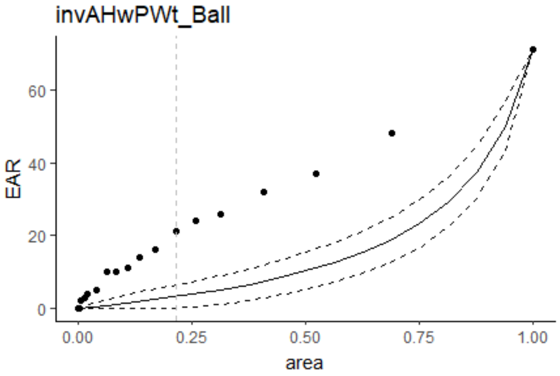
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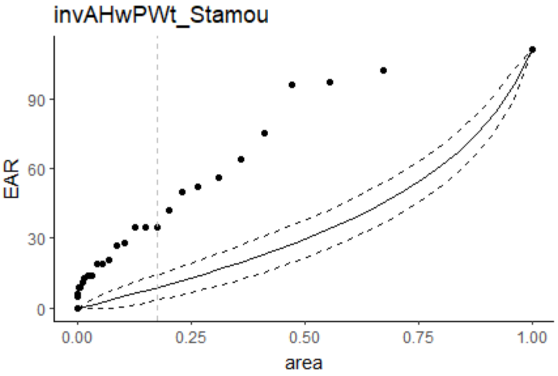
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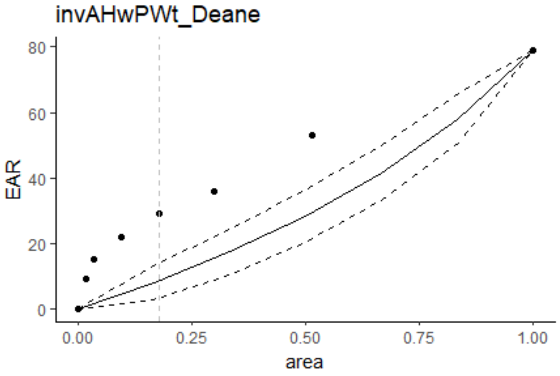
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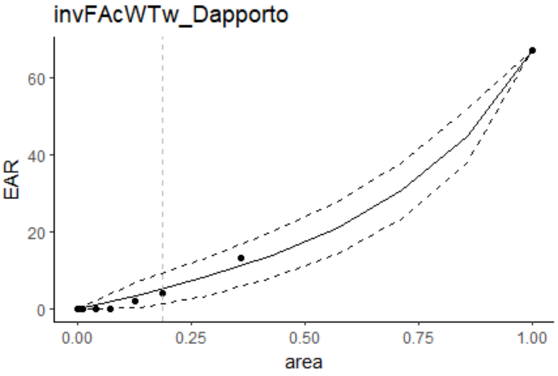
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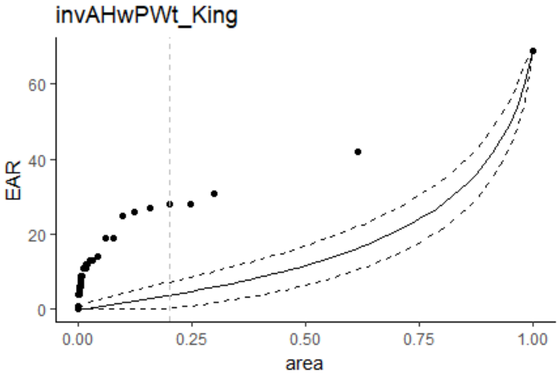
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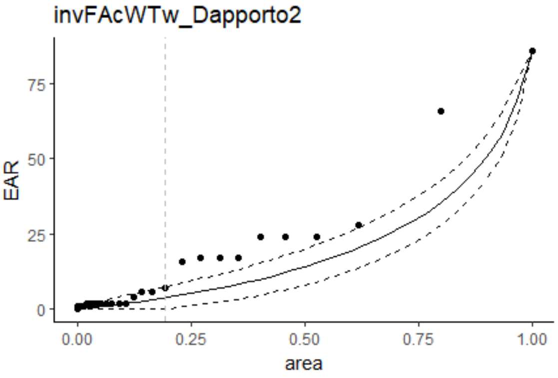
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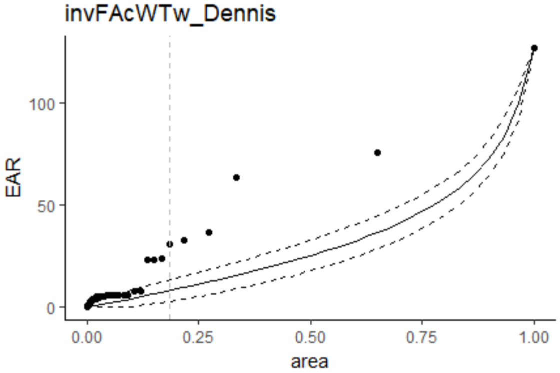
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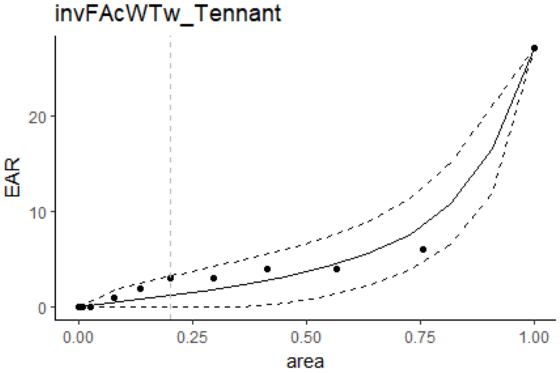
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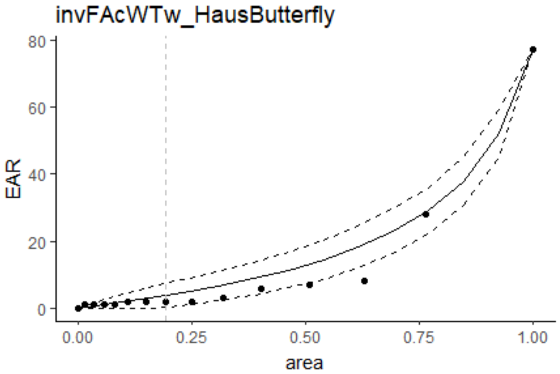
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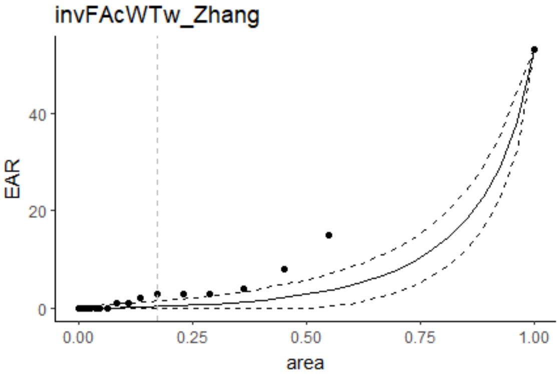
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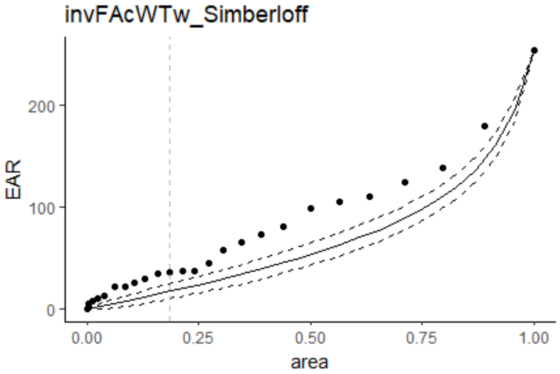
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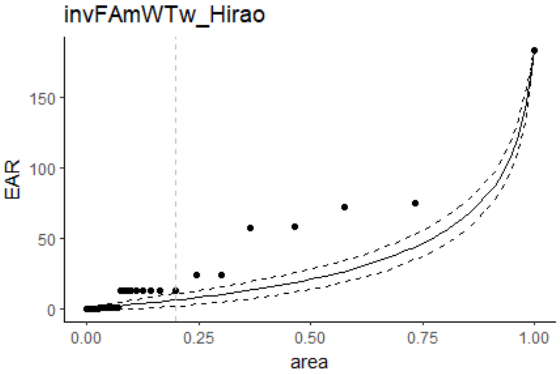
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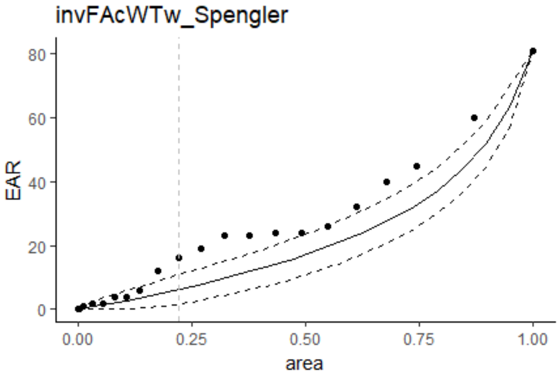
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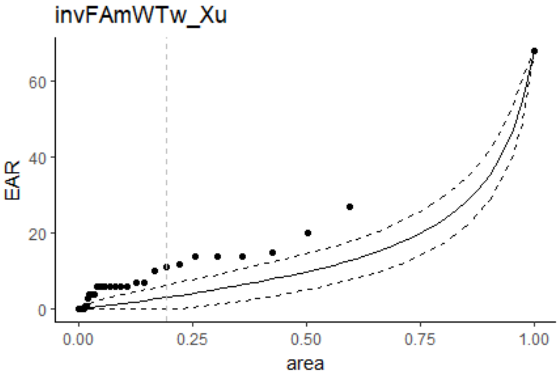
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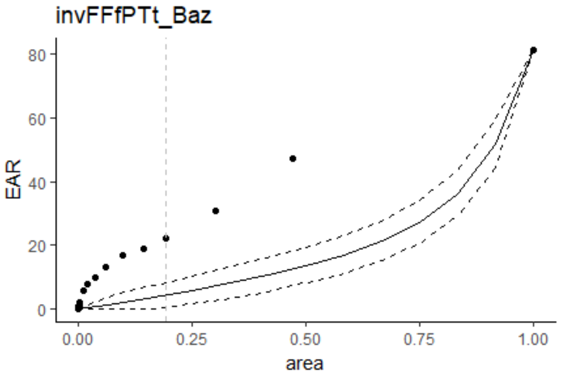
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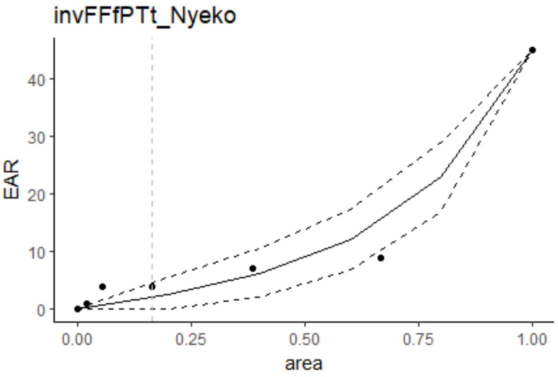
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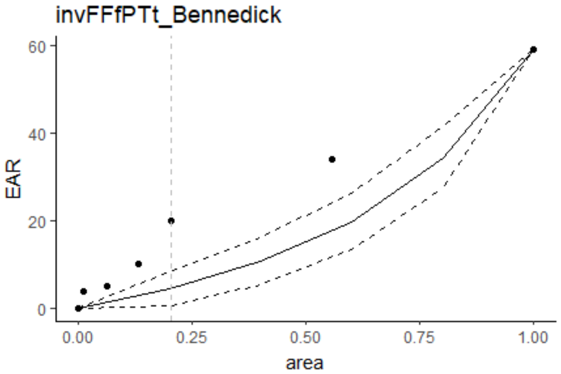
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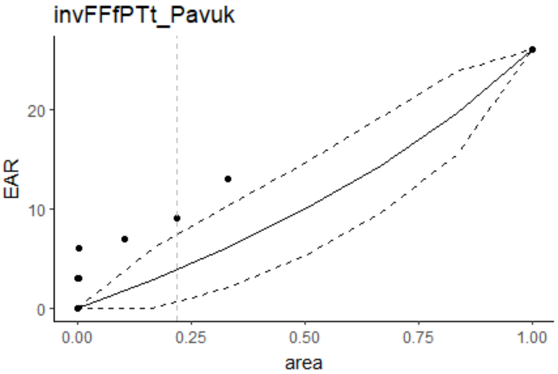
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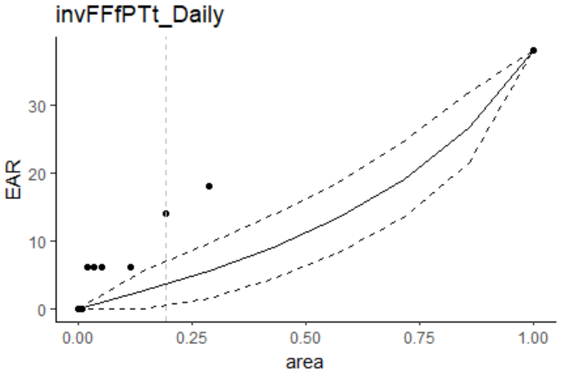
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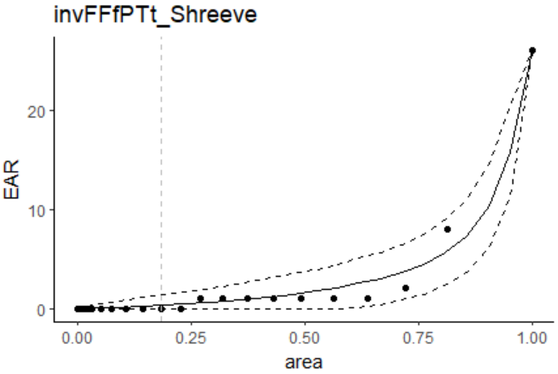
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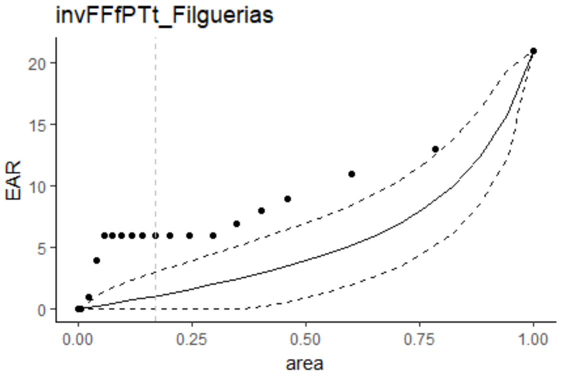
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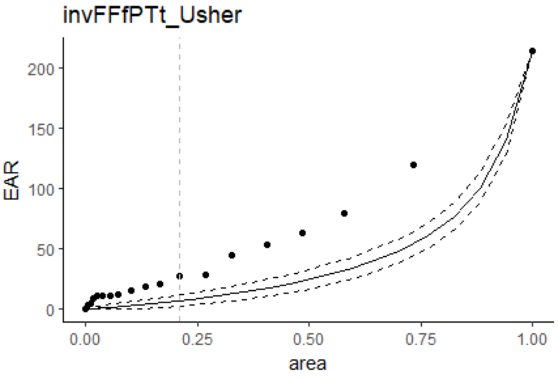
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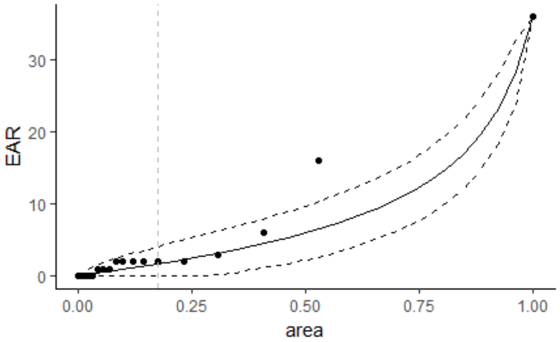

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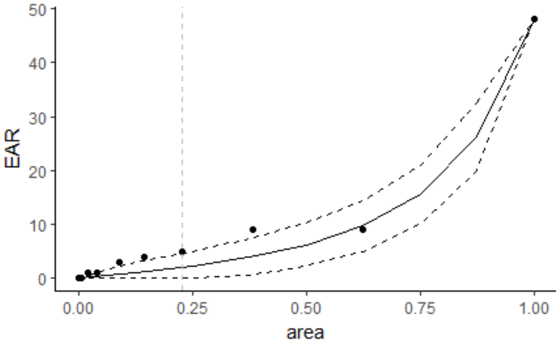

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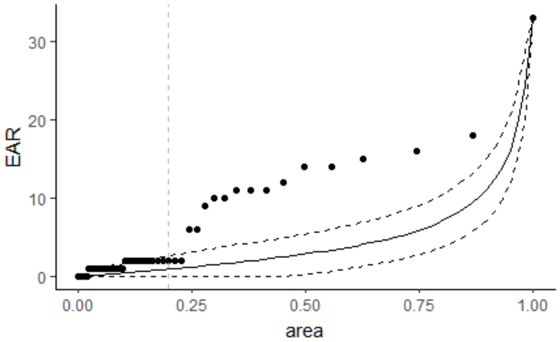

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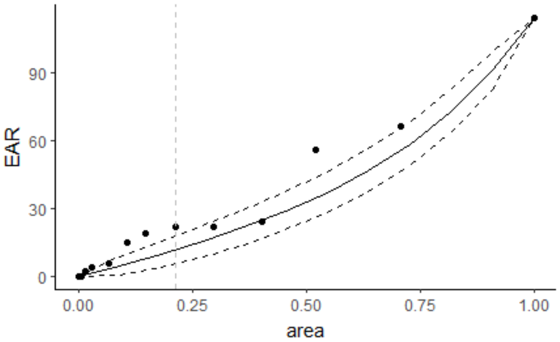

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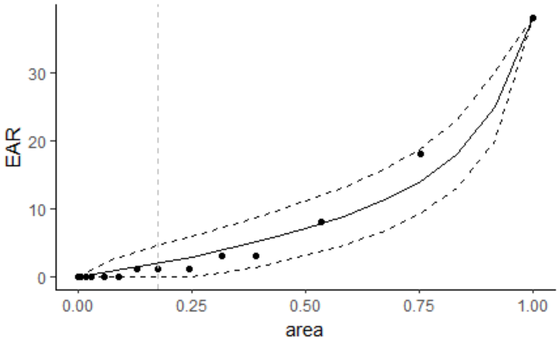

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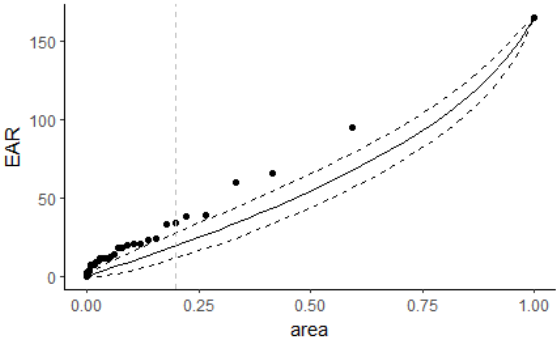

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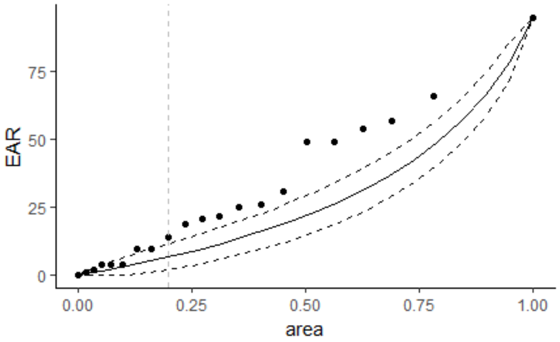

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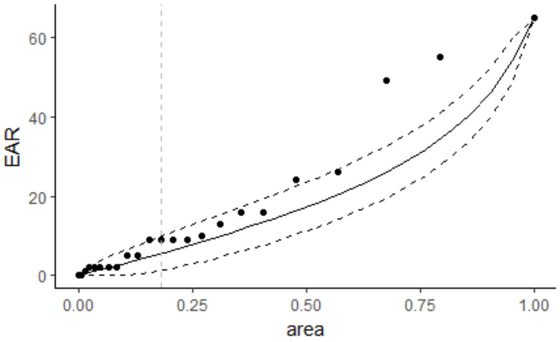

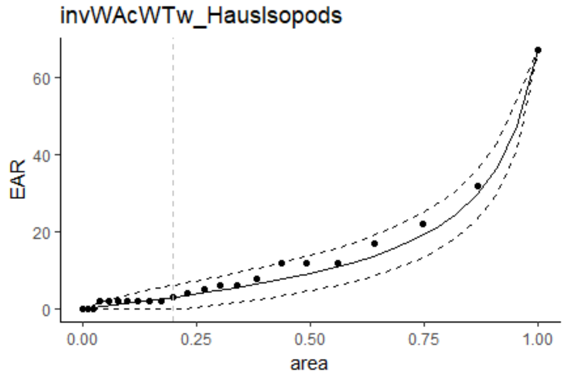

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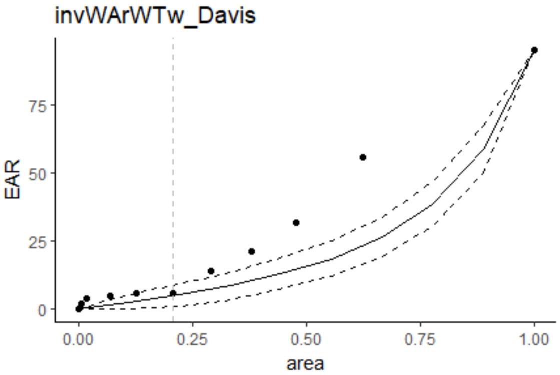

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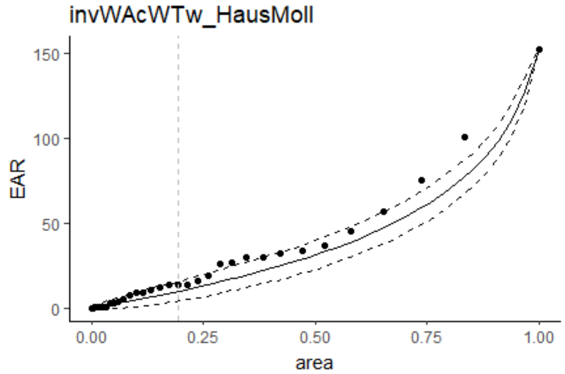

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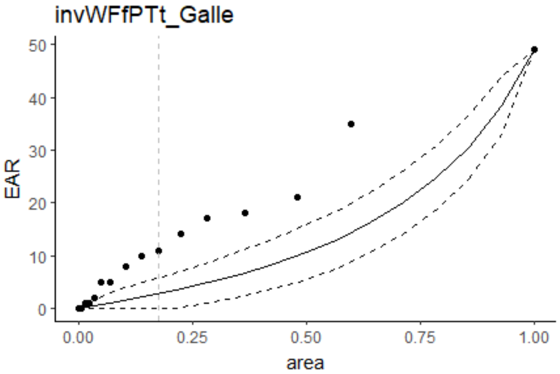

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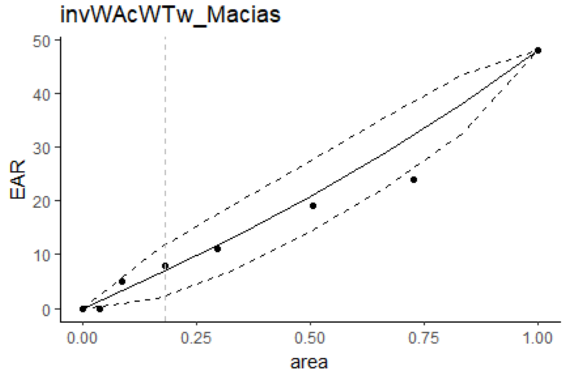

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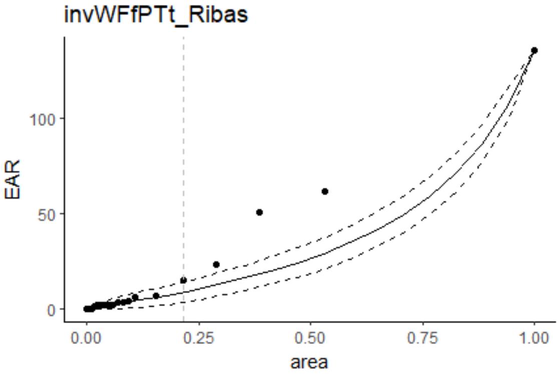

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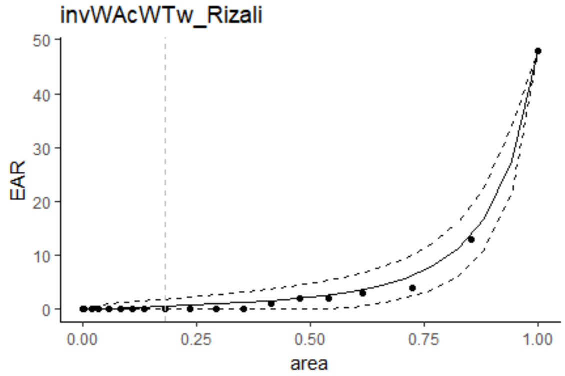

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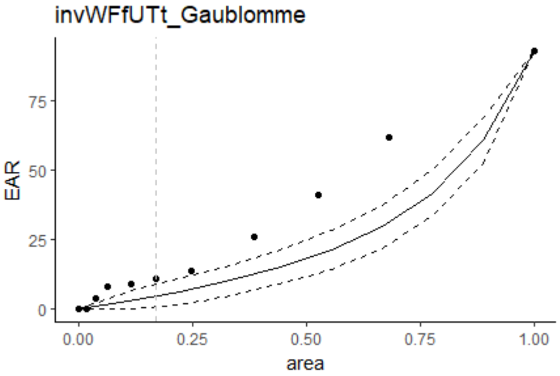

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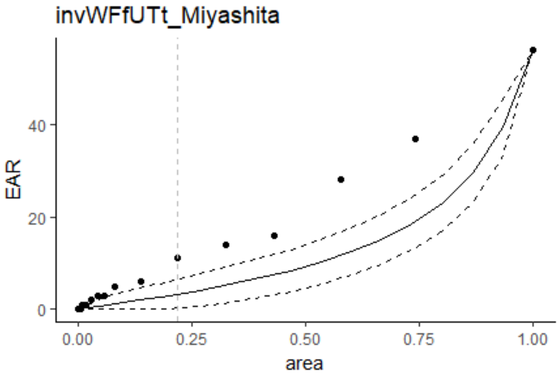
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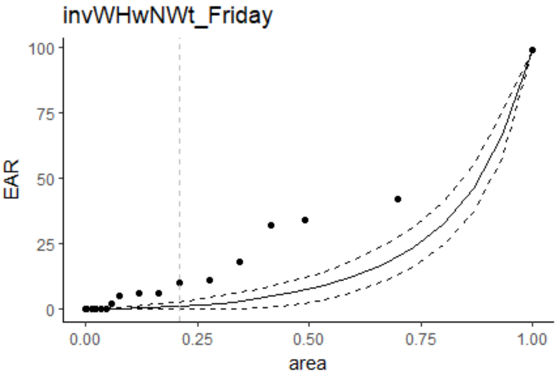
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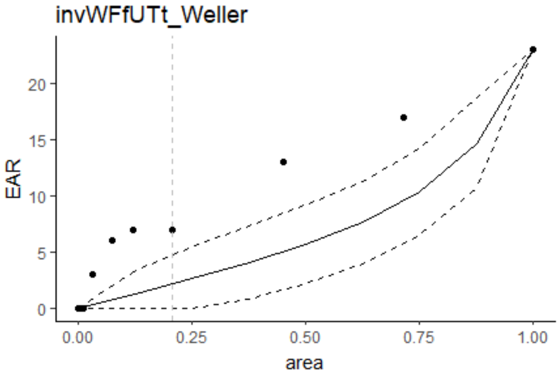
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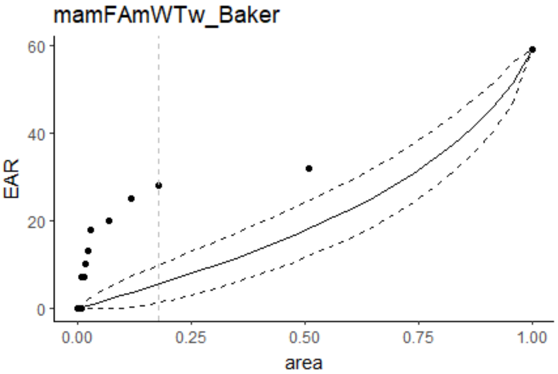
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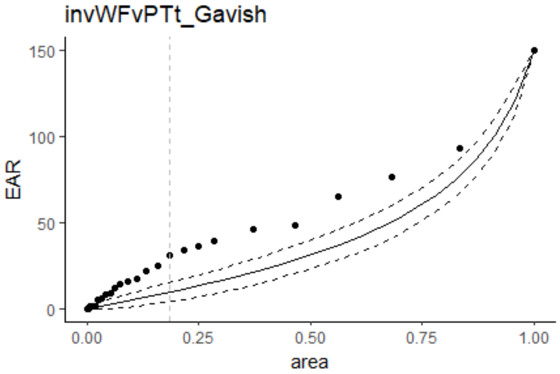
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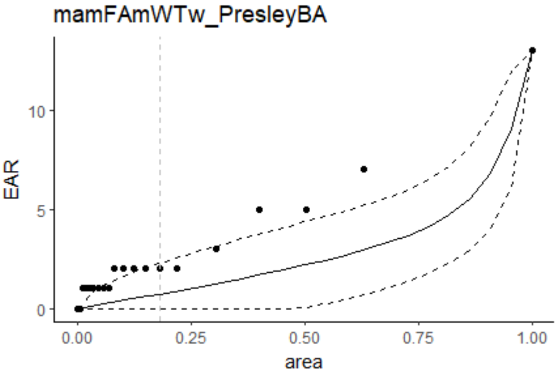
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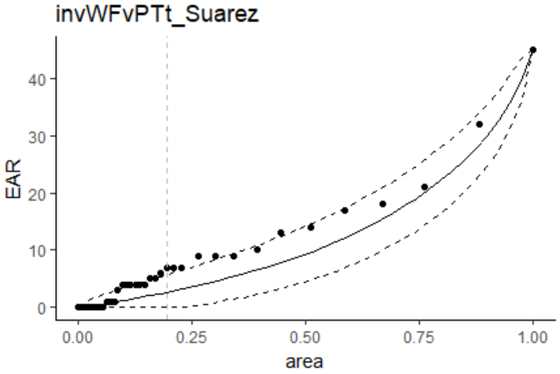
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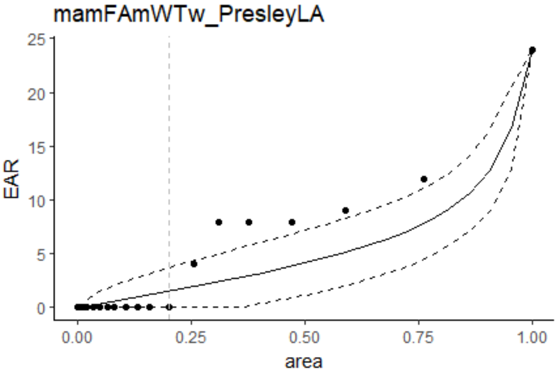
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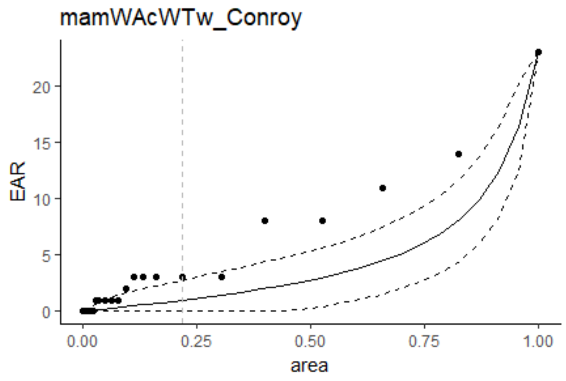
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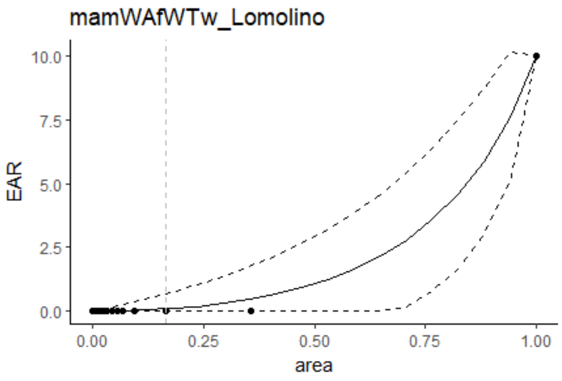
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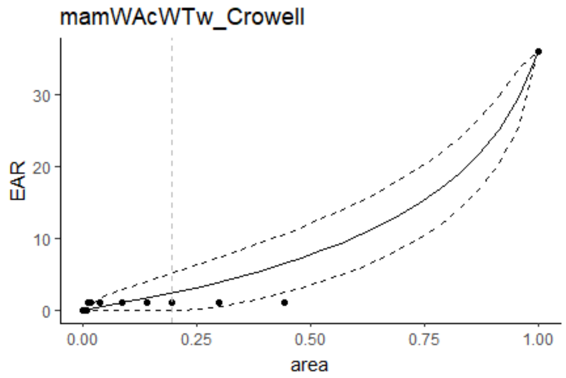
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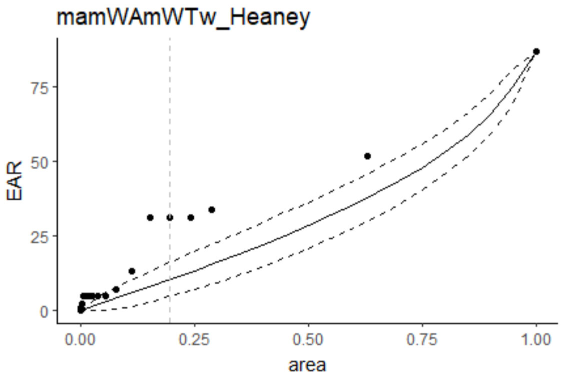
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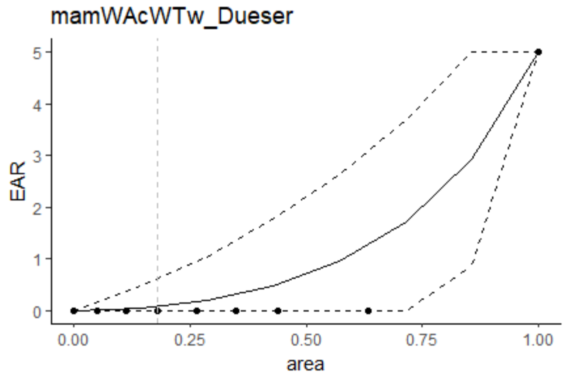
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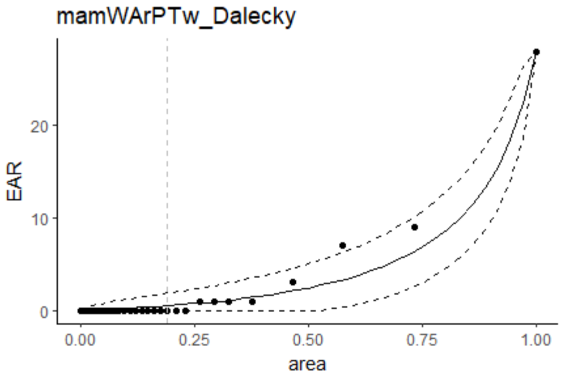
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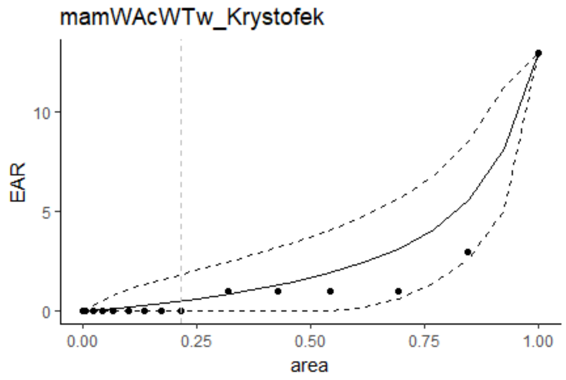
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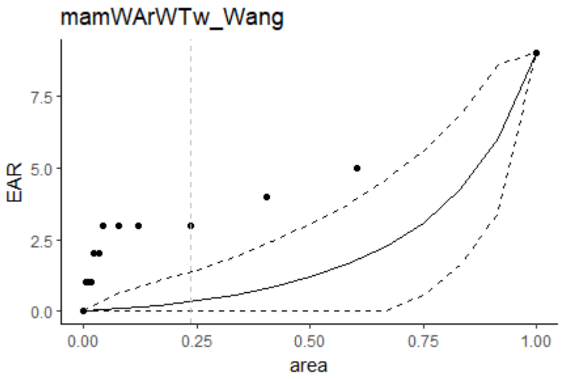
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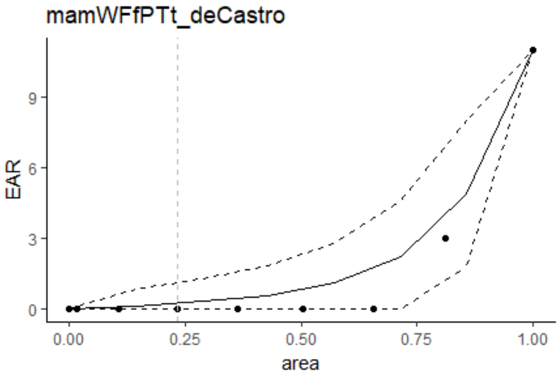
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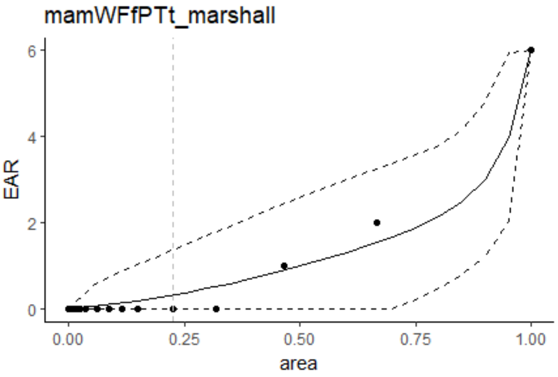
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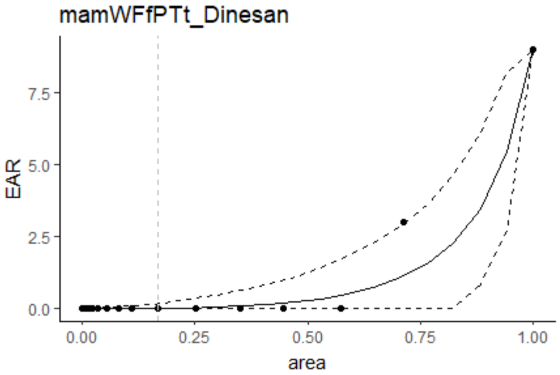
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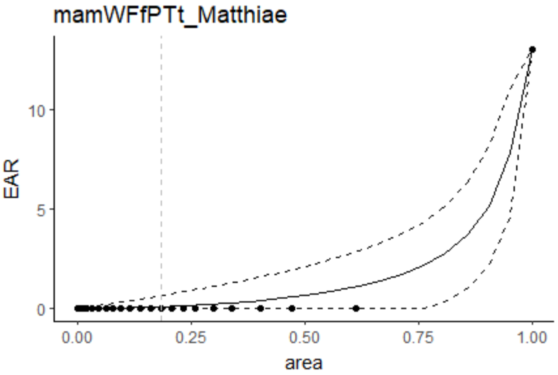
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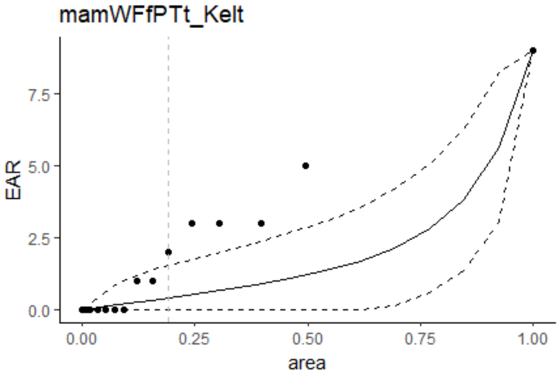
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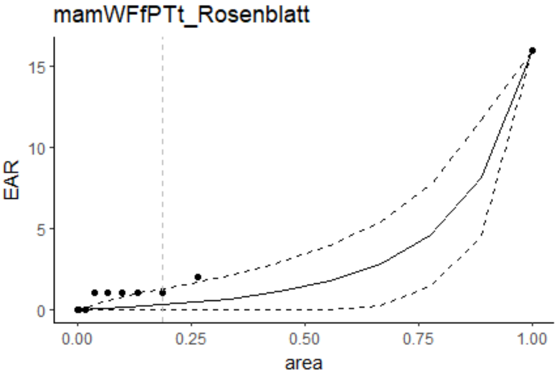
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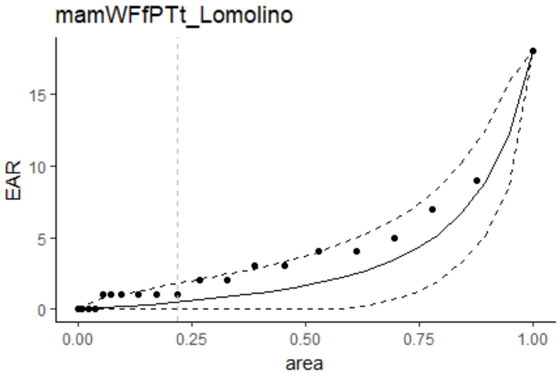
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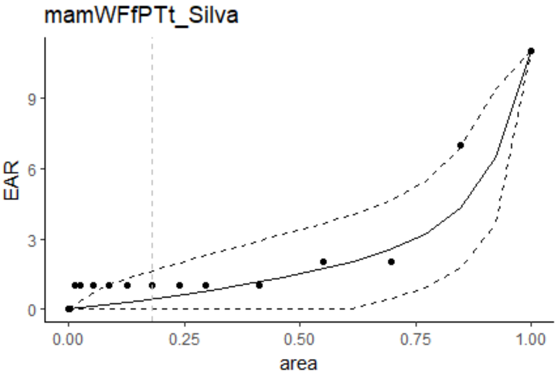
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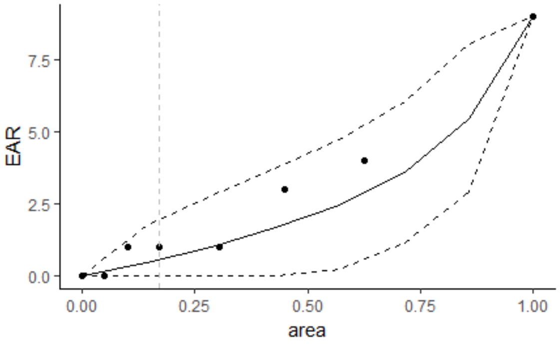
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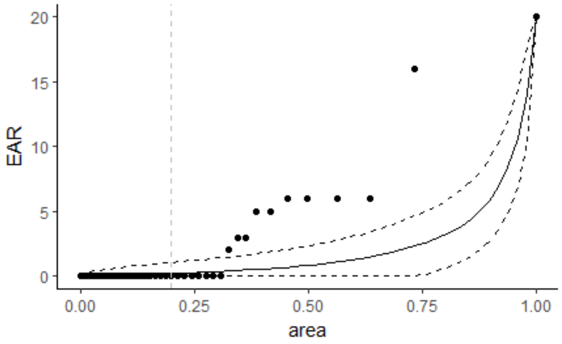
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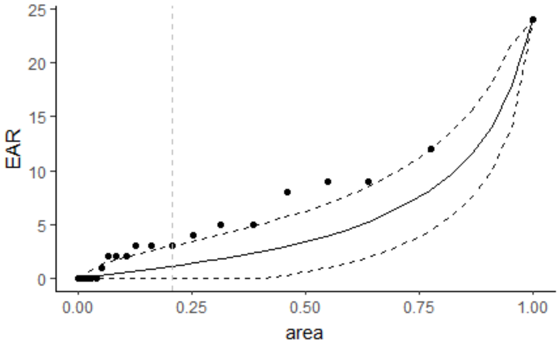
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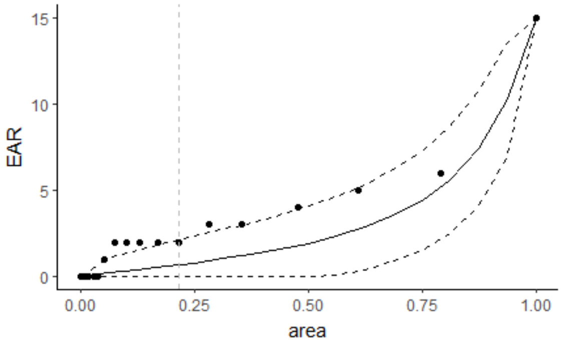
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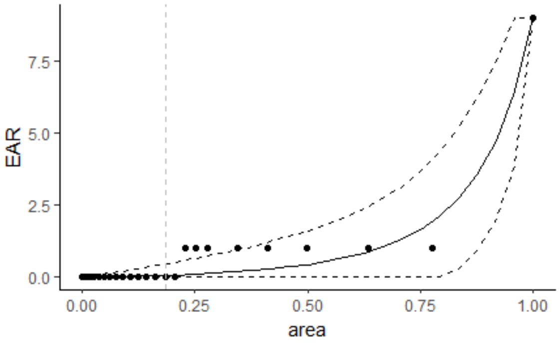
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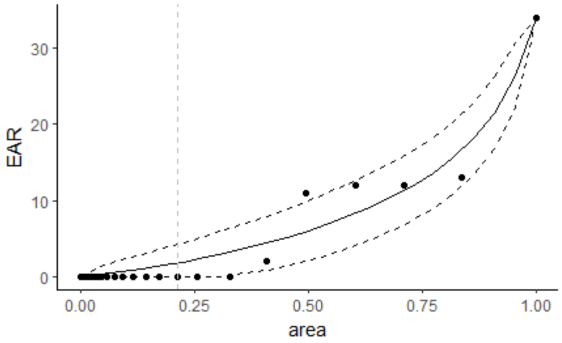
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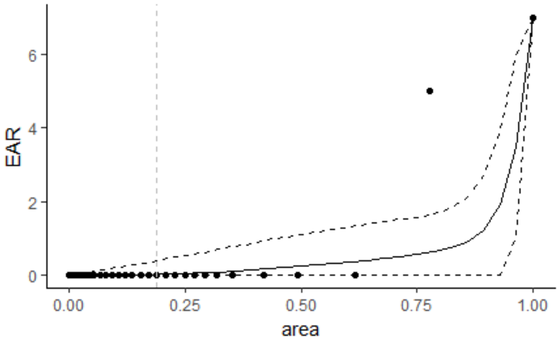
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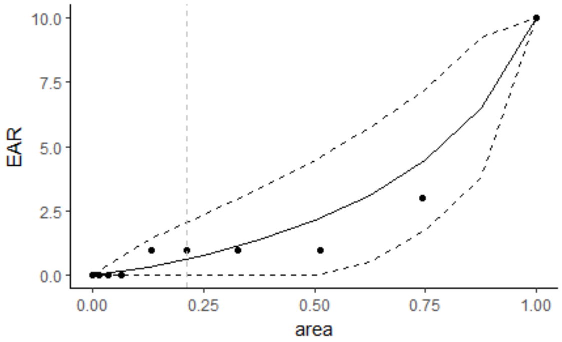
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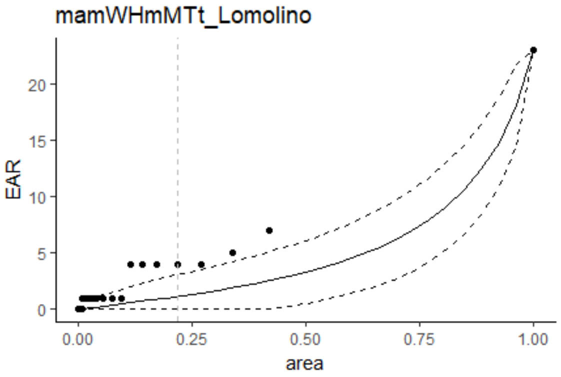
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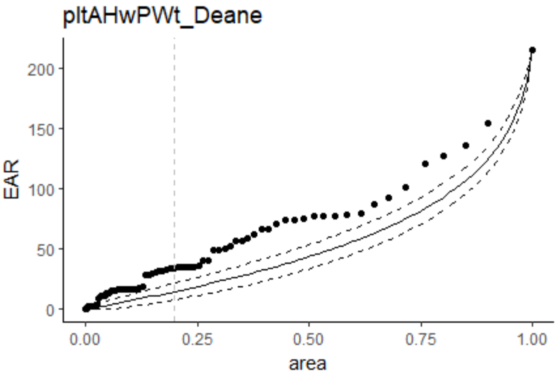
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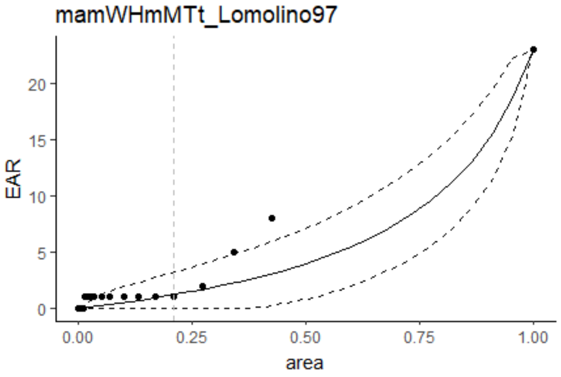
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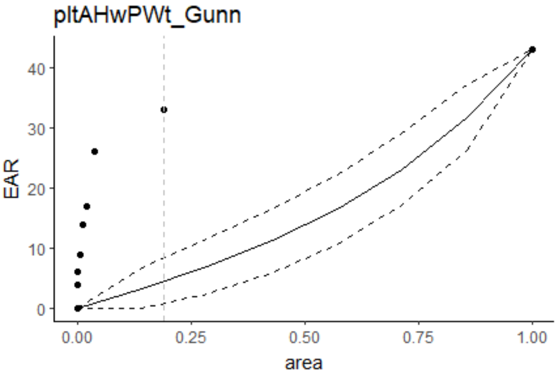
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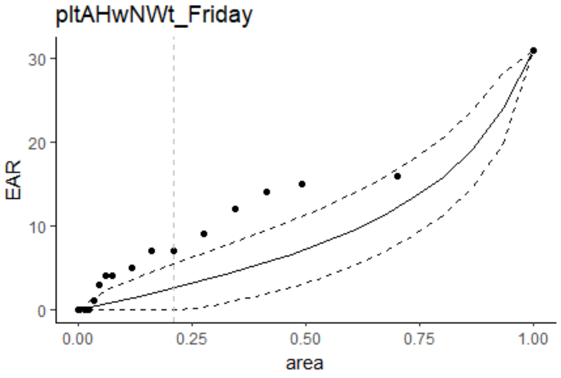
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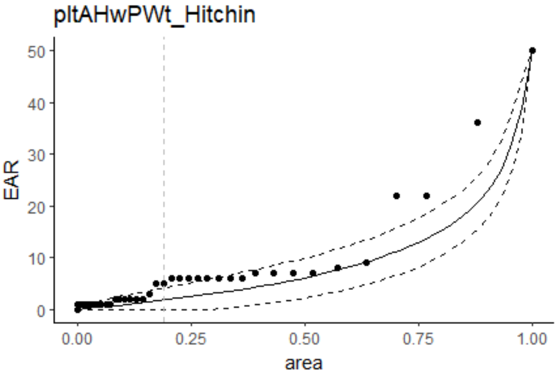
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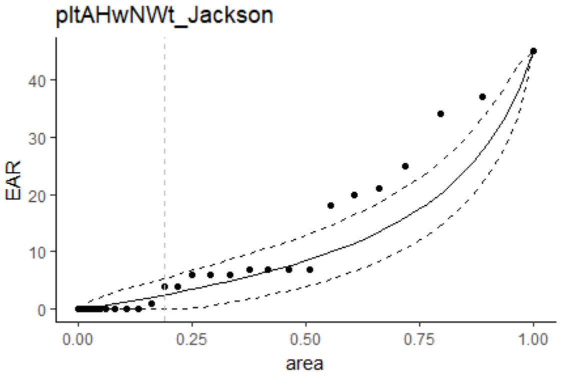
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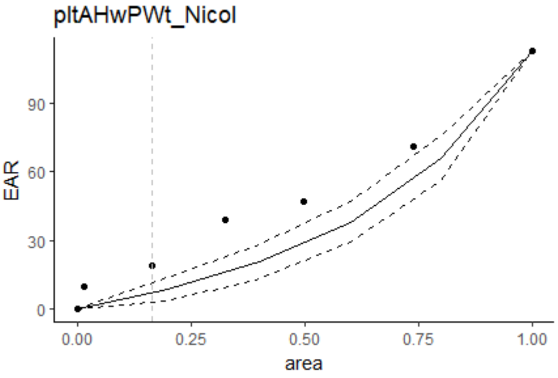
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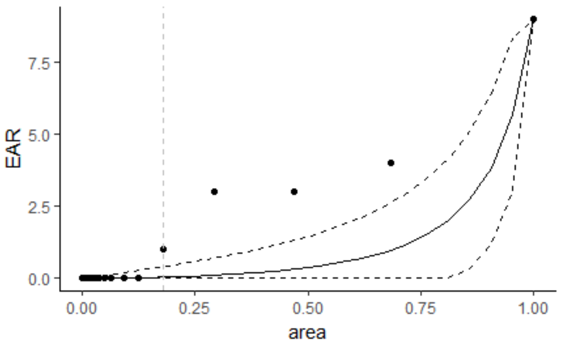

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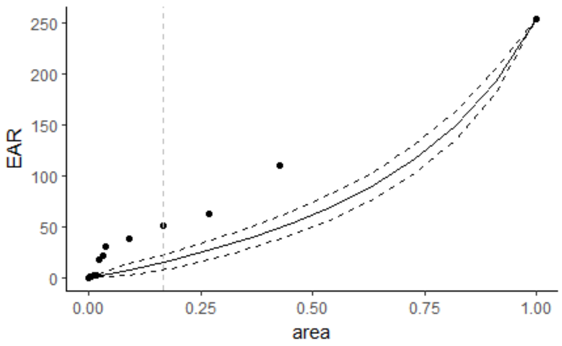

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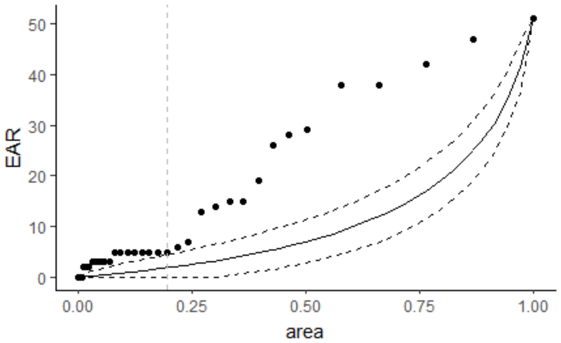

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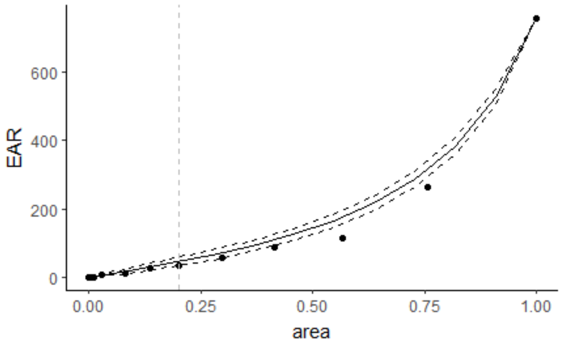

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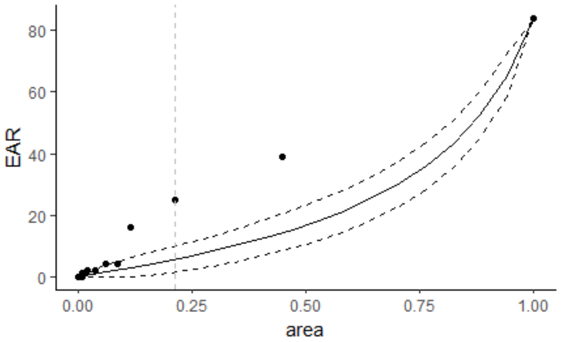

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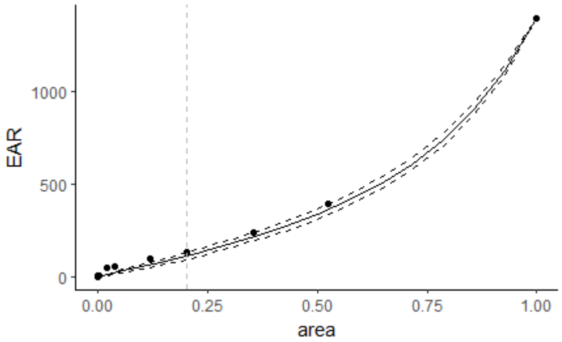

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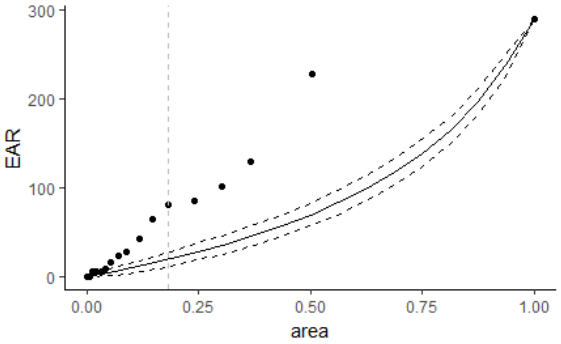

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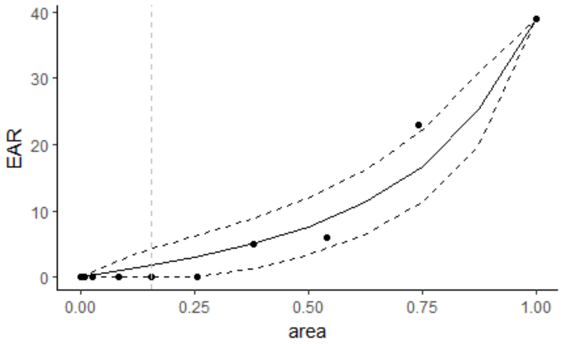

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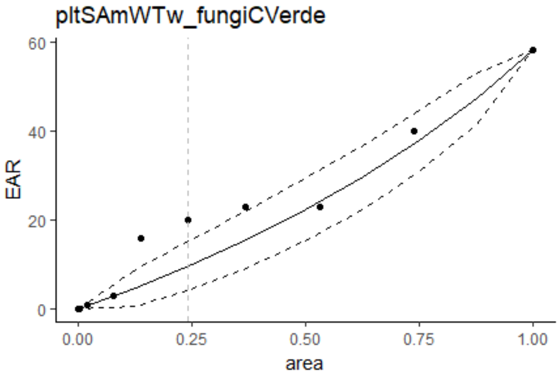
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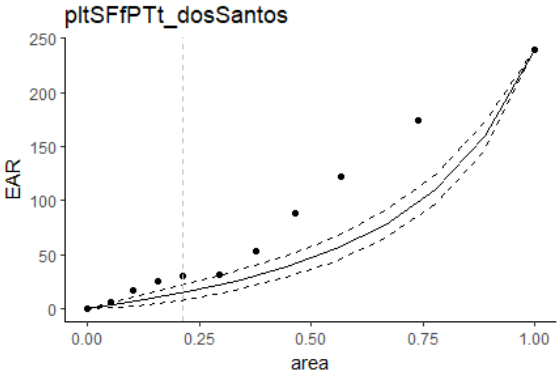
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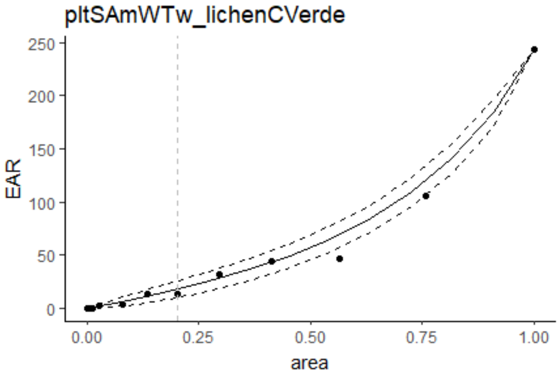
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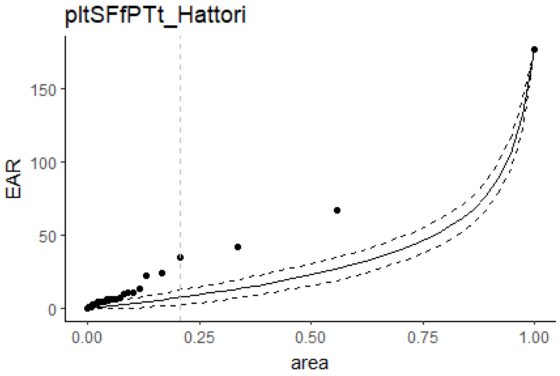
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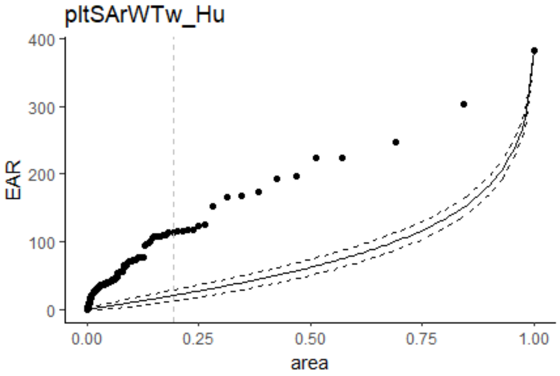
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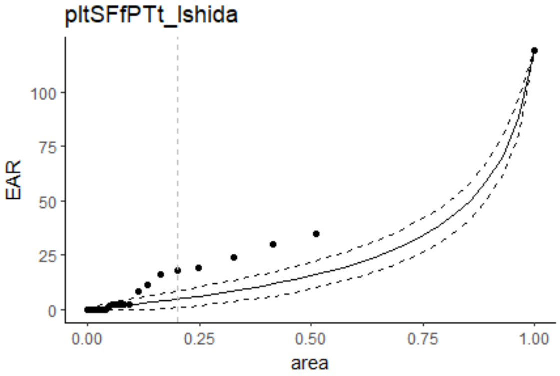
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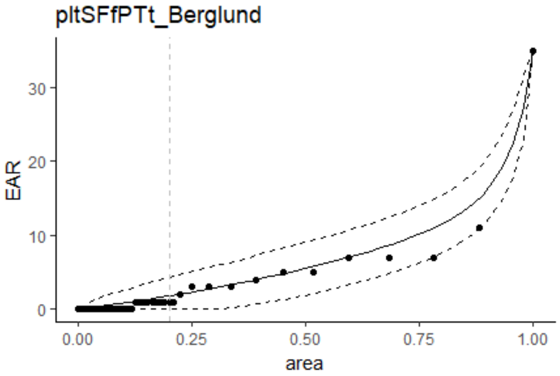
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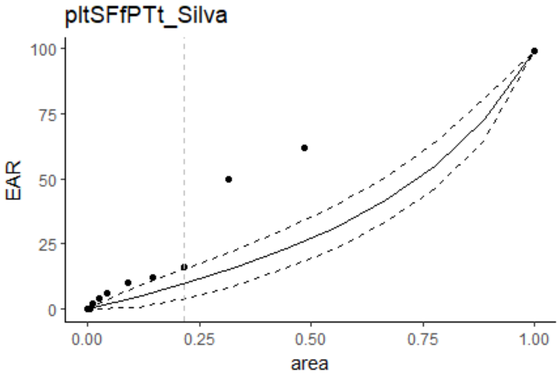
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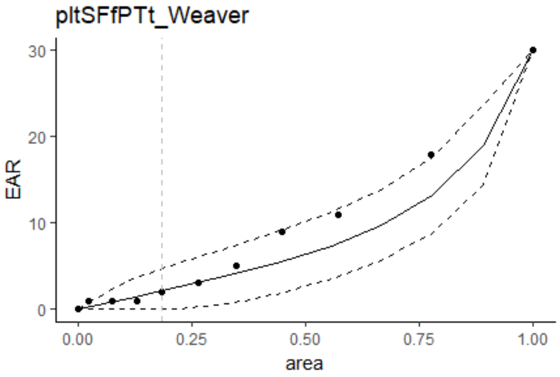
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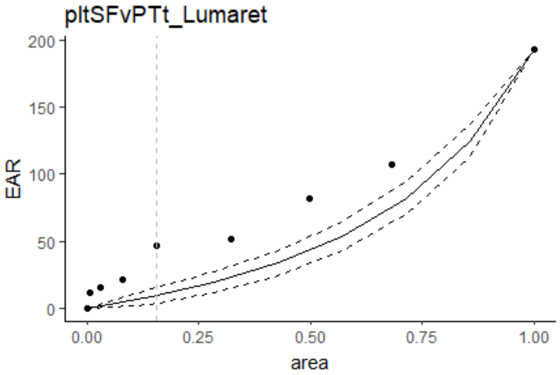
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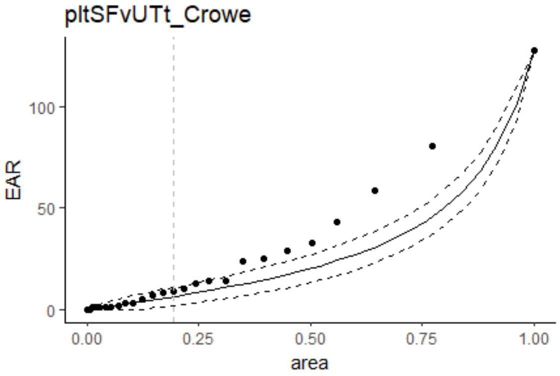
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APPENDIX B: CHAPTER 3 METADATA

Table B.1 Data sources for Chapter 3. See Table A.1 for full citation information.

study	slife	patch	Source	summary	Country	nSpp	nPatch	Effort control
1	bird	island	Haila, Haila et al 1983	Birds in a continental archipelago	Finland	63	44	Multiple census over multiple years; authors express some doubt over single visit islands
1	bird	island						
1	bird	island						
2	bird	fragment	Capizzi et al 2015	Birds in forest fragments	Italy	42	17	Each site 17 point counts, but larger sites were more widely spaced;
2	bird	fragment						
3	bird	fragment	Daily et al 2001	Birds in forest fragments vs open ag landscape	Costa Rica	131	8	Filled areas with survey patches, many as possible
4	bird	fragment	Haila 1993	Birds - forest fragments	Finland	29	13	The mapping method - search the whole fragment
4	bird	fragment						
4	bird	fragment						
4	bird	fragment						
5	bird	fragment	Holbech et al 2005	Birds in logged forest fragments	Ghana	147	15	Multiple sampling methods, area-based; used statistical re-sampling in analysis
6	bird	fragment	Wang et al 2013	Wintering birds in urban woodlots	China	93	42	Transects per area; number of transects per woodlot decided roughly according to its size
7	bird	fragment	Mohd-Azlan 2011	Mangrove birds in Darwin harbour	Australia	70	13	Length of ts; more transects in larger patches

study	slife	patch	Source	summary	Country	nSpp	nPatch	Effort control
8	bird	habitat island	Edenius 1997	Breeding birds in forest and mire natural mosaic	Sweden	23	18	Territory mapping; multiple visits
9	bird	habitat island	Gotmark 1986	Breeding birds in bogs and meadows	Sweden (SW)	18	62	Repeated survey to attain a census of pairs of breeding birds
9	bird	habitat island						
10	vertN	fragment	Vallan 2000	Amphibians in fragmented forest	Madagascar	30	6	Systematic search; multiple visits; search period lasted 40 min to 3 h, depending on patch size
11	vertN	fragment	Pineder & Hallfter 2004	Anurans in cloud forest	Mexico	21	10	Proportional sampling verified by SAC as >80% complete
12	vertN	habitat island	Almeida-Gomez et al 2016	Amphibians in temporary ponds	Brazil	23	11	Chao 1 completeness (all >75%)
13	inv	habitat island	Ball et al 2015	Littoral macroinvertebrates of dune lakes	New Zealand	72	17	Equally spaced around pond
14	inv	habitat island	Deane and Walters 2008	Littoral macroinvertebrates in semi-arid ponds	Australia	79	7	Longer sampling sweeps in larger pools
15	inv	island	Xu et al 2017	Butterflies in the Zhoushan Archipelago, China	East China Sea	68	42	Sampling effort roughly proportional to island area
16	inv	fragment	Baz & Garcia 1996	Butterflies in fragmented landscape	Spain	81	13	Sampled for 9 days, SAC asymptotes at 6
17	inv	fragment	Benedick 2006	Butterflies in fragments in Borneo	Borneo	79	8	Systematic, assume near complete: 2 x 12 days of sampling with 20 baited traps in each patch; 4800 trapping hours across 8 patches

study	slife	patch	Source	summary	Country	nSpp	nPatch	Effort control
18	inv	fragment	Filgueiras 2011	Dung beetles in Atlantic forest frags	Brazil	30	18	Systematic, assume near complete: 10 x 4 baited traps spread over 200 m in center of each patch plus flight interception trap
19	inv	fragment	Nyeko 2009	Dung beetles in forest frags	Uganda	45	6	Systematic, assume near complete; 8 baited traps at 50-m intervals in center of each patch visited monthly for 13 months
20	inv	fragment	Usher & Keiller 1998	Moths in artificial woodland patches	UK	214	18	Systematic, assumed near complete; 24 UV light trapping nights, multiple locations at each site
21	inv	fragment	Baldi & Kisbenedeck 1999 (1992 survey)	Orthopterans, shrub fragments in grass matrix	Hungary	32	26	Adjusted length of transect to size of patch
21	inv	fragment	Baldi & Kisbenedeck 1999 (1993 survey)	Orthopterans, shrub fragments in grass matrix	Hungary	36	26	Adjusted length of transect to size of patch
22	inv	fragment	Nufio et al 2011	Orthopterans, grassland frags Colorado	US	38	13	Proportional to fragment area; 2 levels of density sampling
23	inv	island	Davis et al 2003	Termites in f/w land bridge islands from reservoir	French Guiana	99	10	Systematic but assume near complete; 100 m transects sampled multiple times
24	inv	fragment	Galle 2008	Spiders in forest frags among grassland	Hungary	13	15	No. of traps/patch; 5-15 depending on size
25	inv	fragment	Gaublomme et al 2008	Beetles in urban forest frags	Belgium	94	10	Trap numbers; 9-15 depending on size
26	inv	fragment	Melliger et al 2018	Ants in urban/ag. forest frags	Swiss	28	26	Systematic, assume near complete; 60 trapping weeks per site 12 x 5 traps moved regularly

study	slife	patch	Source	summary	Country	nSpp	nPatch	Effort control
26	inv	fragment	Melliger et al 2018	Spiders in urban/ag. forest frags	Swiss	109	26	Systematic, assume near complete; 60 trapping weeks per site 12 x 5 traps moved regularly
27	vertN	fragment	Matthiae 1981	Mammals in woodland forest fragments	US-Wisconsin	13	22	Multiple methods; intensive spring observation; fall-trapping proportional to patch area
28	vertN	fragment	Silva 2001	Mammals in forest frags in a National Park	Canada	11	14	Trapping grid representing ~9–10% of the area covered by the whole fragment
29	vertN	fragment	Bolger et al 1997	Birds in chaparral scrub fragments, urban matrix	US-California	9	25	Not stated - assume near complete. Matched mainland areas to patch size distribution

APPENDIX C: EFFECTS OF SPATIAL AGGREGATION AND SPECIES ABUNDANCE ON SHARED SPECIES MODEL PARAMETER SCALING PROPERTIES

C.1. INTRODUCTION

To model the effects of sub-division and any change in this due to variations in species abundance and spatial aggregation it is necessary to use the non-random models from Chapter 4. For the estimates to produce realistic patterns of diversity under these different constraints requires that suitable values are assigned to the scaling exponent (z) and base-scale estimate of the c-parameter (c_0) used to scale c with spatial grain. This analysis seeks to identify any systematic variations in these parameters that occur with changes in evenness and aggregation such that suitable parameter sets to model realistic levels of evenness and aggregation can be obtained.

In theory, each species should have a unique value for k_i, the parameter in the shared species models derived in Chapter 4 based on the negative binomial and finite negative binomial distributions controlling spatial pattern. However, a single community-level parameter, c, used to convert mean density to spatial pattern allows for an adequate fit to data where (Chapter 4): $k_i = N_i a/Ac$. This is then used in the shared species model (here based on the negative binomial distribution):

$$E(SS_{m|a}) = \sum_{i=1}^{S}(1-(1+c)^{-k_i})^m \qquad (1)$$

However, a unique value of c is required at every spatial grain of interest. Fortunately, the value of k in the negative binomial distribution (equivalent to c in Eq. 1) follows a predictable scaling relationship with area (Plotkin and Muller-Landau, 2002, He and Hubbell, 2003) according to:

$$c_a = c_0 \left(\frac{a}{a_o}\right)^z \tag{2}$$

where c_i is the value of the scaling parameter at the spatial grain to be estimated, a_i; c_0 is the value of the parameter at base scale a_0 and z is a fitting constant describing the scaling relationship. Note that the ratio removes the need to consider area units; the scaling relationship only relies on the ratio of the base scale and the scale of interest in modelling. This relationship simplifies the use of the shared species model at different spatial grains, as c can be calculated using Eq. 2 at any scale, provided the base scale estimate c_0, and the exponent of the relationship z, are known. It is the aim of this study to (*i*) confirm the scaling relationship observed for the negative binomial distribution described by Eq. 2. is reliable for the shared species model based on the negative binomial distribution (Eq. 1); (*ii*) determine how the two parameters of interest (c_0 and z) vary under different conditions of spatial aggregation and evenness in species abundance.

C.2. METHODS

C.2.1. Validation landscapes

As with Chapter 4 I created simulated 50-ha landscapes based on the empirical data for Barro Colorado Island (2005 census, 211845 living stems, 301 species). While maintaining the observed value of individuals and species, I systematically varied both the distribution of abundance and the spatial placement of individuals on the landscape. This provided a ‘crossed’ dataset with which to explore the effects of varying both evenness and aggregation and their effects on one another. I randomly sampled species richness for each simulated landscape at different spatial grains and fit the shared species model with $m = 1$ (i.e., the equivalent species-area model) to estimate c at each grain. Then, selecting one value of a as the base scale (and thereby defining c_0 for that landscape) I used Eq. 2 to predict the observed values by estimating scaling exponent z in each landscape.

C.2.2. Generating simulation landscapes

I used the same approach to generate aggregated landscapes as in Chapter 4, using the Thomas point pattern process. Here I used a wider range of values for the sigma parameter controlling the dispersal kernel for the Thomas process, varying this from 10 - 50 in 5-m increments. As the observed BCI data produce species richness values that are similar to simulated landscapes with sigma in the range 30-40 m, I assume this range of aggregation covers the gradient one would expect to observe in nature from the highest levels of intraspecific aggregation close to that expected under random placement.

To systematically vary evenness of species abundance I used the zero-truncated negative binomial distribution (TNBD), varying the parameter gamma, which controls the shape of the distribution and the evenness of the resulting SAD. As a result, the TNBD is a commonly used distribution in applications where a systematic variation in evenness is desired without changing the underlying distribution model (e.g., He and Legendre, 2002, Wilber et al., 2015), and a number of widely used SAD models can be obtained by varying the value of gamma. For example, a value for gamma of 1 is equivalent to Macarthur's broken stick apportionment model and a value of zero is the log series, while intermediate values are close to the log normal (Wilber et al., 2015). I used values for gamma = 0.1 – 1.0 in increments of 0.1, yielding ten different species abundance distributions of increasing evenness (Table C.1). I quantified relative evenness in the different SAD using Pielou's measure, $H'/\ln S$, where $H'$is Shannon information and S is the total number of species (Pielou, 1975). I created landscapes using every combination of each spatial and species abundance distribution (i.e., a crossed factorial study), yielding 80 landscapes in total (Table C.2). Species abundance distributions were modelled using R package 'sads' (Prado et al., 2017) and simulated aggregated landscapes using the rThomas function in R package 'spatstat' (Baddeley et al., 2015).

I sub-sampled each landscape using square quadrats at 5-m increments from 5 x 5 to 50 x 50 yielding ten sampling grains (25, 100, 225, 400, 625, 900, 1225, 1600, 2025, and 2500-m^2), repeating this sampling 100 times and estimating mean species richness at each grain for each landscape. I then fit the species-area model for each model at each grain to estimate the best-fitting c-parameter for that grain (all species richness values were correct to 2 decimal places). I then used non-linear least squares to fit Eq. 2 to the observed *c* values at each spatial grain, using the fitted value at 400 m^2 as a base level. I test the fit of Eq. 2 to each set of c-parameters in each landscape using the coefficient of determination. Finally, I inspected the effects of varying evenness and spatial aggregation on the observed value of *c* at the base scale and scaling exponent *z*. All simulations and modelling were done in R 3.5.1 (R Core Team, 2019).

C.3. RESULTS

The ten SAD represented a gradient of evenness according to Pielou's measure (0.67-0.93; Table C.1). In terms of their similarity with commonly used SAD models, distributions with gamma < 0.4 were most like a log series SAD, while values from 0.4-0.5 resembled the log normal SAD and larger values were more like the broken stick (Table C.1**Error! Reference source not found.**). For comparison, the best fitting model for the empirical SAD was the log normal (ΔAIC to second ranked model = 9.5). The TNBD using the best fit estimate for gamma to the empirical data (gamma = 0.14) did not fit the empirical data well, although it had around the same support as the log series (ΔAIC = 1.0).

Table C.1 Statistics and best fitting SAD model for simulated abundance distributions. Gamma is the gamma parameter used to simulate SAD, evenness is Pielou's evenness, Top and 2nd ranked SAD are the best and second-best fitting species abundance distribution model, ranked according to AIC from log series, log normal, broken stick, negative binomial and geometric series models. All models based on 301 species and 211 845 individuals.

Gamma	Evenness	Top SAD	Second ranked
0.1	0.67	log series	TNBD
0.2	0.77	log series	TNBD
0.3	0.82	TNBD	log series
0.4	0.85	TNBD	log normal
0.5	0.87	TNBD	log normal
0.6	0.89	TNBD	broken stick
0.7	0.9	TNBD	broken stick

0.8	0.91	TNBD	broken stick
0.9	0.92	broken stick	TNBD
1.0	0.93	broken stick	TNBD

For all simulated landscapes, the scaling relationship described variation in the c-parameter with sampling grain well (all $R^2 > 0.970$, mean = 0.993; Table C.2).

Table C.2 Results for all 80 simulated landscapes. Each row represents a different landscape with spatial aggregation determined by the sigma parameter of the Thomas point pattern process (Sigma), evenness of abundance distribution determined by the gamma parameter of the TNBD (Gamma). SR$_0$ is the mean species richness at the base scale (400 m^2); c0 is the corresponding estimate for the c-parameter in each landscape; z is the estimated scaling exponent in Eq. 2; R^2 is the coefficient of determination for the fit of the scaling relationship to the observed data.

Simulation	Sigma	Gamma	c_0	z	R^2	SR$_0$
1	10	0.1	5.228	0.503	0.976	31.24
2	15	0.1	2.427	0.631	0.986	38.235
3	20	0.1	1.287	0.658	0.988	42.95
4	25	0.1	0.8	0.708	0.988	45.69
5	30	0.1	0.495	0.799	0.993	47.78
6	35	0.1	0.34	0.8	0.995	48.995
7	40	0.1	0.328	0.632	0.994	49.09
8	50	0.1	0.173	0.746	0.974	50.45
9	10	0.2	5.146	0.542	0.978	38.925
10	15	0.2	2.325	0.665	0.986	49.645
11	20	0.2	1.237	0.749	0.994	56.755
12	25	0.2	0.85	0.694	0.996	60.155
13	30	0.2	0.514	0.776	0.994	63.715

14	35	0.2	0.379	0.72	0.988	65.355
15	40	0.2	0.303	0.711	0.984	66.35
16	50	0.2	0.169	0.774	0.97	68.24
17	10	0.3	4.827	0.573	0.976	43.73
18	15	0.3	2.334	0.677	0.992	55.465
19	20	0.3	1.235	0.74	0.993	64.255
20	25	0.3	0.761	0.756	0.997	69.535
21	30	0.3	0.551	0.749	0.997	72.345
22	35	0.3	0.375	0.765	0.993	75.005
23	40	0.3	0.259	0.813	0.995	76.935
24	50	0.3	0.151	0.834	0.993	78.89
25	10	0.4	4.621	0.587	0.98	46.895
26	15	0.4	2.267	0.702	0.993	59.645
27	20	0.4	1.293	0.744	0.995	68.43
28	25	0.4	0.73	0.814	0.998	75.54
29	30	0.4	0.485	0.846	0.994	79.4
30	35	0.4	0.377	0.775	0.993	81.32
31	40	0.4	0.277	0.788	0.998	83.2
32	50	0.4	0.208	0.651	0.985	84.605
33	10	0.5	4.885	0.565	0.986	47.45
34	15	0.5	2.173	0.739	0.991	63
35	20	0.5	1.187	0.795	0.995	73.065
36	25	0.5	0.761	0.824	0.998	79.03
37	30	0.5	0.509	0.825	0.999	83.31
38	35	0.5	0.324	0.873	0.997	86.935
39	40	0.5	0.264	0.826	0.996	88.225
40	50	0.5	0.16	0.837	0.99	90.595
41	10	0.6	4.639	0.6	0.983	49.645

42	15	0.6	2.205	0.741	0.992	64.66
43	20	0.6	1.136	0.816	0.992	76.305
44	25	0.6	0.741	0.814	0.991	82.33
45	30	0.6	0.504	0.826	0.997	86.665
46	35	0.6	0.351	0.853	0.998	89.84
47	40	0.6	0.262	0.854	0.996	91.86
48	50	0.6	0.16	0.871	0.995	94.365
49	10	0.7	4.758	0.593	0.987	49.995
50	15	0.7	2.193	0.728	0.995	66.245
51	20	0.7	1.229	0.791	0.995	77.015
52	25	0.7	0.766	0.816	0.996	84.19
53	30	0.7	0.509	0.821	0.998	89.095
54	35	0.7	0.399	0.766	0.998	91.465
55	40	0.7	0.272	0.809	0.998	94.43
56	50	0.7	0.149	0.878	0.993	97.61
57	10	0.8	4.612	0.606	0.986	51.36
58	15	0.8	2.139	0.741	0.993	67.935
59	20	0.8	1.188	0.816	0.993	79.15
60	25	0.8	0.788	0.811	0.998	85.63
61	30	0.8	0.504	0.854	0.999	91.24
62	35	0.8	0.37	0.82	0.999	94.275
63	40	0.8	0.268	0.825	0.996	96.795
64	50	0.8	0.203	0.721	0.988	98.52
65	10	0.9	4.648	0.601	0.993	51.75
66	15	0.9	2.189	0.743	0.995	68.415
67	20	0.9	1.139	0.829	0.996	81.18
68	25	0.9	0.698	0.887	0.998	88.845
69	30	0.9	0.485	0.854	0.998	93.345

70	35	0.9	0.325	0.906	0.998	97.185
71	40	0.9	0.262	0.849	0.999	98.84
72	50	0.9	0.172	0.82	0.995	101.325
73	10	1	4.653	0.593	0.988	52.19
74	15	1	2.176	0.729	0.993	69.325
75	20	1	1.17	0.828	0.998	81.785
76	25	1	0.741	0.853	0.998	89.275
77	30	1	0.487	0.888	0.999	94.71
78	35	1	0.352	0.851	0.998	97.995
79	40	1	0.262	0.85	0.998	100.4
80	50	1	0.161	0.876	0.997	103.305

Estimates for base scale c_0 at 400 m^2 were a decreasing function of aggregation, particularly over the range of sigma values from 10-30 m. For landscapes simulated with sigma > 30 m, values for the parameter changed little (Fig. C.1a, 8.3). The scaling exponent showed the opposite pattern, increasing rapidly over the range in sigma from 10-25 m and then remaining constant, albeit with some suggestion of increasing scatter as landscapes became less aggregated (sigma values > 0.4; Fig. C.2b, C.4). This suggests it is unnecessary to explore landscapes with c_0 or z values corresponding to landscapes with aggregation exceeding that simulated at sigma ≈ 50, as their behaviour will be effectively modelled with the random placement model.

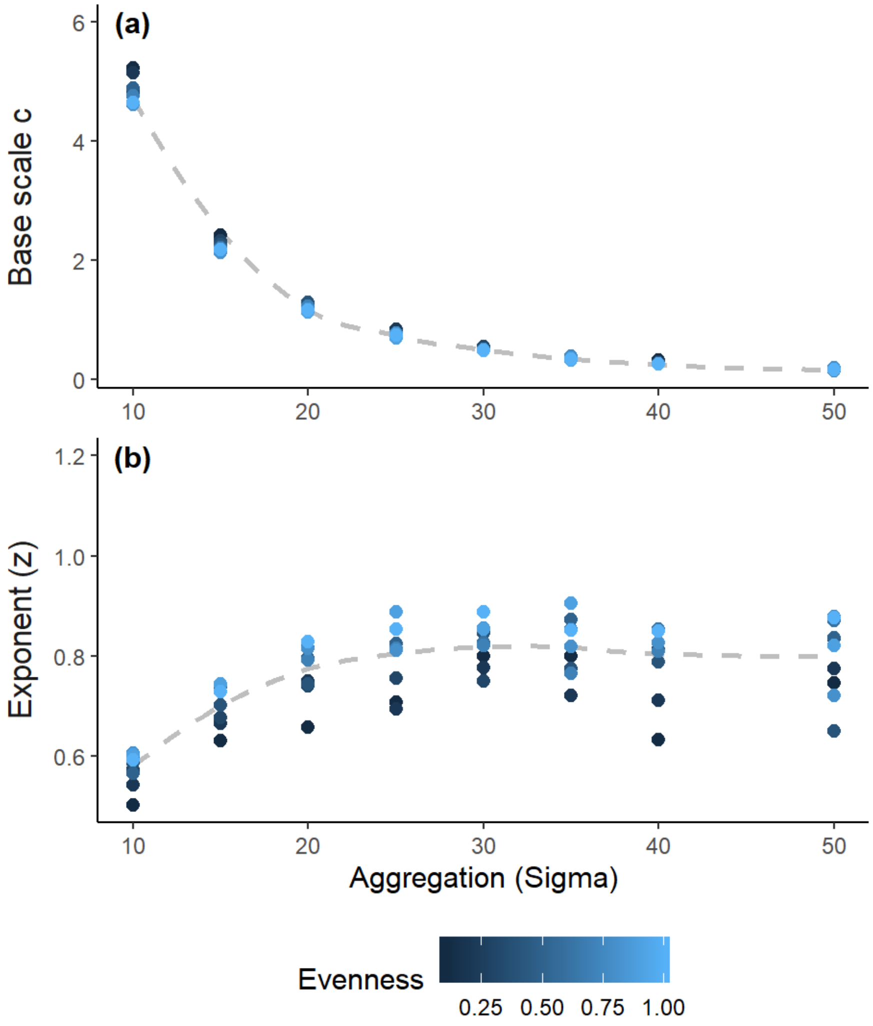

Fig. C.1 Effect of spatial aggregation on (a) the *c*-parameter estimated at base scale of 400 m^2 and (b) the exponent used to scale the parameter with spatial grain. In contrast with the effect of aggregation, evenness of SAD in the underlying landscape had relatively little effect on the estimates of c_0 or z (Fig. C.2). There was a slight positive increase in the exponent value with increasing evenness but there was considerable overlap at all levels of evenness modelled. This suggests that evenness of abundance distribution can be largely ignored in simulations.

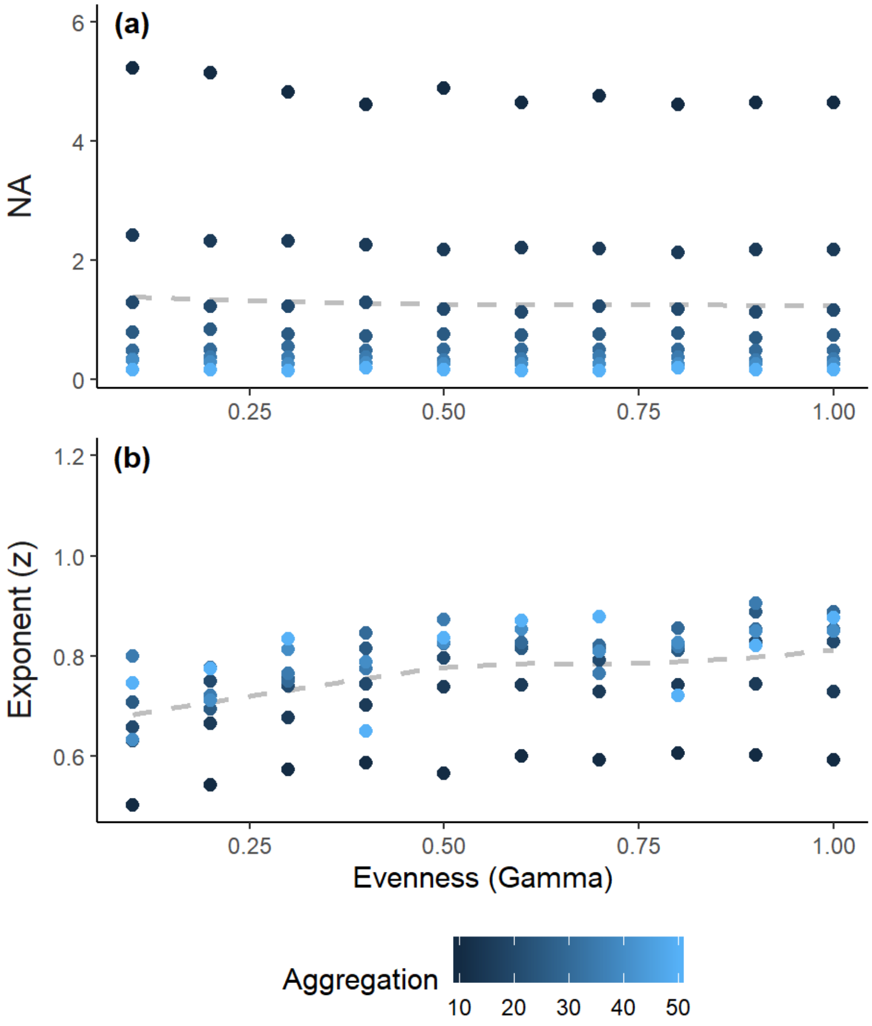

Fig. C.2 Effect of evenness on (a) estimated *c*-parameter at base scale of 400 m^2 and (b) the exponent used to scale the parameter with spatial grain.

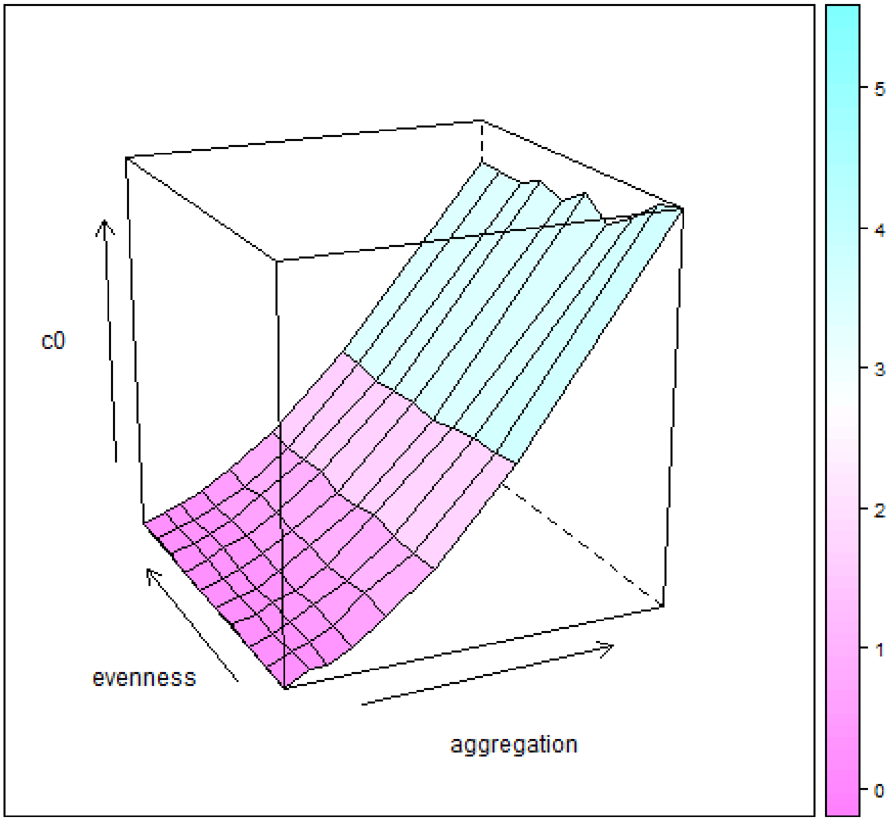

Fig. C.3 Effects of evenness and aggregation on the base scale estimate of *c*. Colour bar shows changes in the value of c_0.

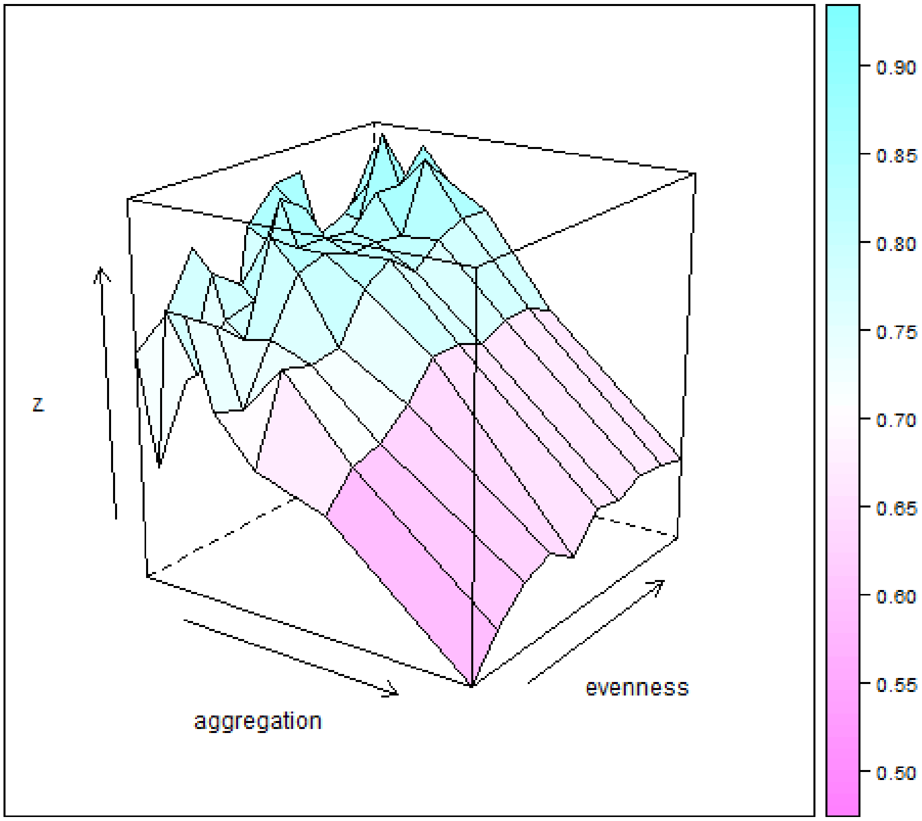

Fig. C.4 Effects of evenness and aggregation on the fitted scaling exponent, z. Colour bar shows the values of the exponent.

C.4. CONCLUSIONS

The results confirm the scaling relationship is a reliable means to predict the value of *c* at any spatial grain once a base scale value is established, consistent with previous findings on the negative binomial distribution aggregation parameter, *k*, in other applications (Plotkin and Muller-Landau, 2002, He and Hubbell, 2003). Results also demonstrate an opposing non-linear dependence of both c_0 and *z* on aggregation and a small linear dependence on evenness. This makes sense in terms of what is known about model derivation and how c fits into the non-random model, i.e.: $k_i = N_i a/Ac$. Parameter *c* alters mean species density under a random assumption ($N_i a/A$) to a lower value consistent with the amount of aggregation present in the community. Larger values for *c* increasingly attenuate mean density as expected in more highly clustered spatial patterns. This analysis suggests that values of sigma that result in simulated communities with a much higher level of aggregation than present (at least) in the Barro Colorado Island tree assemblage result in values for a base scale of 400 m^2 around 5-6. In simulated landscapes this value rapidly declines as a negative exponential function of sigma in these simulations (where $c_0 = 17.1exp^{-0.13\sigma}$; $R^2 = 0.99$). As increasing values of sigma produce spatial patterns approaching that of random placement, the value for c_0 becomes extremely small, consistent with expected model behaviour, where random placement of individuals is represented by larger values of k_i (requiring small values of *c*; Chapter 4).

It is expected that aggregation should decrease with census area (Conlisk et al., 2012) and the scaling exponent describes this change in aggregation from the perspective of the model. Concurrent with the rapid decrease in c_0 as spatial patterns change from highly aggregated to nearly random, the scaling exponent *z* initially increases rapidly from around 0.6 to a value near 0.8. This range in values is consistent with other empirical fits of the aggregation-scaling relationship to BCI and other data (Wright, 1991, Plotkin and Muller-Landau, 2002, He and Hubbell, 2003).

This analysis has implications for modelling aggregated scenarios using the modelling framework of Chapter 4, where suitable values need to be selected to produce realistic results. Based on this analysis, and a base scale corresponding to a similar proportion of the total area (i.e., 400 m^2 in 50-ha = 0.08%), highly aggregated assemblages could adopt values in the range

$c_0 = 4\text{-}5$ and $z = 0.5\text{-}0.6$, while weak aggregation could be modelled using values near to $c_0 = 0.2\text{-}1.0$ and $z = 0.8\text{-}0.9$. If intermediate levels of aggregation were desired, these ranges could be interpolated linearly. The random placement model requires no fitting and can therefore provide a qualitative verification of model predictions independent of the spatial scale being considered.