Assessing the Impacts of Habitat Fragmentation on Biodiversity Across Scales:

The Case of Thousand Island Lake, China

by

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ABSTRACT

Habitat fragmentation, the loss of habitat in the landscape and spatial isolation of remaining habitat patches, has long been considered a serious threat to biodiversity. However, the study of habitat fragmentation is fraught with definitional and conceptual challenges. Specifically, a multi-scale perspective is needed to address apparent disagreements between landscape- and patch-based studies that have caused significant uncertainty concerning fragmentation's effects on biological communities. Here I tested the hypothesis that habitat fragmentation alters biological communities by creating hierarchically nested selective pressures across plot-, patch-, and landscape-scales using woody plant community datasets from Thousand Island Lake, China. In this archipelago edge-effects had little impact on species-diversity. However, the amount of habitat in the surrounding landscape had a positive effect on species richness at the patch-scale and sets of small islands accumulated species faster than sets of large islands of equal total size at the landscape-scale. In contrast, at the functional-level edge-effects decreased the proportion of shade-tolerant trees, island-effects increased the proportion of shade-intolerant trees, and these two processes interacted to alter the functional composition of the regional pool when the total amount of habitat in the landscape was low. By observing interdependent fragmentation-mediated effects at each scale, I found support for the hypothesis that habitat fragmentation's effects are hierarchically structured.

To the forest, my first love.

ACKNOWLEDGMENTS

If it takes a village to raise a child, then it takes a lot more to make a doctor. As such, I have a great many people to thank. First thank you to my family, in particular my loving wife, Angie, whose constant support kept my head above water over many years of study, my first son, Jack, who taught me humility, my second son, Henry, who taught me joy, my mother, Michele, who offered love and understanding, my father, Mark, who would drop everything whenever I needed him, and my sister, Amanda Moore, who I have always looked up to. I also thank my friends, especially Mark and Jenna Golab, Matt Curry, Sarah and Alan Tippins, and Badingqiuying for providing support when they could and Scotch when they couldn't.

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Finally, I am deeply indebted to the National Science Foundation, the School of Life Sciences, and the Graduate College Completion Fellowship, each of whom financially supported me during my doctoral studies.

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CHAPTER 1: INTRODUCTION, DISSERTATION STRUCTURE, and STUDY SYSTEM

1 Introduction

The question of why smaller, more isolated patches have fewer species than those that are larger and less isolated has intrigued biologists for generations. In the middle-to-late 1700s European explorers had already recognized the fundamental components of what would become the field of island biogeography, including the species-area and species-isolation relationships (Lomolino et al. 2010). However, while these relationships were studied extensively over the following 200 years (Lomolino et al. 2010), a sufficiently parsimonious and dynamic explanation for their existence was not proposed until the publication of MacArthur and Wilson's *The Theory of Island Biogeography* (IBT) in 1967.

MacArthur and Wilson's accomplishment was far reaching, and only shortly after the publication of IBT, ecologists and conservation biologists began applying IBT principals to the study of habitat fragmentation (Laurance 2010) with the assumption that spatially isolated patches of habitat were in fact very similar to islands, embedded in a sea of human activity rather than the ocean. However, the application of IBT principals to habitat fragmentation has resulted in significant definitional and conceptual challenges.

The first among these challenges is the definition of fragmentation itself. The most commonly used definition of habitat fragmentation is that habitat fragmentation is the process by which large continuous tracts of habitat are broken up into smaller, more isolated remnant patches (e.g., Wilcove et al. 1986, Wu 2009, Didham 2010). As pointed out by Fahrig (2003) in her seminal review, this suggests that fragmentation is first and foremost a process (Fig. 1a). However, in matching IBT, most studies of fragmentation have focused on landscapes that have been fragmented, with landscape composition and configuration held constant throughout the study period (e.g, Haddad et al. 2015), which suggests that fragmentation can also be considered a state (Fahrig (2003), Figs. 1b and 1c). The focus on fragmented, rather than fragmenting, ecosystems has driven many to attempt to isolate the effects of habitat loss from those of fragmentation's purely spatial components (e.g., Fahrig 2003) in a snapshot or across snapshots of time in a static landscape, neglecting that fragmentation's spatial effects are, by definition, derived from habitat loss (Didham et al. 2012).

Second, the study of fragmentation has generally focused on only one form of diversity, species diversity. However, it has become apparent that species loss within fragments is not random (Laurance et al. 2011). This process can be caused by a myriad of forces, ranging from dispersal limitation driving selective colonization at the patch-scale (e.g., Cook and Quinn 1995, Butaye et al. 2001) to fine-scale responses to fragmentation-mediated changes in abiotic conditions (Laurance et al. 2006, Laurance et al. 2007, Ewers and Didham, 2008, Laurance et al. 2011, Haddad et al. 2015). Regardless of the cause, it is clear after decades of study that not all types of biota respond to habitat fragmentation equally, or even similarly, and a focus purely on species richness has proved insufficient for disentangling the causal effects underlying community responses to fragmentation (Wilson et al. 2016). Worse, while habitat fragmentation alters biodiversity, abiotic conditions, and ecosystem functioning (Haddad et al. 2015), the broader biodiversity ecosystem functioning literature has shown that functional diversity, not species diversity, is a more directly related to biodiversity-ecosystem functioning (BEF) relationships (Diaz and Cabido 2001, McGill et al. 2006, Cadotte et al. 2011). This makes connecting fragmentation science to BEF studies a challenge. Therefore, an expansion of fragmentation science beyond simple measures of species diversity is a critical research area for the years to come (Wilson et al. 2016).

The third challenge is centered around the scale at which habitat fragmentation is studied. Using the definition above, fragmentation is a landscape-scale process (Fahrig 2003, 2017). However, despite occurring at the landscape-scale, fragmentation may drive biological changes at other scales (Lafortezza et al. 2010, Didham et al. 2012, Valdés et al. 2015). Many studies of fragmentation have occurred at the scale of the fragment, comparing the communities within patches to themselves and each other (Fahrig 2003, Wilson et al. 2016). Such studies have consistently found that habitat fragmentation has strong negative effects on most ecologically relevant parameters (Haddad et al. 2015). In particular, the study of communities within patches has shown that edges can have marked effects on community composition (e.g., Laurance et al. 2006, Laurance et al. 2011), which suggests that fragmentation’s effects on community structure are at least partially deterministic (e.g., “species sorting” *sensu* Holyoak et al. 2005).

However, extrapolating relationships from one scale to others is an uncertain proposition. To take an obvious example, while it is well established that small fragments have decreased α-diversity relative to large fragments, a recent review by Fahrig (2017) found that more spatially fragmented landscapes almost always have more γ-diversity than less spatially fragmented landscapes if the total amount of habitat was held equal, suggesting that landscape configuration plays a more important role than patch-level effects in controlling diversity at regional scales. Further, studies which attempt to integrate spatial information from multiple scales generally only predict fragmentation effects at a single scale, often very local (e.g., Lafortezza et al. 2010). While such studies are certainly interesting and relevant to conservation planning, they do not explore the scale-dependence of fragmentation's effects.

Missing from this debate is a recognition that the variables which control biological responses to fragmentation likely vary across scales. An alternative hypothesis is that fragmentation's effects on biological communities are hierarchical and scale-dependent (e.g., Bowers and Dooley Jr. 1999, Lomolino 2000, Fig. 2), which is consistent with the Hierarchical Patch Dynamics Paradigm (Wu and Loucks 1995). Such a hypothesis would suggest that at very small spatial scales, community composition should be controlled by both local abiotic filters and the relative fitness of the species attempting to compete for resources. Larger, less isolated patches should have more diverse species assemblies due to IBT principles, altering inter-specific competition, and harboring more total niche space, as they contain more types of habitat, allowing for divergent community compositions within the patch. These local and patch factors will interact with each other to alter the relative diversity of patch communities, which will in turn control regional diversity. While the proceeding sentences described the hierarchical structure from the bottom up, a top down description would be equally valid: if there are no species in the regional pool that can survive in the niche-space that fragmentation creates, niches at local and patch scales will go unoccupied. This scenario suggests that fragmentation's effects on biodiversity are constantly interacting within and across scales, dynamically shaping and modifying communities at all scales all the time.

In this dissertation I test the hypothesis that fragmentation modifies biological communities through hierarchically nested, scale-dependent controls by simultaneously assessing the effects of fragmentation on woody plant communities at plot-, patch-, and landscape-scales in Thousand Island Lake, China.

2 Dissertation Structure

I will answer this question in three steps. First, I will introduce the study region, data sources, and methods shared between chapters in section three below. Then, in Chapter 2, I will begin by quantifying the historical and current landscape context of the study region, which will provide the independent variables necessary to complete further chapters. In Chapter 3 I will assess the core hypothesis at the species-level. In Chapter 4 I will reassess the core hypothesis at the functional-level, categorizing species into functional-groups. This approach will test whether interdependent effects of habitat fragmentation are observed at each level and, because the functional groups are made up of unequal numbers of species, the observed patterns are stronger at the functional-level than at the species-level. Finally, I conclude in Chapter 5 by summarizing and synthesizing my findings. To avoid repetition, chapters will begin directly with methods specific to the analysis contained within the chapter, rather than a formal introduction for each chapter.

3 Study System, Data Sources, and Shared Methods

Thousand Island Lake (TIL) is a large, man-made lake located in Chun'an County, Zhejiang Province, China, with a sub-tropical monsoonal climate. Forests throughout the TIL region have long been modified by humans. These modifications culminated in the late 1950s, when trees were completely or near-completely clear-cut prior to lake formation. Lake formation resulted in the isolation of more than 1,000 habitat remnants, which have since undergone secondary succession. The age of contemporary forests in the lake region are similar (approximately 60 years old; unpublished tree ring data, Yu personal communication), roughly corresponding to the end of the Great Leap Forward and the implementation of immigration policies for local people during dam construction (Wilson et al. 2016).

This work uses two datasets of woody plant richness and abundance. At the island-scale, I utilize a version of the woody plant dataset introduced in Hu et al. (2016), updated to correct errors recognized in subsequent sampling. This dataset measured woody plant community structure on 29 islands in 2009-2010 by tagging and identifying each plant with diameter at breast height greater than or equal to 1 cm within 5x5 m sampling cells. Total sampled area for each island was roughly correlated to island size and ranged from 0.0225 ha to 1.495 ha. Rarefaction analysis has shown that this dataset is sufficient for capturing the vast majority of species on the islands (Yu et al. 2012).

To capture variation in community structure within islands, 400 m^2 sampling plots identical to those described above were set up along an edge gradient on 28 islands. Small islands (those smaller than 1 ha received when water level is at 105 m above sea level) received one to two plots. Large islands (those greater than 1 ha when water level is at 105 m above sea level) received two additional plots, each more than 40 m from the island edge. To account for its much greater size the largest island, JSE, received five additional plots, all more than 40 m from the island edge, and one additional edge plot. The division between small and large islands was selected because a study in a similar forest identified that 1 ha is the minimum size patches that maintain interior communities (Young and Mitchell 1994). All these plots were sampled during the summers of 2014 and 2015 and this work was carried out by the lab of Professor Mingjian Yu of Zhejiang University, Zhejiang, China.

As mentioned above, one of the islands, JSE, is far larger (two orders of magnitude, Fig. 3) than the second largest island. To avoid over-leveraging this single data point, JSE was eliminated from all analyses that used island size as a continuous variable throughout this dissertation. Data from JSE were retained in all other cases.

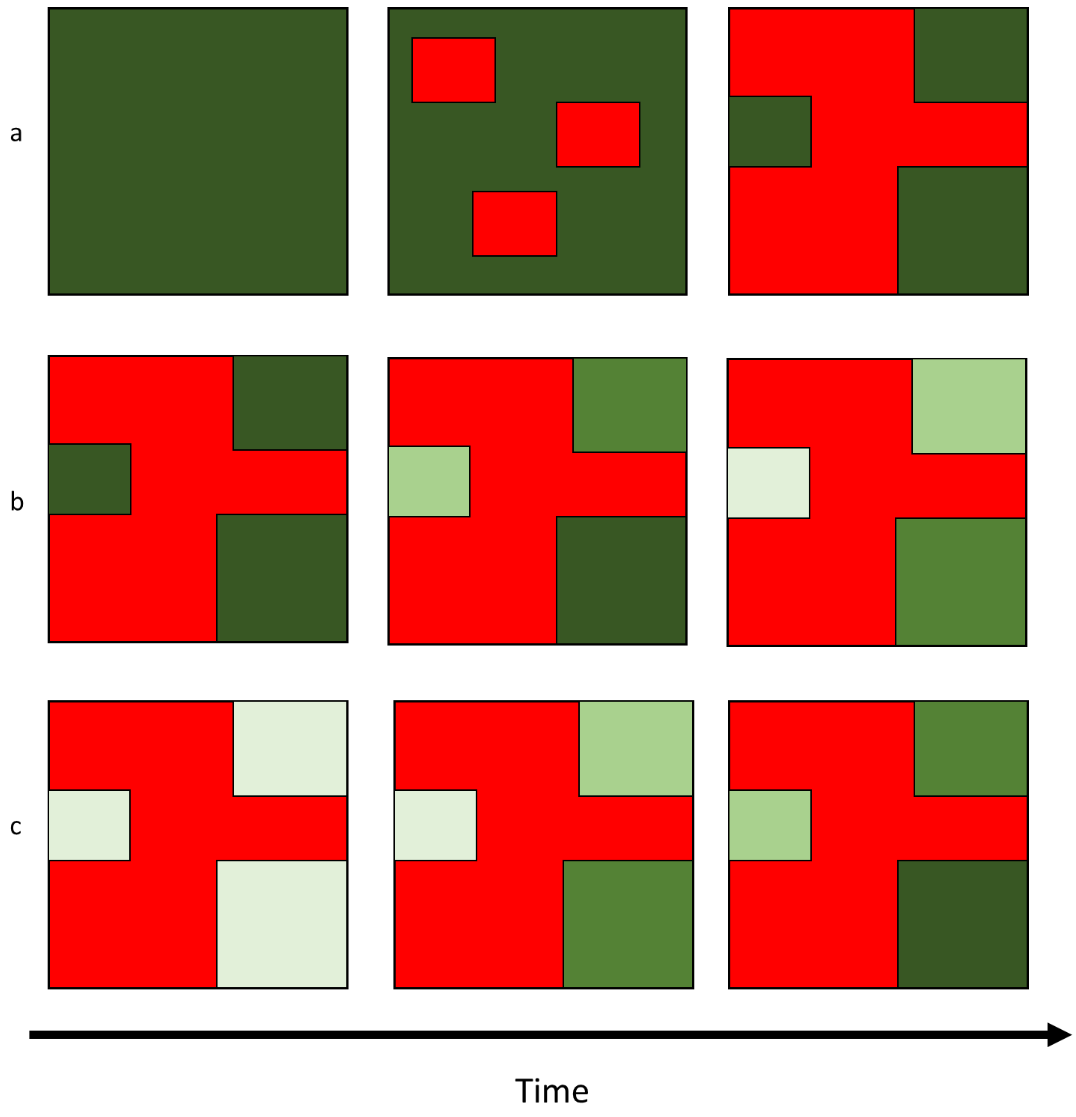


Figure 1. Diagram showing three conceptualizations of habitat fragmentation with (a) showing habitat fragmentation as the process by which habitat loss causes the spatial isolation of remnant patches (modified from Fahrig (2003)), (b) where habitat loss has already occurred in an intact landscape and community relaxation is the dominant process, and (c) where habitat loss in an area without life has already occurred, isolating potential habitat areas which are then allowed to recover with community assembly as the dominant process. Green signifies patches, red matrix, and the shade of green denotes the extent to which communities one each patch are biologically similar to those in intact forest, with darker shades being more similar than lighter shades.

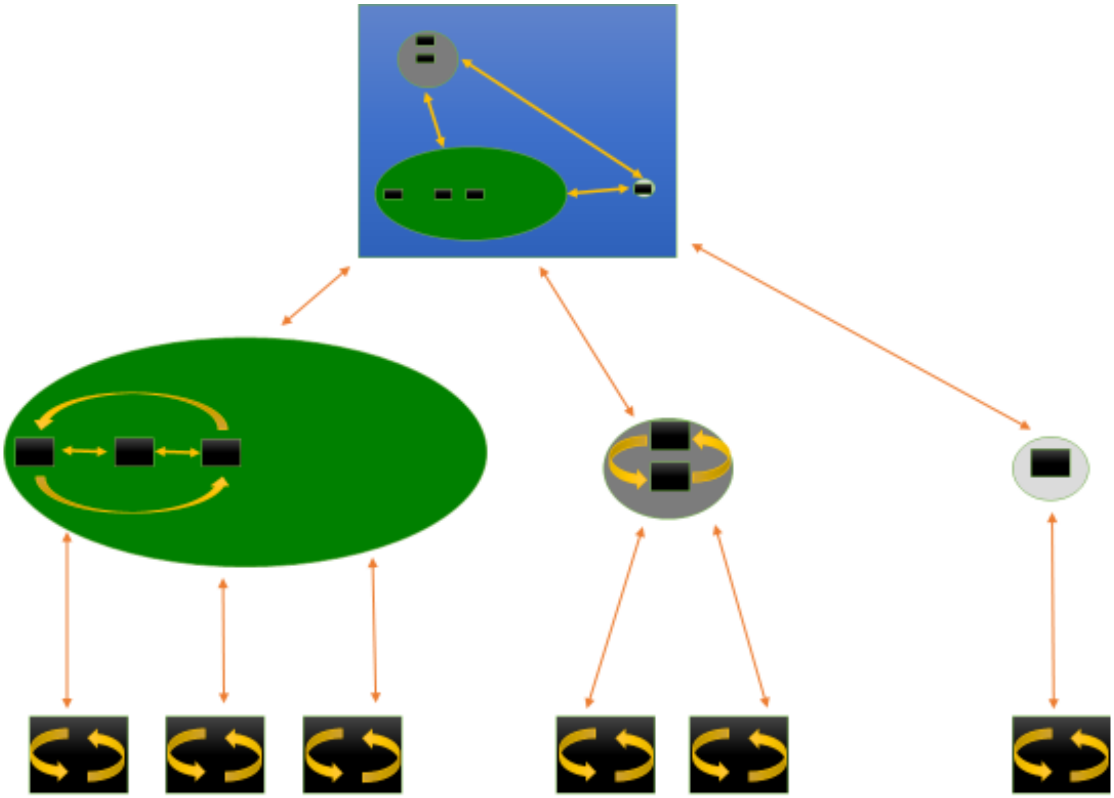


Figure 2. A conceptual diagram showing how local and landscape processes could interact with one another hierarchically. Green areas represent patches, blue areas, matrix, and black areas, local plots. Light orange arrows represent selective processes occurring at a given scale, dark orange arrows represent selective processes occurring across scales.

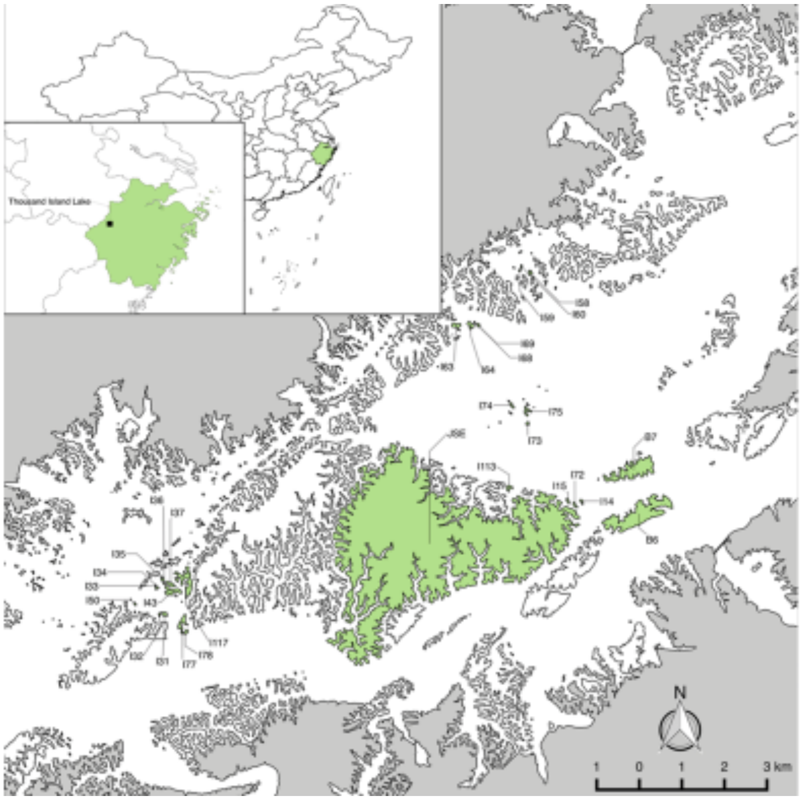


Figure 3. Map of central Thousand Island Lake, China. Study islands in green.

CHAPTER 2: QUANTIFYING HISTORICAL LAND-USE-LAND-COVER AND MODERN LANDSCAPE PATTEREN IN A SEVERLY FRAGMENTED LANDSCAPE, THOUSAND ISLAND LAKE, CHINA

1 Preface

Any study of habitat fragmentation must begin with an adequate quantification of both historical landscape context and modern landscape conditions. In this chapter I complete such a work, providing the building blocks necessary for this and future studies of the TIL system, while simultaneously elucidating the relationship between habitat loss and the spatial configuration of the landscape.

2 Methods

2.1 Historical Land-Use-Land-Cover Change (LULCC)

Classified LULCC data covering Chun’an County were acquired from the labs of Professors Jiyuan Liu and Wenhui Kuang in the Chinese Academy of Sciences for the years 1990, 1995, 2000, 2005, and 2010. In addition, a classified image composited from several years of the 1980s was acquired from these labs.

These data are described in detail in Liu et al. (2005). To summarize they were created through manual digitalization LANDSAT TM data at a 1:100,000 scale, which was then rasterized to a 30x30 m resolution. They use a two-level classification system, each level retaining the 30x30m resolution described above. The first level consists of six LULC types: Cropland, Woodland, Grassland, Water body, Built-up land, and Unused Land. The second level consists of 25 additional LULC types, each nested within a level-one type (Cropland: Paddy Land and Dry Land Agriculture; Woodland: Forest, Scrublands, Woodlands, and Other; Grassland: Dense Grass, Moderate Grass, and Sparse Grass; Water Body: Streams and Rivers, Lakes, Reservoirs and Ponds, Permanent Ice and Snow, Beach and Shore, and Bottomland; Built-up Land: Urban Built-Up Land, Rural Settlements, and Other; and Unused Land: Sandy Land, Gobi, Salina, Swampland, Bare Soil, Bare Rock, and Other). These data have a reported accuracy of 92.9% (Liu et al. 2005).

Upon initial inspection one significant alteration to the raw data was deemed necessary. Large sections of the 1980s images were classified as “bottomland,” which Liu et al. (2005) defined as “Lands between normal water level and flood level,” suggesting that this area was sometimes above and sometimes below the water level of the lake. As the characteristic “beaches” clearly visible along island edges suggest that these forests are highly flood intolerant, these “bottomland” areas were reclassified as reservoir to be consistent with the ecological conditions experienced by flooding intolerant communities and for ease of comparison with other time periods. Data for each time period were cropped to the boundaries of Chun’an county in ArcGIS 10.3, and landscape pattern was assessed by calculating four metrics (number of patches, median patch size, median nearest-neighbor distances, and median radius of gyration (the mean distance between each pixel within a patch and the centroid of the patch)) using FRAGSTATS 4.2 (McGarigal et al. 2012).

2.2 Current Day Landscape Pattern

Current day landscape pattern was assessed in the central TIL's Jeishou Archipelago (Fig. 3). This region was selected because it contains the islands most commonly studied in the lake, and thus forms the basis of the patterns described in the TIL literature. Island and mainland boundaries were assessed using high resolution SPOT-6 satellite imagery. As island size is dependent on water level, island boundaries were defined as the vegetated edge of each island. Vegetated areas and mainland borders were digitalized at 1:5,000 scale from SPOT-6 imagery in ArcGIS 10.3 by Bingbing Zhou of ASU's School of Sustainability. These digitalized maps were then rasterized and processed to identify relevant patch level metrics using FRAGSTATS 4.2. Distance to mainland, which is not measurable natively in FRAGSTATS, was calculated using the Near tool in ArcGIS 10.4.

3. Results

3.1 Historical Land-Use-Land-Cover Change

Landscape structure is generally defined using two components: landscape composition and landscape configuration.

Landscape composition, measured here as the proportion of the landscape for each class, varied little from the 1980s to 2010 (Fig. 4). Of particular interest to the biological communities of the TIL region, the relative abundance of natural LULC types was stable throughout time.

Landscape configuration, however, showed marked variation in time. At the landscape-level, the number of patches decreased significantly while median radius of gyration, median patch size, and median nearest-neighbor distance all increased (Fig. 5). At the class-level, variation was far less dynamic and more idiosyncratic. Here I focused on six classes (paddy land, dry land agriculture, forest, shrub lands, woods, dense grass, and reservoir) as these classes made up almost the entire landscape. The single largest change at the class level was the significant decrease in the number of small agricultural patches between 1990 and 1995 (Fig. 6). Median patch size increased slightly for both agricultural and forest classes (Fig. 7), median radius of gyration increased slightly for agricultural and forest classes (Fig. 8), while median nearest-neighbor distances were either stable or idiosyncratic for all classes (Fig. 9).

3.2 Current Landscape Patten

The digitalization of central TIL identified 504 islands (Fig. 3). Island areas within TIL display an extremely right skewed distribution (Fig. 10). Mean Island size is 8.21 ha; however, 305 of the 504 islands identified were less than 1 ha, and the median island area is 0.59 ha. Eigen Nearest-Neighbor (ENN, the straight-line distance between two island edges), also displayed a right skewed distribution (Fig. 11), with a mean ENN of 87.91 m and a median of 56.37 m. Distance to mainland displayed a right skewed, multi-modal distribution (Fig. 12) with a mean distance to mainland of 935.06 m and a median of 664.57 m.

Special care was taken to identify fragmentation relevant landscape parameters for commonly studied islands in the TIL. These parameter values can be found in Appendix A.

4 Discussion

4.1 Historical Land-Use-Land-Cover Change

China has changed rapidly since the 1980s, with urbanization being a particularly large driver of socio-ecological changes at both regional and landscape scales (Zhang and Song 2003). In this context, my results from the LULCC assessment are not particularly surprising. Over the study period the number of dryland agriculture patches decreased significantly, while the total amount of dryland agriculture remained relatively stable across the landscape. These findings are indicative of rural abandonment and urban migration, processes by which small, relatively unproductive agricultural areas are abandoned as local people seek better opportunities in nearby cities.

From a fragmentation perspective, the LULC analysis revealed two critical findings. First, I found little evidence of succession occurring during the study period. Given the fact that islands were completely or nearly-completely clear cut prior to lake formation (see Chapter 1 and Wilson et al. 2016), this suggests that secondary succession reclaimed most forested areas by the 1980s, supporting other analyses which have found forest ages within the lake to be similar to the age of the reservoir (unpublished tree ring data). Second, I found that the amount of forest throughout the landscape was fairly stable throughout the study period. The impacts of habitat loss are known to dominate most fragmentation-mediated responses, whether measured by a strict habitat loss vs. habitat fragmentation *per se* paradigm (e.g., Fahrig 2003), or through more complicated interdependence paradigms (e.g., Didham et al. 2012), which take habitat loss as the core driver of the spatial changes in fragmented landscape. As the amount of natural habitat throughout the landscape was fairly consistent over the study period, it is likely that interactions between the time delayed fragmentation mediated responses and historical LULC will be relatively unimportant to TIL studies. This result will facilitate direct comparison with other truly experimental systems, in which landscape context is controlled throughout the study period, but will limit the usefulness in applying lessons learned at the TIL to real world habitat fragmentation, which is a dynamic process.

4.2 Current landscape pattern

TIL is a severely fragmented landscape. In my study area more than half of the islands were less than 1 ha and nearly all are less than 100 ha (Fig. 10). However, distance to mainland and nearest islands also presented a strongly right skewed distribution (Figs. 11 and 12), suggesting that most islands are relatively close to each other and source populations. This distribution helps explain many of the patterns observed in the TIL system, in which area effects have nearly always dominated isolation effects. For example, on the species level Wang et al. (2010, 2012b) showed that both lizard and snake communities were nested across gradients of area but not isolation. Hu et al. (2011) showed that island area was the primary driver explaining the nestedness of plant communities, although the nestedness of both herbs and shade intolerant plants were impacted by isolation. Si et al. (2015) showed that the beta-diversity of birds and lizards was area, not isolation, dependent, and Si et al. (2014) showed that the immigration and extinction rates of birds were similarly area, not isolation, dependent. On the functional level, Ding et al. (2013) showed that the functional evenness of bird communities was correlated with island area, and Su et al. (2014) showed that edge effects, which impact small islands more than large islands, altered plants communities at the functional level. On the genetic level, Zhang et al. (2012) observed that the genetic diversity of a tree species was impacted by habitat loss, not habitat fragmentation *per se*. Though there are some notable exceptions (for example, Wang et al. (2012a) showed that the dispersal of frogs was limited by island isolation and Yu et al. (2012) showed that although isolation has little impact on species richness, it was a meaningful predictor of community composition), results from TIL are not in opposition to the hypothesis that habitat loss is the dominate cause of fragmentation-mediated biological responses.

It should be noted, however, that TIL is a unique system. My complete census of islands in the Jeishou Archipelago (where nearly all the aforementioned studies were carried out) showed that island area varied on the order of tens of millions of m^2, while distances to mainland and distances to nearest neighbor only varied on the order of the thousands of m. Therefore, the dominance of area effects and the absence of isolation effects when measured at the patch level should not be particularly surprising and should not be treated as the "rule" when applying the TIL's lessons to conservation planning. Further study on systems with more balanced variation in area and isolation are needed to fully understand the interplay between area and isolation on patch communities.

4.3 The Relationship Between Habitat Loss and the Spatial Configuration of the Resulting Landscape

One of the great debates in the biological literature concerns the relationship between habitat loss and landscape configuration. Since Fahrig's (2003) seminal work, countless studies have attempted to partition the effects of habitat loss and habitat fragmentation *per se* as if they were independent of each other. This framework was countered by Didham et al. (2012), who pointed out that changes in landscape structure that occur during fragmentation are caused by, not independent of, habitat loss.

On a fundamental level Didham et al. (2012) is correct: had humans not altered the landscapes of Chun'an County the area would, presumably, be a contiguous forest with little spatial partitioning of patches. Therefore, the modern-day configuration of the landscape is a result of habitat loss. However, as pointed out by Fahrig (2003), habitat loss can take on a great many spatial forms. Therefore, the connection between habitat loss and the spatial configuration of the landscape is not direct, but rather interactive with the socio-economic pressures and development policies shaping the spatial components of habitat loss. Here I saw relatively little habitat loss over the study period, but documented significant changes in habitat fragmentation *per se* driven by land-use intensification (e.g., the loss of small farms, growth of large farms, and growth of urban areas). Failing to take these forces into account would have relatively little impact on studies which cover a single time period, as landscape configuration is not changing. However, applying models which assume a direct relationship between habitat loss and the altered spatial configuration of the landscape across time-sets could lead to the attribution of fragmentation-mediated changes in biological communities to habitat loss when they actually arise from changes in landscape structure driven by socio-economic forces.

5 Conclusion

Habitat fragmentation, the loss of habitat and spatial isolation of remnant patches (Wilcove et al. 1984, Wu 2009, Didham 2010), has long been considered to be one of the most serious threats to biodiversity at a global scale. However, despite the fact that fragmentation's effects can take years or decades to become apparent (Collins et al. 2017), few studies have explicitly quantified both historical and current day landscape patterns for their study regions. Here I performed such a work in a severely fragmented landscape, Thousand Island Lake, China. I found that landscape composition has varied little, but landscape configuration has changed significantly. Given that the impacts of habitat loss are considered to be far more important than habitat fragmentation *per se* (Fahrig 2003), and that most studies in TIL have found area effects to be far more important than isolation effects, I doubt that historical land-use-land-cover change will be an important driver of biological dynamics on TIL remnants. It is my hope that this work will be a foundational component of future study in the TIL region, providing both accurate quantifications of current landscape patterns and historical landscape context.

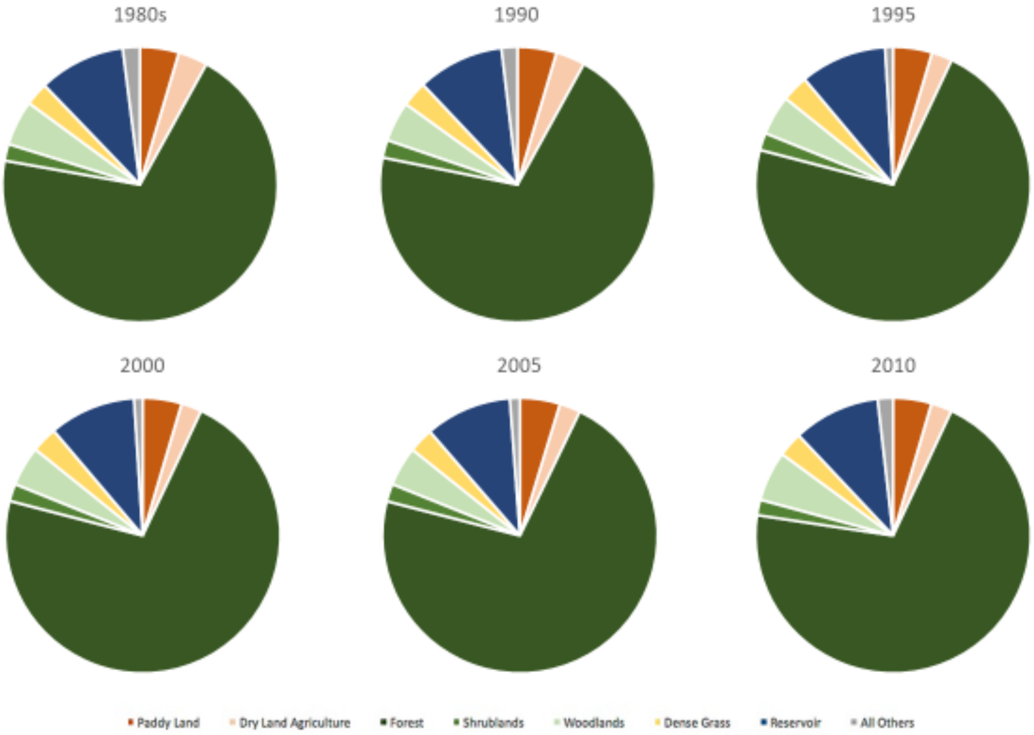


Figure 4. Landscape composition of Chun’an County from the 1980s to 2010.

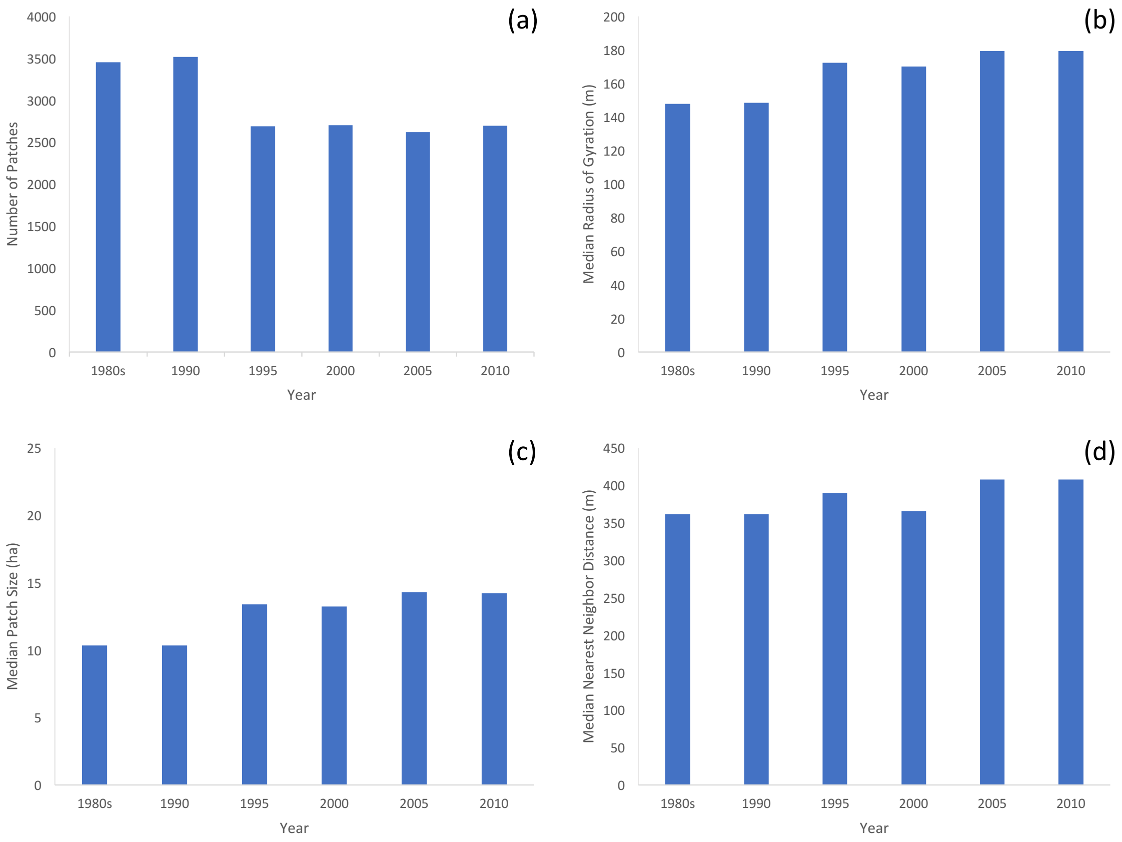


Figure 5. Landscape level configuration metrics for Chun’an County from the 1980s to 2010.

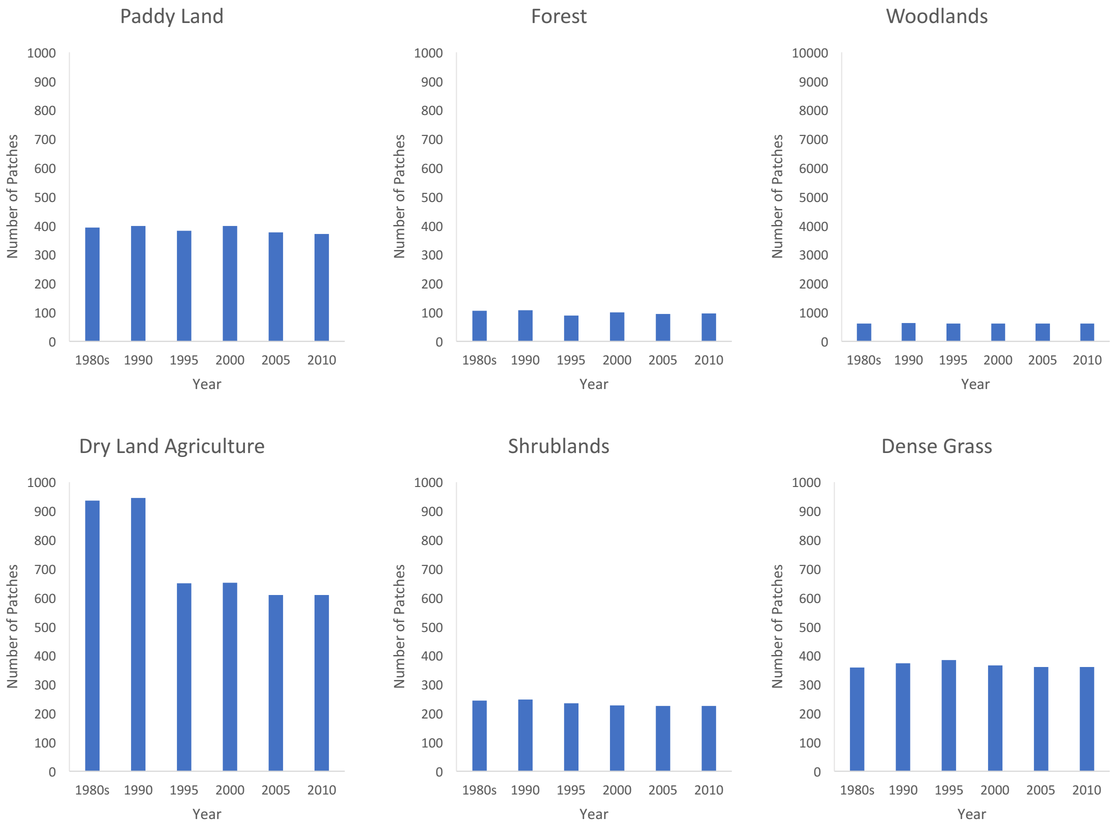


Figure 6. Number of patches for the six most common land-use-land-cover classes in Chun’an Country from the 1980s to 2010.

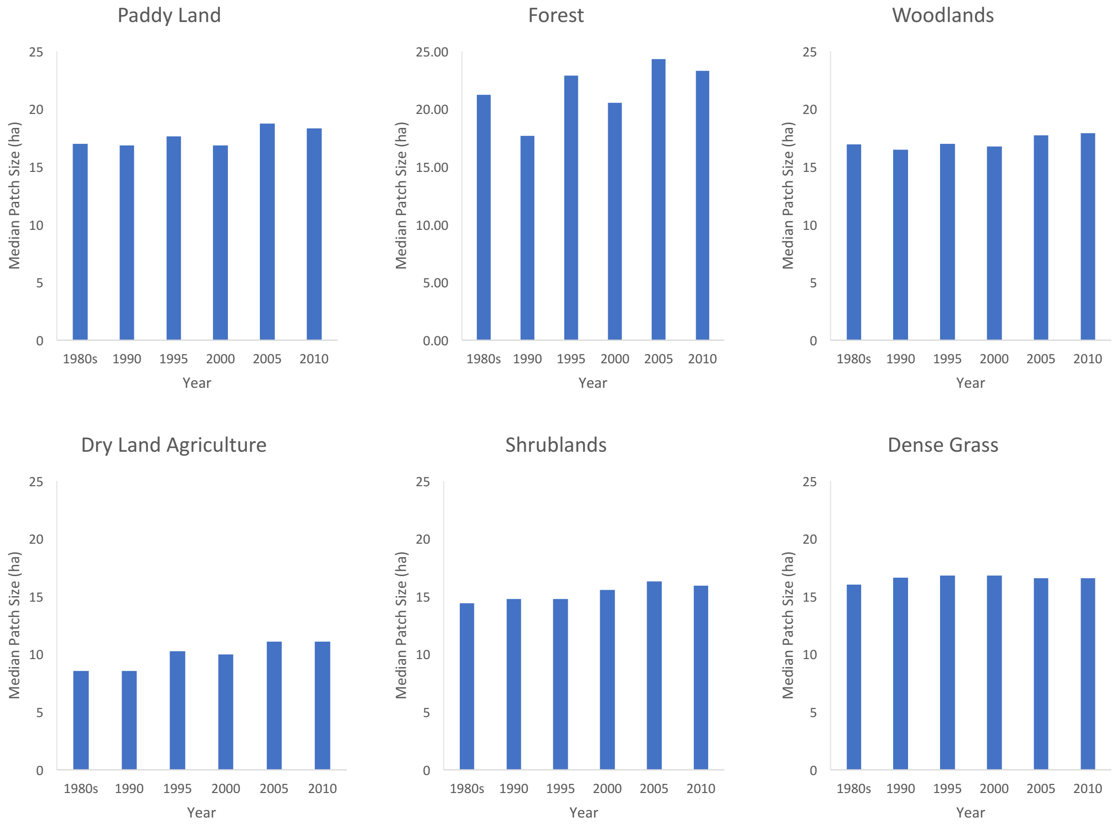


Figure 7. Median patch size for the six most common land-use-land-cover classes in Chun’an Country from the 1980s to 2010.

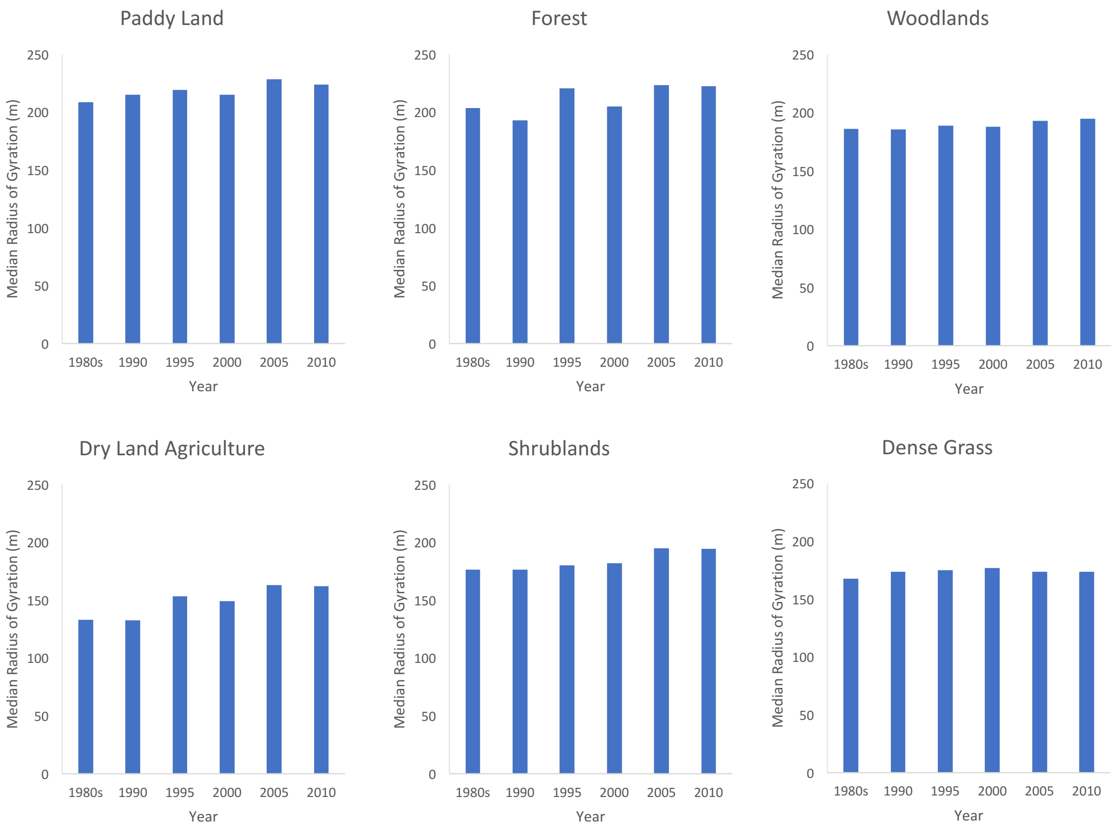
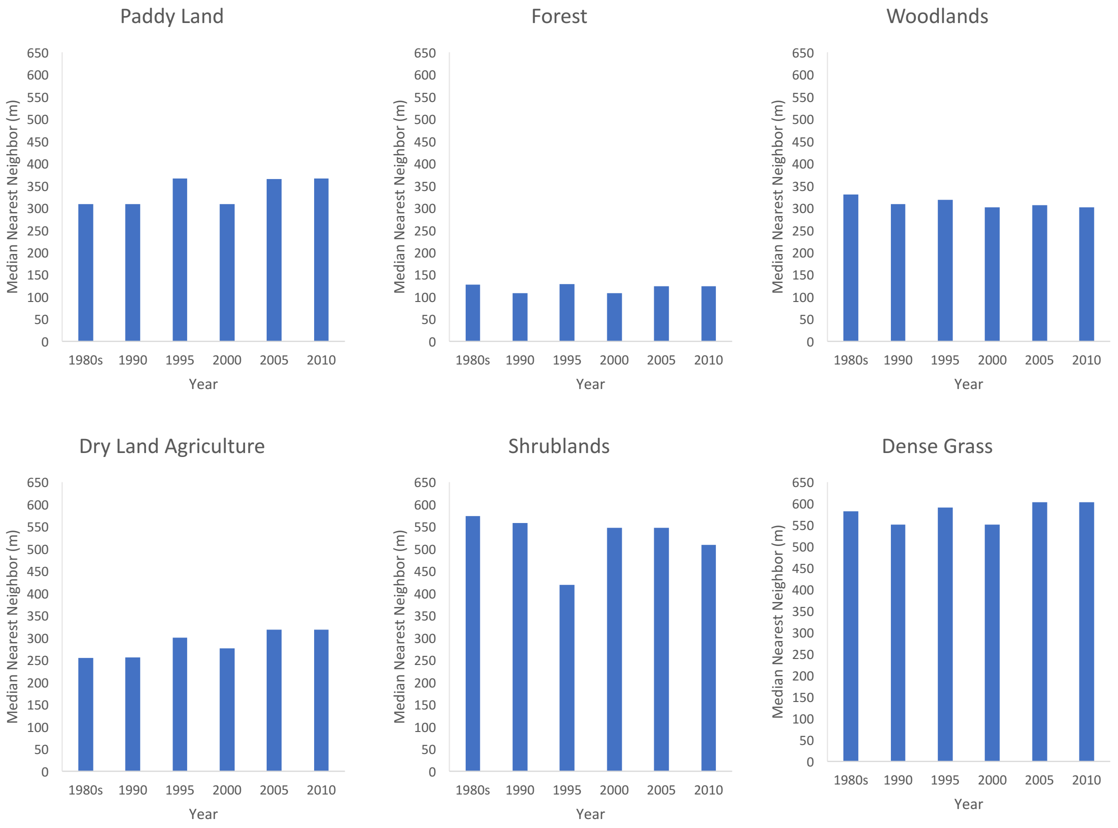


Figure 8. Median radius of gyration for the six most common land-use-land-cover classes in Chun'an Country from the 1980s to 2010.



Paddy Land

Forest

Woodlands

Dry Land Agriculture

Shrublands

Dense Grass

Figure 9. Median nearest neighbor distance for the six most common land-use-land-cover classes in Chun'an Country from the 1980s to 2010.

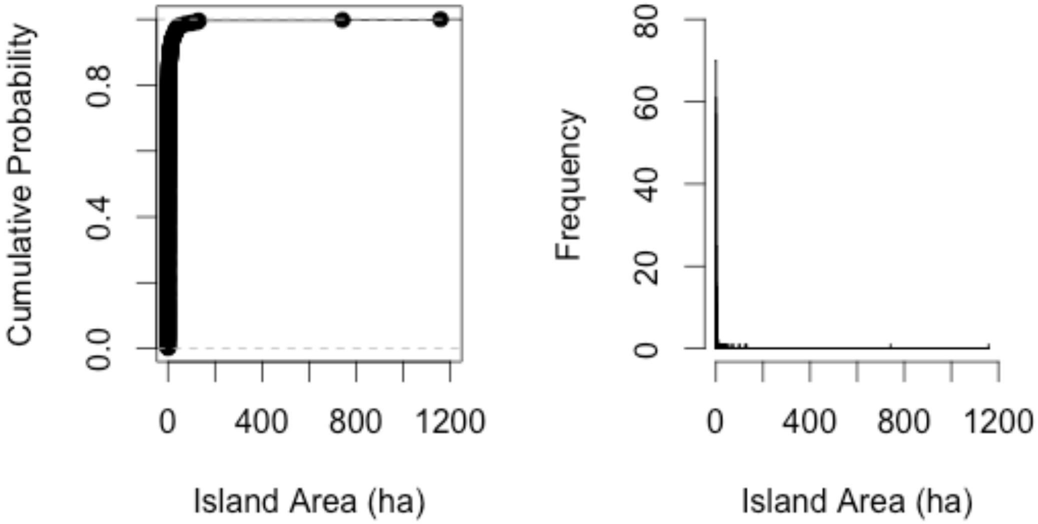


Figure 10. Empirically derived cumulative probability function (left) and histogram (right) of 504 island areas in central Thousand Island Lake.

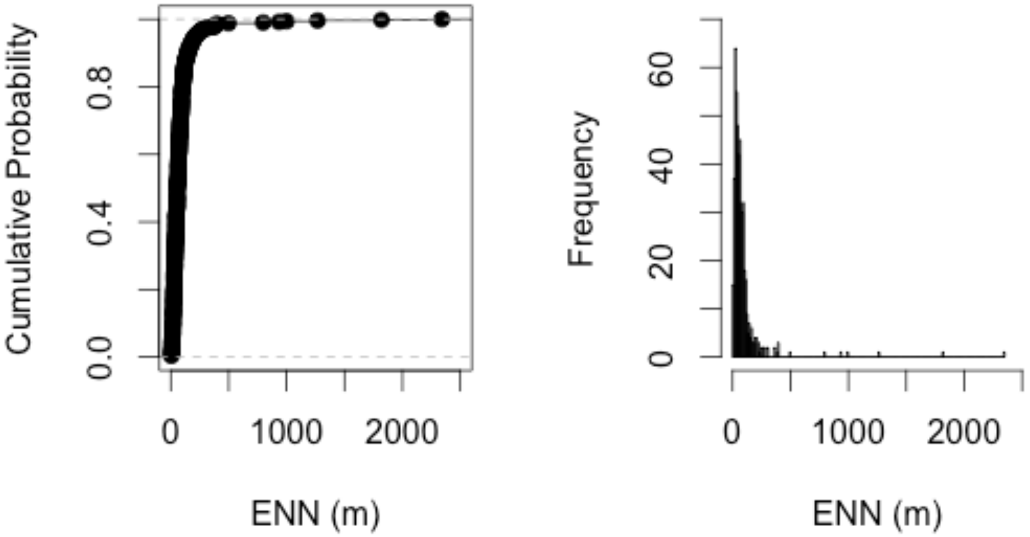


Figure 11. Empirically derived cumulative probability function (left) and histogram (right) of Eigen nearest-neighbor (ENN) distances for 504 islands in central Thousand Island Lake.

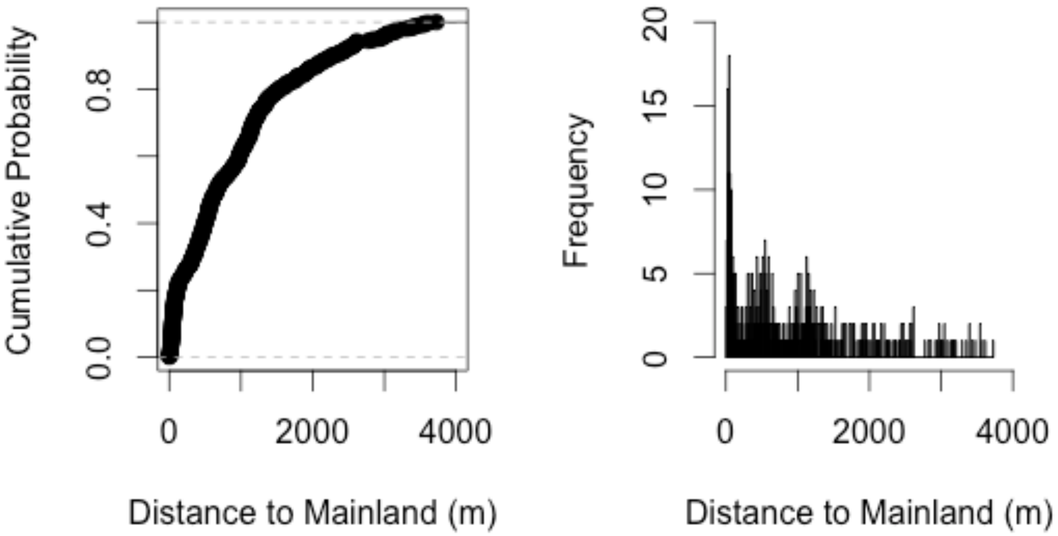


Figure 12. Empirically derived cumulative probability function (left) and histogram (right) of distance to mainland for 504 islands in central Thousand Island Lake

CHAPTER 3: NO ISLAND IS AN ISLAND: ASSESSING HABITAT FRAGMENTATION'S HIERARCHICAL EFFECTS ON SPECIES DIVERSITY AT MULTIPLE SCALES IN THOUSAND ISLAND LAKE CHINA

1 Preface

As discussed in Chapter 1, one of the most significant challenges in the study of fragmentation is that it has been studied at a variety of scales. In this chapter I test the hypothesis that habitat fragmentation impacts biological communities by creating selective pressures which are hierarchically structured by comparing communities across plot-, island-, and landscape-scales at the species level.

2 Methods

2.1 Plot-Scale Effects

Plot-scale effects were measured as the difference in α- and β-diversity between edge and interior plots. α-diversity was measured using two complementary processes: first, as the difference in α-diversity between edge and interior plots regardless of island identity using Wilcoxon test, and second, as the difference in mean α-diversity, paired by island for islands large enough to contain both edge and interior plots using a paired Wilcoxon test. As using average pairwise comparisons of community composition can be misleading (Baselga 2013), β-diversity was measured using the Sorensen form of

Baselga's multi-site dissimilarity index (Baselga 2010, 2017). Baselga's multi-site β-diversity assesses the variation in community composition within a group and decomposes these dissimilarities into their nestedness and turnover components. Multi-site dissimilarities were assessed using the 'betapart' package (v. 1.4-1) in R (v. 3.02-3.4.0). Because computing multi-site dissimilarities requires equal sample sizes, the number of edge plots selected had to be reduced to the maximum number of interior plots (n = 23). This procedure was done using the function 'beta.sample,' which iteratively and randomly samples sites to provide dissimilarities for each sample. To assure accuracy, this random sampling was done with 100 iterations, and multi-site beta-diversity was taken as the average of these 100 random samples. To assure that my results were not skewed by using presence/absence data, I also repeated this analysis using abundance-based data (see Appendix B).

To measure the effect of island size on plot-level community composition, I first divided islands into small and large groups, using the 1 ha line of demarcation described above. The difference in plot α- and β-diversity for small and large islands was then assessed using the same methods described above for measuring edge effects. In this case sample size had to be limited to the number of plots on small islands (n = 28).

2.2 Island-Scale Effects

The effects of habitat fragmentation on woody plant communities at the island-scale is well studied in the TIL system (e.g., Hu et al. 2011, Yu et al. 2012, Hu et al. 2016). These works have almost universally found that area effects dominate the response of plant communities to habitat fragmentation (see Wilson et al. 2016). Further, Hu et al. (unpublished data) and Liu (2017) both found that woody plant communities on small islands were less similar to one another than large islands were to one another. Rather than replicating this deep literature, I elected to simply create a semi-log species-area curve, as it was a necessary component for the analyses described below.

Due to the lack of high quality remote sensing imagery, few studies have explored the impact of the surrounding landscape on TIL islands beyond relatively coarse isolation metrics (e.g., distance to nearest island, distance to nearest neighbor). Therefore, I elected to quantify the impact of landscape composition and configuration on island-scale species richness after first controlling for island size using the GIS database created in Chapter 1. To do so I selected three landscape metrics: 1) Percent habitat in the landscape, 2) Landscape shape index, and 3) Coefficient of variation of habitat patch size. These indices were selected to represent landscape composition, aggolmeration, and diversity, respectively. Each of these metrics was measured for landscapes within 500, 1000, 1500, 2000, 2500, and 3000 m buffers around each island using FRAGSTATS 4.2 (McGarigal et al. 2012). For the purposes of my study I considered all patches within the lake as potential habitat. When buffers overlapped with the mainland, mainland habitat and matrix patches were classified using an unsupervised classification created by Bingbing Zhou of ASU’s School of Sustainability. After intensive post-classification processing, which resulted in a classification with an accuracy of 98.1%, I assessed the impact of these variables on the species richness at each buffer size after controlling for island area by calculating the residual of the semi-log species area relationship using two generalized linear models, one with each with each landscape variable as an independent variable and simplified model which only included the amount of habitat in the landscape. Model performance was assessed using the Akaike Information Criterion (AIC) (Akaike 1973), which gives a measure of model performance but also penalizes models which include variables that negligibly add to model fit (Johnson and Omland 2004) So that these metrics are available for future studies of TIL I have included them in Appendix A.

2.3 Landscape-Scale Effects

An assessment of landscape-scale effects requires controlling for the total amount of habitat in the landscape (Fahrig 2017). To do this I performed a single-large or several-small (SLOSS) analysis, comparing two sets of virtual landscapes, one created by aggregating both island area and species richness from the smallest island to the largest island, and another created by aggregating from the largest island to the smallest island. Such analyses are commonly used to study the landscape-scale effects of habitat fragmentation (Fahrig 2017), resulting in two dichotomous extremes, with the small to large aggregation representing the virtual landscape which has undergone the most habitat fragmentation *per se*, while the large to small aggregation has undergone the least habitat fragmentation *per se* for any given amount of habitat.

3 Results

3.1 Plot-Scale Results

When comparing edge plot and interior plots without controlling for island identity, edge plots tended to have fewer species than interior plots (p = 0.03, Fig. 13a). However, when comparing mean plot species richness paired by island, this difference became negligible and statistically insignificant (p = 0.56, Fig. 13b). Further edge and interior plots were approximately equally dissimilar to one another (β_{sor} = 0.83 vs. 0.81, Fig. 14a). β-diversity was primarily dependent on turnover, not nestedness, between plots, though the proportion of total β-diversity caused by the nestedness was 42% higher in edge plots than in interior plots. These results did not change when β-diversity was assessed using abundance-based metrics, though nestedness became slightly more important when β-diversity was measured using abundance metrics compared to presence/absence metrics (Appendix B).

Island size had a weak positive effect on plot species richness (Spearman's rho = 0.40, p = 0.04). Further, plots on large and small islands were approximately equally dissimilar from one another (β_{sor} = 0.84 vs. 0.85 for plots on large vs. small island, respectively, Fig. 14b). Similar to edge vs. interior comparisons, plot β-diversity was primarily dependent on turnover, not nestedness, between plots, with the nestedness component making up between 7-8% of total β-diversity. Again, similar to edge vs. interior comparisons, these results did not change when β-diversity was assessed using compositional metrics, though nestedness became slightly more important when β-diversity was measured using abundance metrics compared to presence/absence metrics (Appendix B).

3.2 Island-Scale Results

As expected, island species richness significantly increased with island area ($R^2 = 0.73$, $p < 0.001$, Fig. 15).

I found that the inclusion of landscape configuration metrics did not improve the ability of my models to predict residual island species richness at any scale (Table 1), and therefore I elected to utilize a simplified regression model that excluded configuration metrics (e.g., Fig. 16b). In doing so I found that residual species richness was positively correlated with the amount of habitat surrounding each island (Table 1). This effect was strongest at the 1000 m buffer size, however, it was still detectable at the 500 and 1500 m buffer size, with somewhat small differences between the 500 and 1000 m buffers (Table 1). In no buffers was the percent habitat in the landscape correlated to the island size (Spearman's rho range: -0.07 to 0.16, p-value range: 0.42 to 0.96 for all buffer sizes).

3.3 Landscape-Scale Results

When total habitat was controlled, virtual landscapes consisting of small islands had more species than virtual landscapes of large islands (Fig. 17). Further, the shape of the species-accumulation curves were far different from one another, with the smallest to largest agglomeration presenting a roughly logarithmic curve and the largest to smallest agglomeration presenting a roughly exponential curve until nearly all species in the regional pool were accounted for. Therefore, the most rapid periods of species accumulation (as a function of total habitat area) occurred when relatively small islands were added to the virtual landscape regardless of aggregation method.

4 Discussion

4.1 Scale Specific Results

Though designed to show the scale-dependence of fragmentation-mediated effects on biological communities, my study revealed several interesting results within each scale.

At the plot-scale, I found that edge effects slightly reduce species richness when island identity is ignored but have no effect when edge and interior plots within a given island are compared (Fig. 13). This suggests that the plot-level declines in edge plot species richness represent a cross-scale effect on plot species richness caused by island size. This is reinforced by my finding that plot species richness is positively correlated with island area. Further, I found that plots on large islands were no more different from one another than plots on small islands were from one another, despite the fact that large islands contained both edges and interiors. This finding is dissimilar to results from the Biological Dynamics of Forest Fragments Project (BDFFP), which found that edge areas had significantly higher turnover rates than interiors (Laurance et al. 2006). One possible explanation for this result is that habitat heterogeneity between plots on small islands and plots on large islands was approximately equal, which is reasonable given that plots were aggregated by island size regardless of their location in space. However, the proportion of β-diversity due to nestedness increased by 42% in edge plots relative to interior plots and nestedness was always a larger component of beta-diversity when measured using abundance based, rather than presence-absence based, metrics (Appendix B). This suggests that edge-mediated non-random biodiversity loss is stronger in edge, rather than interior, areas and at the individual, rather than species, level. This disparity could occur because some species continue to persist in small numbers in edge plots but cannot establish robust populations there, suggesting that some amount of edge-mediated species sorting is occurring. In contrast, I found that plots on large islands were no more different from one another than plots on small islands were from one another, despite the fact that large islands contain both edge and interior areas. This is also dissimilar from many studies of fragmentation, which have shown large differences between edge and interior communities (see Murica (1995) for details and other idiosyncrasies in the edge-effect literature). However, this result may be due to my relatively coarse grain of analysis (400 m^2 plots), as Liu (2017) found a weak positive effect of island size on intra-island β-diversity when working at smaller spatial grains (25 m^2 plots). Further, Hu et al. (unpublished data) and Liu (2017) found that communities on small islands were more different from one another than communities on large islands. These findings could be viewed as disagreeing with my results, however, this is actually a classic scale-effect, as comparing plots *within islands* to one another is a comparison across a gradient of proportional edge, while comparing *islands* to one another is a comparison across a gradient of island size, and therefore richness.

I also found that the landscape surrounding each island had an effect on island species richness. However, I did not find that including landscape configuration variables meaningfully increased the predictive power of my models. Therefore, I elected to simplify my model. This finding is in broad agreement with Fahrig's (2003) classic review, which found that fragmentation *per se* is a weak control of fragmentation-mediated effects on biological communities relative to habitat loss at any particular time step. However, it is important to note that my model simplification was done not because I ignore the indirect effects of habitat loss through time (e.g., Didham et al. 2012, Fig. 6a), but because configuration metrics from my specific case did not add to the explanatory power of my models. Had the inclusion of configuration metrics significantly improved model performance, a more detailed structural equation modeling approach, such as that suggested by Didham et al. (2012) and shown in Fig. 6a, would have been appropriate.

Finally, by comparing virtual landscapes of equal total habitat, I found that groups of small islands had significantly more species than groups of large islands. This finding is in agreement with Fahrig's (2017) literature review, which found this pattern to be nearly universal, and as small islands had more β-diversity than larger islands (Hu et al. unpublished data, Liu 2017) this response was expected. However, it is important to note that these virtual landscapes can only capture the results of possible habitat loss given current conditions, and cannot project how the loss of small vs. large patches would impact the long-term dynamics of the system. For example, although large patches are relatively similar to one another and groups of large patches accumulate species more slowly than groups of small patches, it is possible that these large patches may serve as important source populations for interior species. As fragmentation's effects on community composition can be time-dependent (Collins et al. 2017), it is critical that SLOSS findings are confirmed through experiments which monitor fragmentation-mediated responses through time before they be integrated into conservation planning.

4.2 Habitat Fragmentation's Hierarchical Effects

My core hypothesis was that habitat fragmentation creates hierarchically nested selective pressures across plot-, patch-, and landscape-scales. By observing meaningful variation in biological communities, across and between all three of these levels, I found support for this hypothesis.

Studying community responses at all three scales simultaneously had a significant impact on the interpretation of my results. Had my study simply focused on patch and sub-patch processes, I would have concluded that small patches were of little conservation value, though my landscape scale analysis showed quite the opposite. Similarly, had I focused only on the local landscape around each patch, I would have concluded that fragmentation *per se* had no measurable effect on species richness, though my SLOSS analysis suggests that habitat fragmentation *per se* could significantly alter regional diversity for any given amount of habitat loss. Therefore, it is only by studying the impacts of fragmentation simultaneously at all of these scales that I could recognize how biological communities respond to interacting gradients of intra-patch, inter-patch, and landscape-scale controls.

My study is substantially different from those which use independent variables generated at multiple scales to predict fragmentation effects at a single spatial scale (e.g., Lafortezza et al. 2010). My aim was not to quantify community controls at a given scale, but rather to establish that the impact of these controls are scale-dependent. Valdés et al. (2015) performed a somewhat similar multi-scale analysis; however, they only predicted the impact of fragmentation on plot-, patch-, and within-patch scales. Valdés et al. (2015) found at plot-, patch-, and within-patch scales that patch-scale controls were generally more important than controls occurring at higher levels. This is precisely the response predicted by the Hierarchical Patch Dynamics Paradigm (Wu and Loucks 1995). In addition to this scale dependence, the relative strength of local-, patch-, and landscape-scale controls is also likely to be context specific. For example, systems with strong local filters (e.g., edge effects in the BDFFP) will likely see more significant local and patch scale species sorting than I observed in this study. Further, systems that are significantly isolated, such as oceanic archipelagos, could see dominant controls at the landscape and inter-patch levels. In my study I observed little difference in the dissimilarity between plots across gradients of edge, though other studies have found that edge effects are detectable in the TIL system (e.g., Su et al. (2014)). My finding is reasonable, as TIL is a secondary, assembling, sub-tropical forest, which is likely much more edge adapted than tropical forests, such as those studied at the BDFFP. This species-level analysis would benefit from replication at the functional-level, as unequal richness within functional groups (e.g., unequal numbers of shade-tolerant vs. shade-intolerant plant species) could create significant noise in my results. Therefore, these findings should not be taken as a statement of primacy of one scale over another, but rather as yet another contextual example that the responses of biological communities to selective pressures vary across scales, sometimes in surprising ways.

5 Conclusion

Habitat fragmentation is a spatially and temporally dynamic process. During fragmentation loss of habitat in the landscape alters the regional species pool, creating increasingly smaller, increasingly more isolated patches. These patches sample smaller amounts of the region's biophysical space, contain fewer species to compete with one another, and are increasingly impacted by fragmentation-mediated changes in local biophysical conditions. I hypothesized that these processes interact hierarchically, with bottom up and top down effects each altering biological communities in different ways across scales. My results do not cause me to reject this hypothesis. Plots, patches, and landscapes are likely not islands unto themselves, but rather co-dependent, interacting parts of a whole, as predicted by the Hierarchical Patch Dynamics Paradigm (Wu and Loucks 1995). Future studies of fragmentation should attempt to take these hierarchical effects into account, contextualizing the impacts of fragmentation within the constraints placed on biological communities across scales.

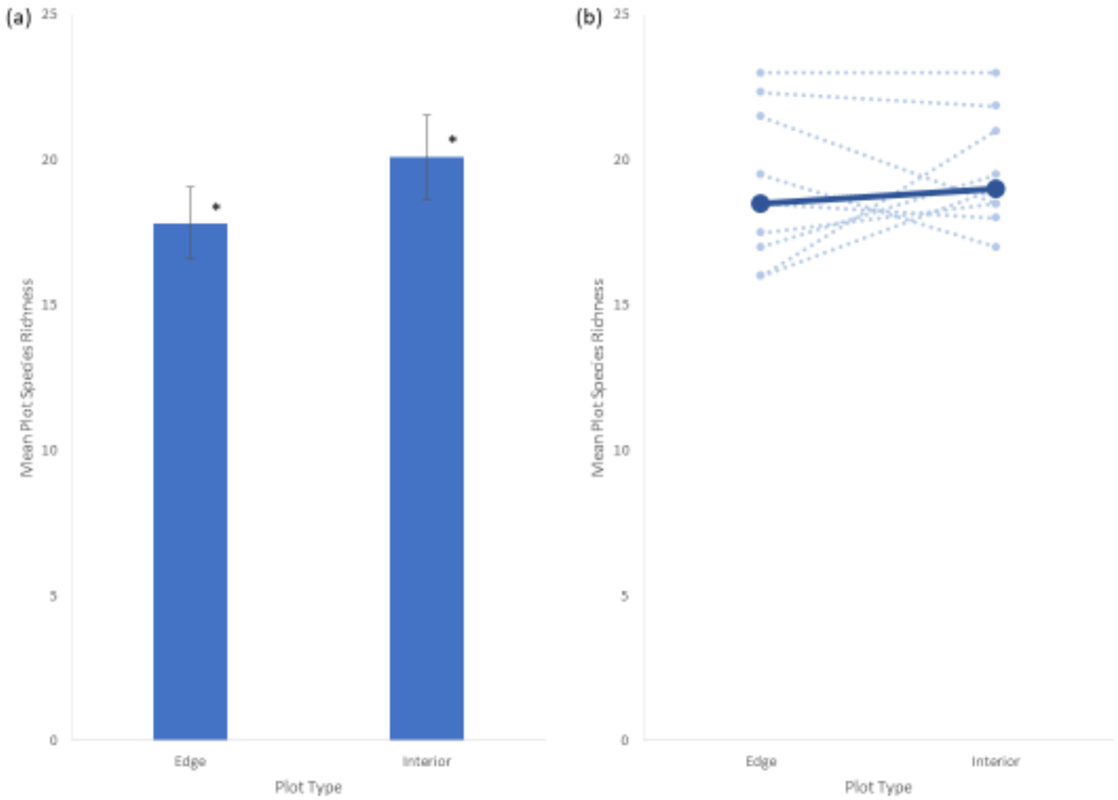


Figure 13. Mean plot species richness for edge and interior plots. (a) Mean plot species richness when all plots are pooled regardless of island identity. Error bars represent two standard errors of the mean. Asterisks represent statistical significance ($p < 0.05$) (b) Mean plot species richness of edge and interior plots paired by island. Dotted lines represent island pairs and the solid line represents the median.

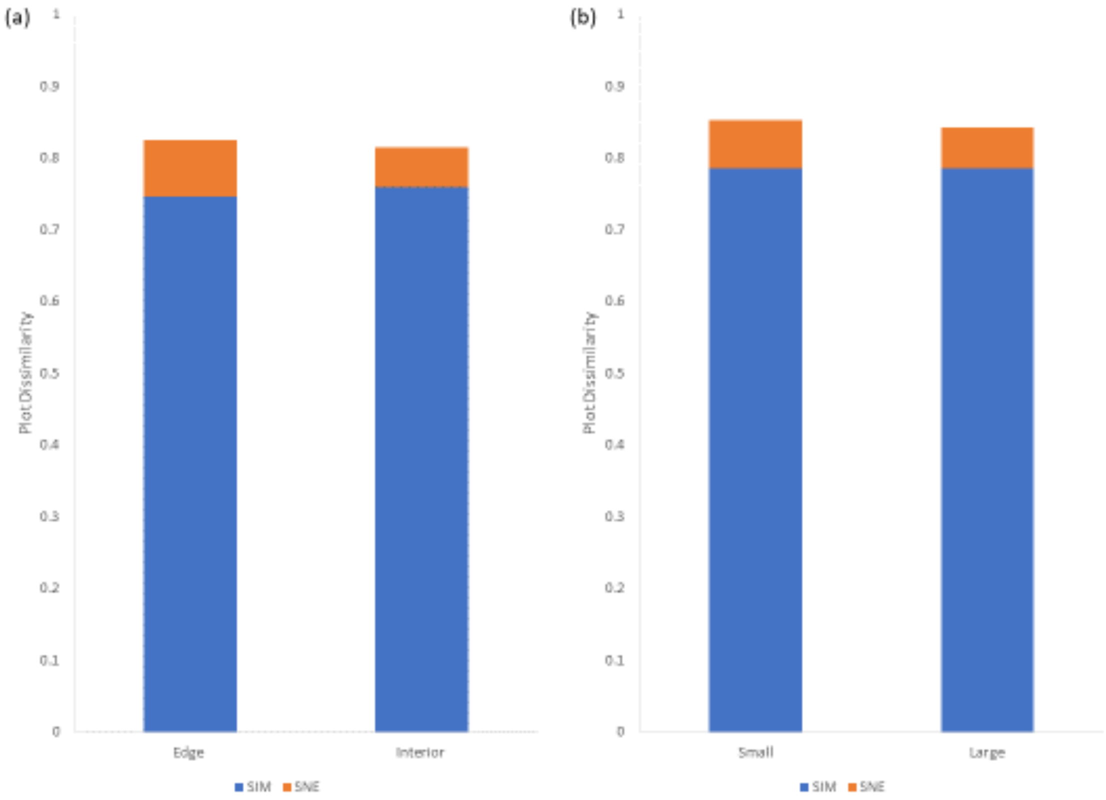


Figure 14. Community dissimilarity at the plot scale. (a) Plot dissimilarity of edge and interior plots measured using the multi-site Sorrensen family of metrics, with SIM representing the turnover component and SNE representing the nestedness component. (b) Plot dissimilarity from plots on large and small islands measured using the multi-site Sorrensen family of metrics, with SIM representing the turnover component and SNE representing the nestedness component.

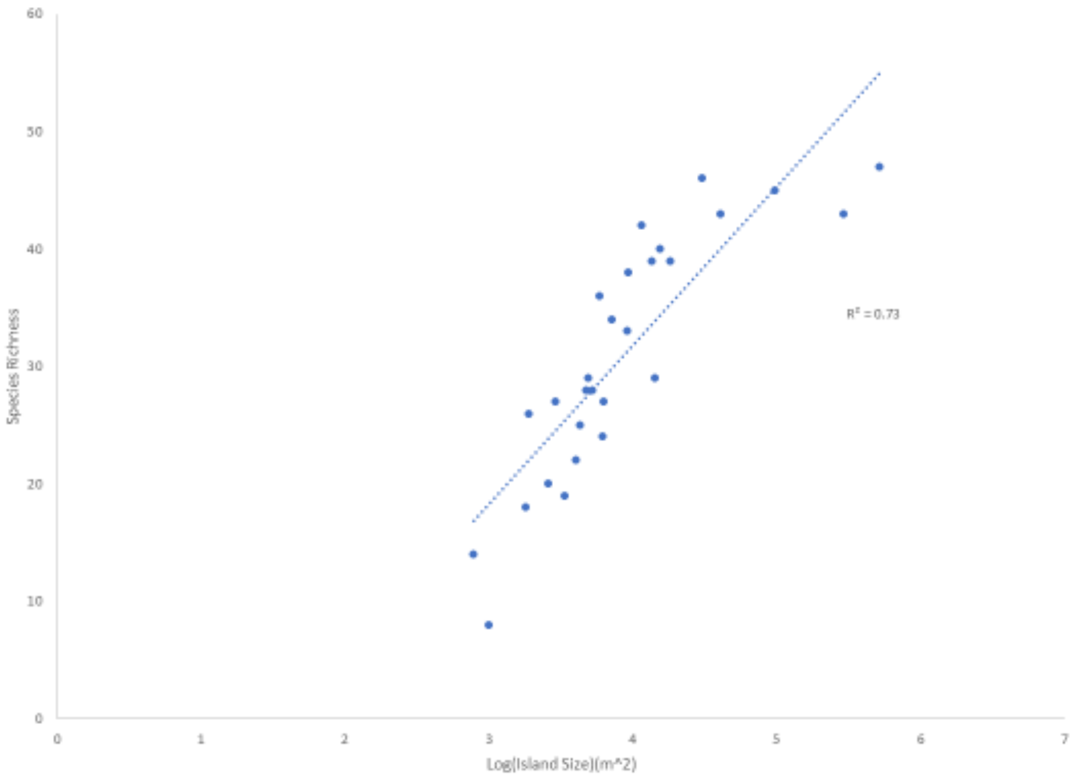


Figure 15. Semi-log species area relationship for studied islands.

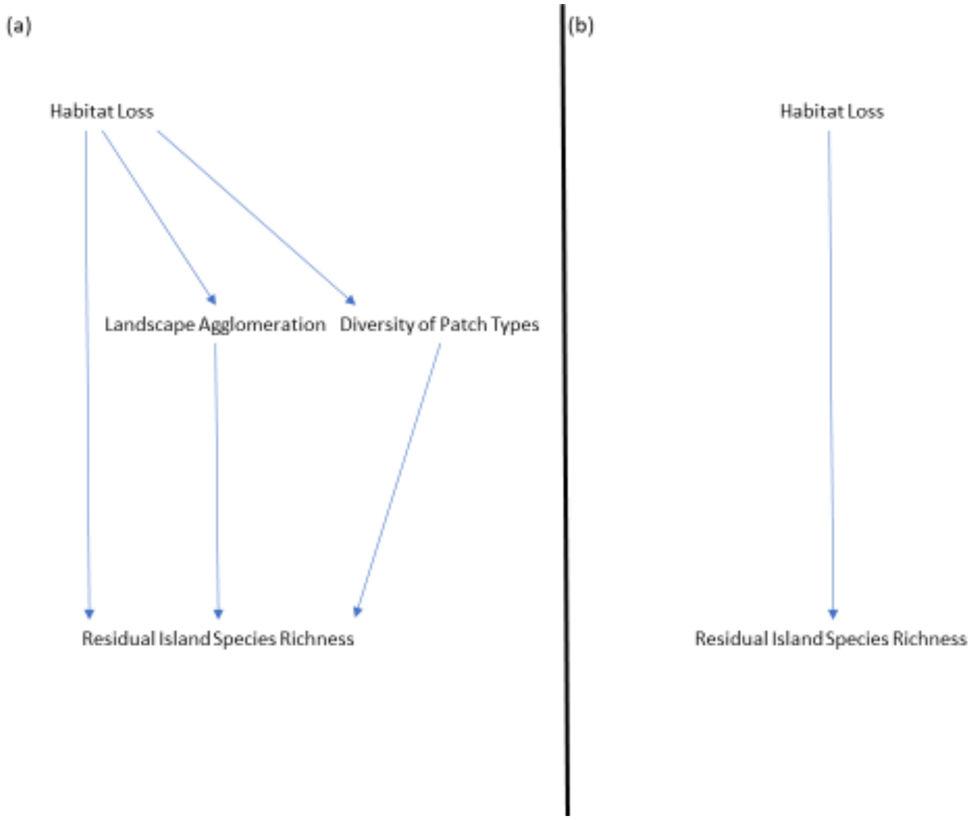


Figure 16. Two path diagrams showing potential ways in which the surrounding landscape could impact island species richness. (a) shows a path diagram in which habitat loss, the agglomeration of habitat, and the diversity of patch sizes surrounding each island have a direct effect on species richness, while habitat loss drives the agglomeration of habitat and the diversity of patch sizes in the surrounding landscape. (b) Shows a simplified model, where habitat composition, but not configuration, in the surrounding landscape has an impact on island species richness.

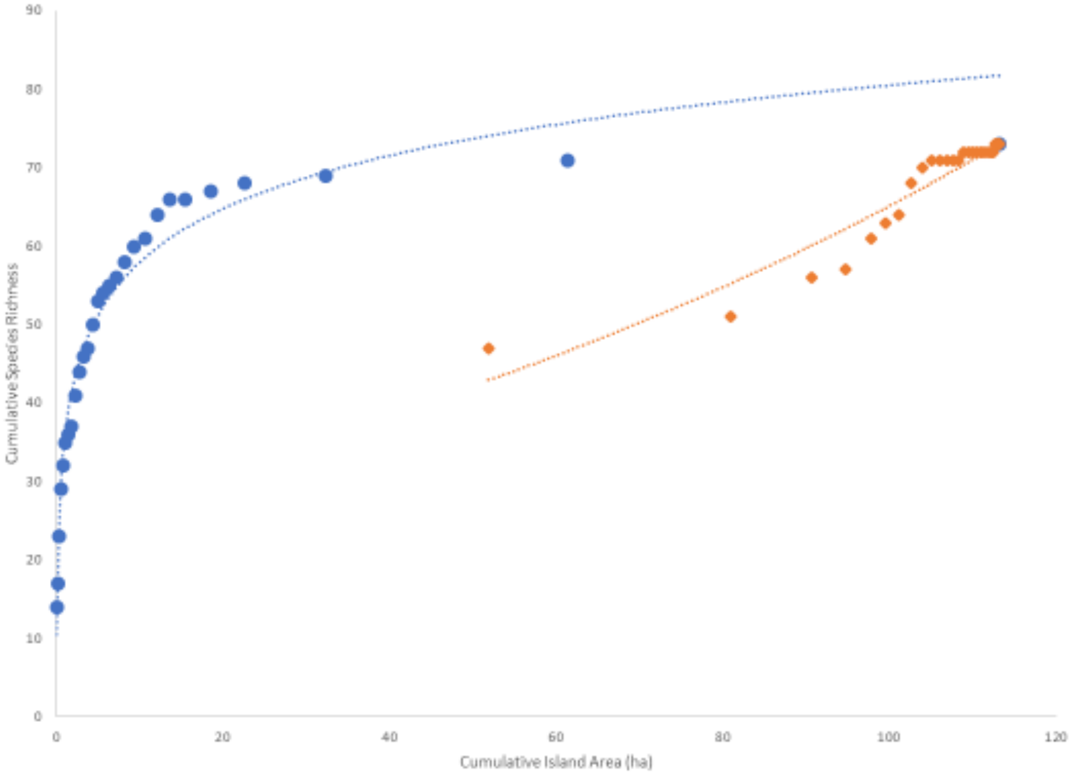


Figure 17. Accumulated species richness in two sets of simulated landscapes, one created by aggregating from the smallest to the largest island (blue circles), the other created by aggregating from the largest to the smallest island (orange diamonds). Fitted lines are logarithmic and exponential functions for the small to large and large to small data series, respectively.

BUFFER SIZE (M)	MODEL TYPE	PERCENT HABITAT IN LANDSCAPE	LANDSCAPE SHAPE INDEX	COEFFICENT OF VARIATION OF PATCH SIZE	AIC
500	a	**0.31**	1.03	-0.01	170.51
500	b	**0.35**			168.24
1000	a	**0.53**	-0.69	-0.02	167.29
1000	b	**0.36**			167.00
1500	a	0.32	-0.55	0.00	175.09
1500	b	**0.25**			172.12
2000	a	0.31	0.15	-0.02	177.29
2000	b	0.19			174.70
2500	a	0.33	0.55	-0.02	178.54
2500	b	0.14			176.70
3000	a	0.35	0.91	-0.01	179.63
3000	b	0.07			177.94

Table 1. Results from generalized linear models, comparing the impact of three landscape variables on species richness for each island across six landscape sizes. Model type refers to the models identified in figure 16. Parameters shown are the slope for each variable, at each scale in the final step of the model (e.g., predicting residual island species richness). Bold parameters are statistically significant ($p < 0.05$).

CHAPTER 4: SEEING THE FOREST THROUGH THE TREES (AND SHRUBS): AN ANALYSIS OF HABITAT FRAGMENTATION'S IMPACT ON THE FUNCTIONAL COMPSITION OF FORESTS ACROSS SCALES

1 Preface

MacArthur and Wilson's IBT was a far-reaching accomplishment that dominated the early study of habitat fragmentation. However, IBT's focuses only on the species-level, and we know relatively little about how fragmentation alters other forms of biodiversity. In this chapter I apply the hierarchical framework assessed in Chapter 2 to the functional-level, analyzing how and why habitat fragmentation alters the functional composition of forests across scales.

2 Methods

2.1 Division of Plants into functional groups

Plants were divided into functional groups using two functional traits, lifeform and shade-tolerance. These functional traits were selected because they are known to be tightly connected to fragmentation-mediated changes in biodiversity (e.g., Laurance et al. 2011) and for ease of interpretation relative to more quantitative, hard-trait based approaches. This resulted in four functional groups, shade-tolerant trees (STT), shade-intolerant-trees (SIT), shade-tolerant shrubs (STS), and shade-intolerant shrubs (SIS) using the functional trait information found in the supplementary materials of Hu et al.

(2011). Four species had to be removed from the analysis, three because they did not appear in Hu et al. (2011) and one because it was classified as an herb. Each of these species was extremely rare, cumulatively only 30 individuals for all four species, and thus their removal should have very little impact on the results described here.

2.2 Multi-Scale Analysis

The functional composition of each community at each scale was derived as the proportion of each functional type of each community in each plot, island, or virtual landscape. This partitioning was done twice for each community at each scale, once using richness data and again using abundance data. Differences between edge and interior plots were assessed using two complementary methods. First, all edge plots and all interior plots, respectively, were pooled regardless of island identity, and differences in the proportion of each group in each plot type were assessed using Wilcoxon rank sum tests. Second, in islands that were large enough to contain both edges and interior plots, the proportions of each functional group in edge plots and interior plots were first averaged and then differences in proportion within each island were as assessed using a paired Wilcoxon rank sum test. Correlations across gradients of island size were assessed using Spearman-Rank Correlation Tests. At the landscape-level I performed two single-large-or-several-small (SLOSS) analyses. First, I completed a traditional SLOSS analysis for each species within functional group, whereby two virtual landscapes were created, one in which habitat area and species are accumulated from the smallest to the largest island, and another where species are accumulated form the largest to the smallest island.

Second, I analyzed how the functional composition of each virtual landscape differed by measuring the proportion of each functional group in each aggregated community as a functional of total accumulated area. Because there is no abundance-based parallel for SLOSS analyses, my landscape-level results were limited to richness only.

3 Results

At the plot-level, I used two complementary analyses to discern possible edge effects, first comparing edge plots to interior plots regardless of island identity, and second by comparing edge and interior plots within an island to one another. Using the pooled method, I found that interior plots contained higher proportions of STT and lower proportions of SIT whether measured using richness or abundance metrics (Figs 18 and 19; STT_{abund} $p = 0.008$, STT_{rich} $p = 0.001$, SIT_{abund} $p = 0.006$, SIT_{rich} $p = 0.02$). In contrast, the proportion of the community consisting of shrubs were not related to plot type ($p > 0.05$), with the notable exception of a higher proportion of STS occurring in edge plots when measured using richness (Fig. 19 $p = 0.02$). These results were generally consistent when edge effects were measured by comparing paired plots within an island to one another using a paired Wilcoxon rank-sum test (Figs. 20-21), with a single important exception: the proportion of STT was not responsive to edge effects when measured on islands which contained both edge and interior plots (Figs. 20-21). Island size also had an impact on plot composition. The proportion of the plot community consisting of STS was positively correlated with island size when using abundance measures (Fig. 22 $p = 0.04$), but not richness (Fig. 22, $p = 0.82$). Similarly, the proportion of the plot community consisting of SIT was negatively correlated with island size when using abundance measures (p = 0.04), but not richness measures (p = 0.52). The proportion of the plot community consisting of SIS and STT were not related to island size whether measured using abundance or richness metrics (Fig. 22, p = 0.98 and 0.21, p = 0.06 and 0.78, respectively).

Island size also had a marked impact on island-scale community composition (Fig. 23). Island size was positively correlated with the proportion of STT when measured using abundance measures (p = 0.01), but not richness (p = 0.50). In contrast, island size was positively correlated with the proportion of STS when measured using richness measures (p = 0.0007), but not abundance measures (p = 0.12). Island size was negatively correlated with the proportion of SIT whether using richness or abundance measures (p = 0.03 and 0.001, respectively). Island size was not correlated with the proportion of SIS whether using richness or abundance measures (p = 0.34 and 0.91, respectively).

On the landscape-scale, I found somewhat idiosyncratic results. For all functional groups virtual landscapes consisting of several small islands contained more species than virtual landscapes consisting of an equal amount of habitat derived from large islands (Fig. 24). However, aggregation method did have a marked effect on the community composition of virtual landscapes. When the amount of habitat in the virtual landscape was low (e.g., only very small islands sampled) community composition was markedly different, with unexpectedly high proportions of SIT and low proportions of STT (Fig. 25). When the amount of habitat in the virtual landscape was high, above approximately 10 ha total habitat, the composition of the aggregated community stabilized (Fig. 25).

4 Discussion

Ecologists have long recognized that habitat fragmentation can alter biological communities at local-, patch-, and regional-scales. Further, it has long been established that habitat fragmentation does not impact all types of biota equally. However, while both these issues have been extensively studied independently, relatively few studies have taken an multi-scale approach while also differentiating between functional clades. This type of analysis is critical because identifying how the responses of biota diverge from one another is an important stepping stone in mechanistically disentangling how the effects of habitat fragmentation vary and interact with one another. Here I performed such a work, identifying local-, patch-, regional- and cross-scale impacts of habitat fragmentation across four plant functional types.

Taking a multi-scale, multi-clade approach had significant impact on the interpretation of my results. On the local level, I found a clear increase of STT in interior plots relative to edge plots. When using a pooled approach, where all edge plots and interior plots were compared regardless of island identity, I found that proportions of SIT plants increased in edge areas (Figs. 18 and 19). However, when controlling for island identity using a paired method, this pattern was not apparent (Figs. 20 and 21). Despite this result, the proportion of SIT in both plots and on the entire islands was negatively correlated to island size (Fig.

22). This suggests that STTs exhibit a true edge effect, while the declines of SITs at both the plot and island scale is in fact an island-scale effect. This distinction would not have been possible without carrying out my study at both local and island scales. Liu (2017) and Liu et al. (2018) found a similar result, with Liu et al. (2018) concluding as part of their broader analysis of secondary successional dynamics in TIL that edge effects controlled species composition in islands large enough to contain interiors, while island-scale patterns were likely caused by slower successional rates on small islands. My results support this view, though it should be noted that the early successional states of small islands may be caused by reduced interspecific competition, which could cause decreased mortality of early successional plants, as shown in Liu (2017). When aggregated these two complementary processes, edge selection against STT and large island selection against SIT, result in SLOSS communities which are quite different from one another when the total habitat in the landscape is small (Fig. 24), though these landscape-level community compositions did eventually stabilize. Tellingly, this stabilization point is roughly correlated to the addition of islands with an area greater than 1 ha, which has been shown to be the point at which interior areas develop in similar forests (Young and Mitchell 1994).

Importantly, these local-, patch-, and landscape-level effects interact dynamically and hierarchically through time and space. Working from the top down, my results suggest that the total amount of habitat in the landscape controls the functional composition of the regional community, and thus the types of immigrants available in the regional pool. Larger islands have more habitat types, more area to contain species, and are more likely to be colonized, thus increasing inter-specific competition and accelerating secondary succession (e.g., Liu 2017). In contrast, smaller islands are dominated by edge areas, which select against STT and contain lower levels of species diversity, reducing the likelihood that strong competitors will occur and subsequently decreasing mortality on the individual level (e.g., Liu 2017). Similarly, this hierarchy could be built from the bottom up, as the type of species that can persist in any location is constrained both by the resource requirements of that species and its ability to outcompete other species that can access local resources. The number of species competing for resources on any patch is constrained by the species-area relationship, immigration to the patch, and the heterogeneity of habitat types within the patch. In aggregate the diversity of the regional pool is defined not only by these competitive processes within patches, but also by the relative diversity of patches. Each of these processes at each of these scales occur simultaneously, but at different speeds. Processes that occur at local-scales (such as mortality) take place relatively quickly, while processes that occur at island- and landscape-scales (such as immigration and extinction) take place relatively slowly. Thus, each process actively shapes communities from the previous time-step through a combination of stochastic and deterministic processes, precisely as predicted by the Hierarchical Patch Dynamics Paradigm.

The strength of these filters will be specific to the life form, species, and to a lesser extent the individual. This can obscure their detection when studied at the species and individual levels. In Chapter 2 I found using the same dataset that, at the species level, edge effects had little impact on diversity between edge vs. interior plots and also within small vs.

large islands. However, by performing a similar analysis at the functional level, I observed significant variation in community composition at all levels of analysis. As a whole, this suggests two complementary conclusions. First, the selective pressures controlling the response of biological communities to fragmentation are hierarchically structured in space-time. Second, that this selection acts on different functional types at different levels of the hierarchy. Further, this study only examined the impacts of habitat fragmentation on woody-plants, which are obviously not mobile and thus strongly impacted by local conditions. Species which are highly mobile, such as birds, would likely be more impacted by filters at the patch- and landscape-scales than at local-scales. In contrast, specialist species will be confined to the areas where their food sources can persist regardless of their own mobility. Context is therefore a critical component in understanding the interplay between local-, patch-, and landscape-level filters.

My results also suggest that it is important to study fragmentation's impact on biological communities beyond richness. Since its inception as a field, fragmentation ecology has largely focused on richness-based responses, possibly due to the influence of MacArthur and Wilson IBT. However, as Wilson et al. (2016) pointed out, fragmentation often impacts community composition even when it does not alter richness *per se*. The vast majority of patterns in this study were only apparent when measured while taking abundance into account. My previous work in Chapter 2 attempted to integrate abundance measures at the species level into a multi-scale analysis of species diversity in TIL. However, despite finding significant species-based responses at the island- and landscape-scales, the analysis presented in Chapter 2 was not able to detect all the effects

I have identified here, possibly because of the inter-specific, intra-functional group variation discussed above. Combined with my previous results, this suggests that including abundance measures may be a necessary part of detecting fragmentation-mediated effects, but that simply including abundance measures at the species-level may not be sufficient in and of itself. Rather it is critical that data are analyzed at a level which pairs the hypothesized selective force with the predicted biological response, in this case pairing edge effects and island size to shade-tolerance and life form.

The observed landscape-scale effects are particularly important to conservation planning. A recent review by Fahrig (2017) showed that SLOSS analyses such as mine nearly always find that virtual communities aggregated from a collection of small patches have more species than virtual communities aggregated from large patches of equal size. I observed this result as well, both at the species level in Chapter 2 and within each functional group as documented here (Fig. 24). However, one of the logical complaints about such an analysis from a conservation planning perspective is that though collections of small patches may aggregate species more quickly than collections of large patches, these aggregated communities found across small patches may be functionally different from those found in large patches and intact tracts of habitat. I found some support for this claim. Though the communities aggregated from small islands did functionally diverge from those found in large islands, the structure of the landscape-scale community stabilized well before the addition of the largest island, which suggests that communities aggregated from several small patches can have both more species and have similar functional structure as those found in aggregations of large islands, but only if the total habitat area in the landscape is above the functional stabilization threshold. On the other hand, if only the smallest islands are retained, and the total habitat threshold is not reached, the functional composition of the aggregated communities will be different from one another. This result suggests that land-sharing could be a viable, perhaps even preferential, conservation planning tool compared to land-sparing from a species maximization perspective, as long as enough total habitat is maintained in the system.

5 Conclusion

The study of insular biotas, including those in fragmented habitats, has been blessed with the minds of many great ecologists, MacArthur and Wilson foremost among them. However, a driving force in the development of IBT was the need for “a biogeography of the species,” (Wilson 1959, quoted in Lomolino et al. 2010), which has led many to focus on the species level. I show here that such an approach may be insufficient for detecting fragmentation’s impacts on biological communities. In concert with the scale-dependence shown here and in Chapter 2, this makes the study of fragmentation a formidable task, as truly assessing how fragmentation impacts biological communities requires not only study at multiple scales, but also study of multiple forms of diversity. Future work should take these lessons to heart, examining biological communities at multiple-scales, using multiple perspectives whenever possible.

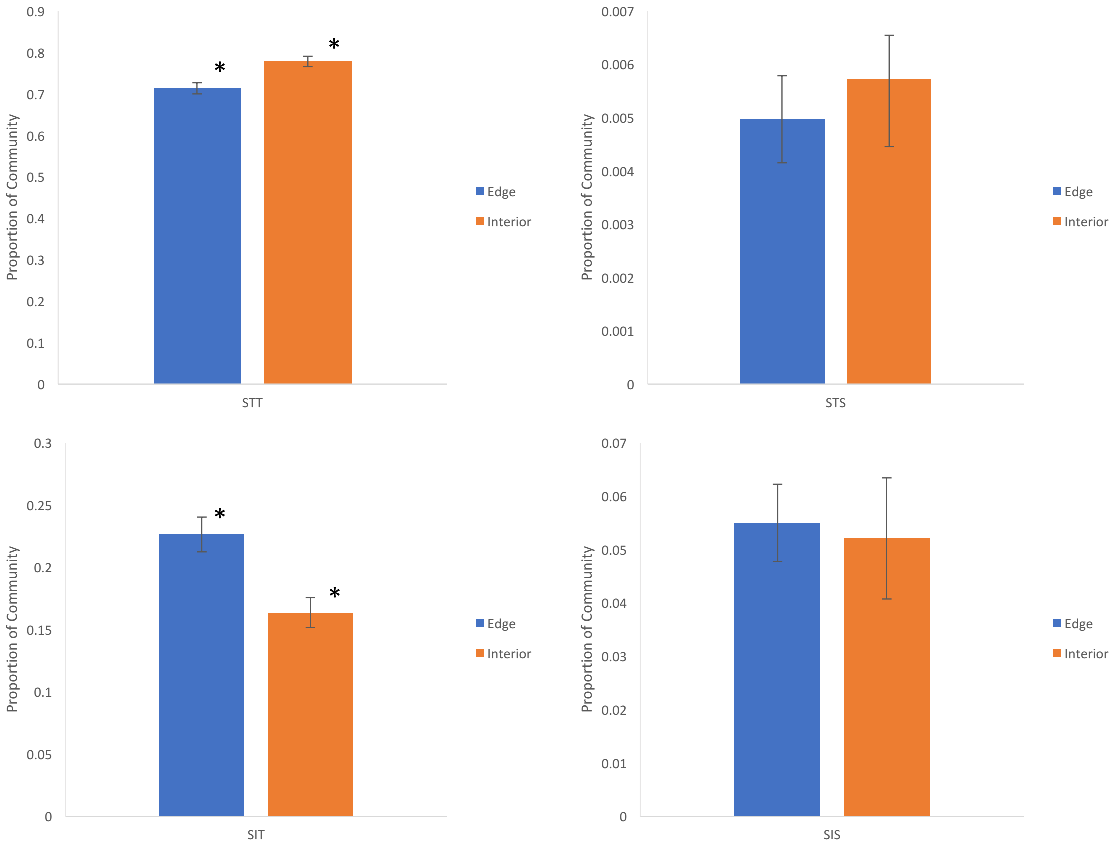


Figure 18. The mean proportion of each community consisting of each functional group in edge and interior plots using abundance measures. Clockwise from upper left, groups are shade-tolerant trees, shade-tolerant shrubs, shade-intolerant shrubs, shade-intolerant trees. Error bars represent one standard error of the mean. Asterisks denote significant differences ($p < 0.05$).

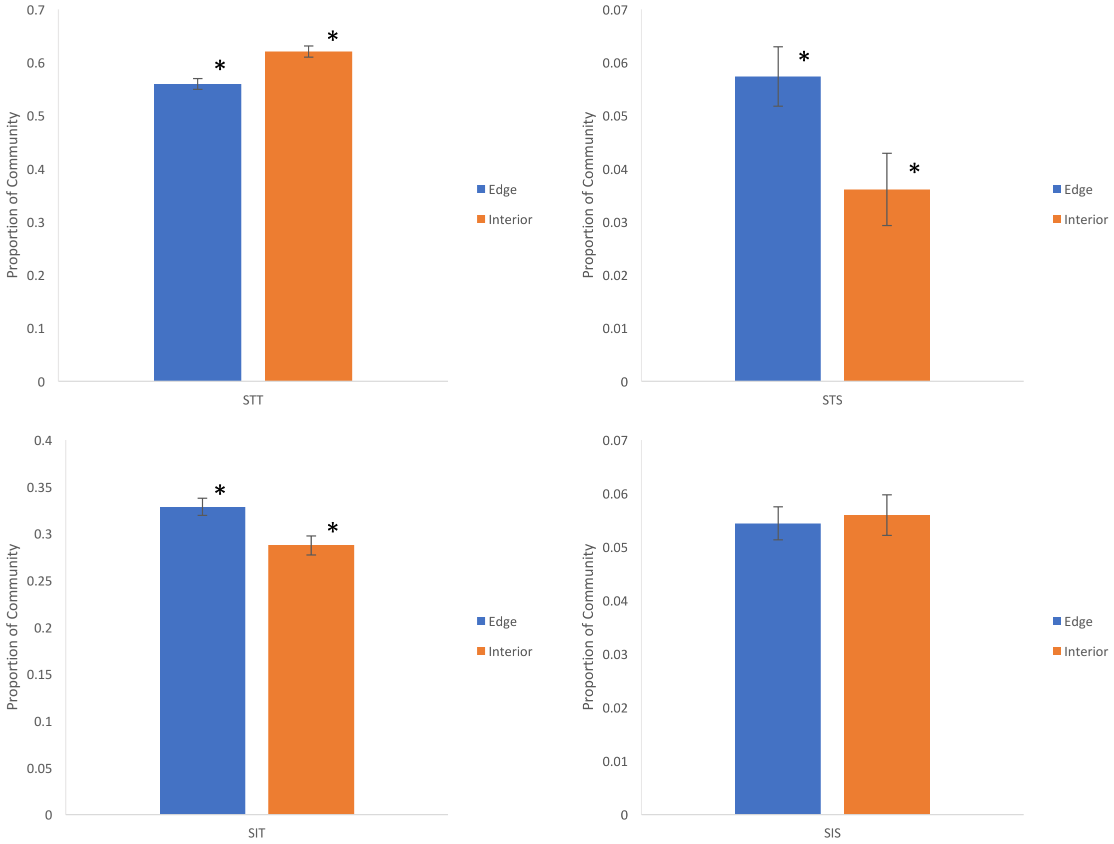


Figure 19. The mean proportion of each community consisting of each functional group in edge and interior plots using richness measures. Clockwise from upper left, groups are shade-tolerant trees, shade-tolerant shrubs, shade-intolerant shrubs, shade-intolerant trees. Error bars represent one standard error of the mean. Asterisks denote significant differences ($p < 0.05$).

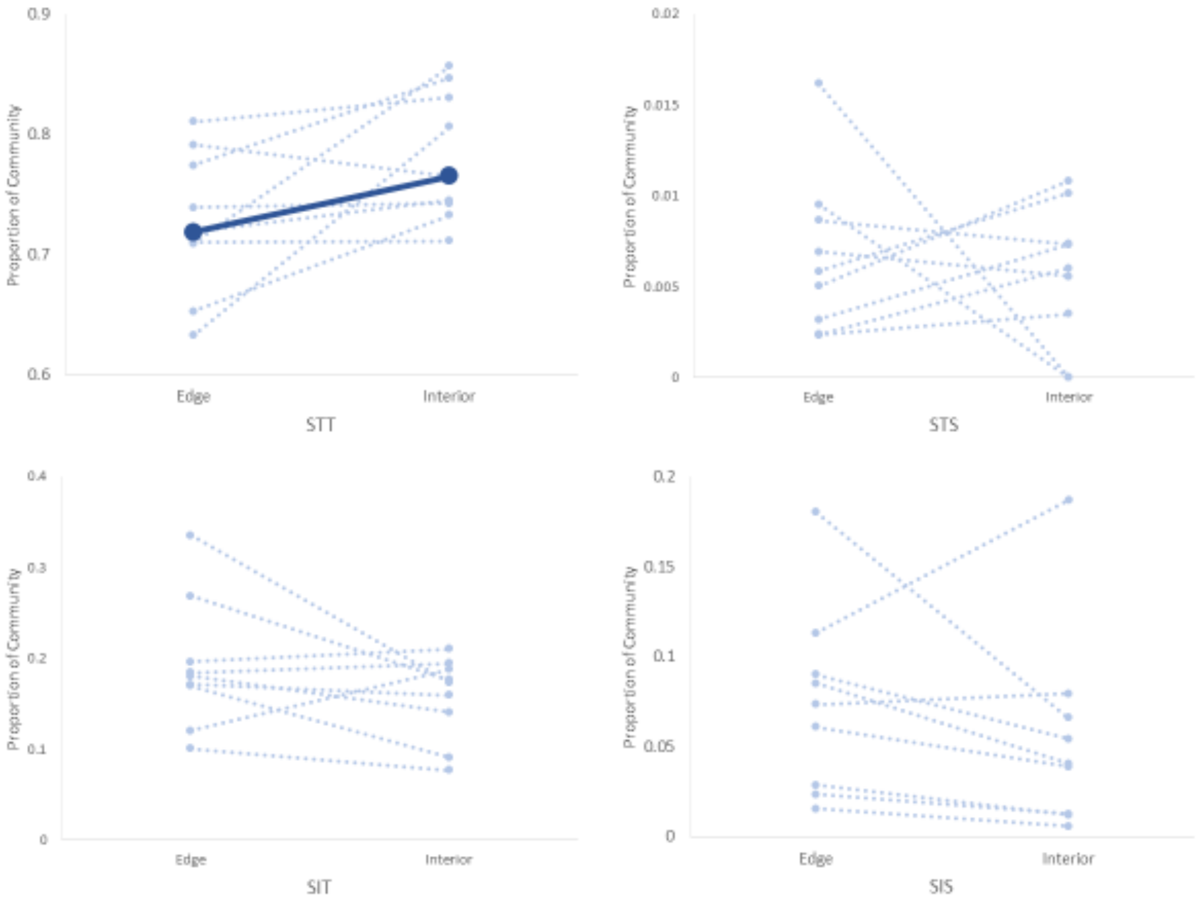


Figure 20. The proportion of each community consisting of each functional group in edge and interior plots across nine islands weighted for abundance. Endpoints represent mean for each plot type on each island. Dotted lines denote island pairs. Solid lines denote a statistically significant relationship ($p < 0.05$) and show the median values for all nine islands. Clockwise from upper left, groups are shade-tolerant trees, shade-tolerant shrubs, shade-intolerant shrubs, shade-intolerant trees.

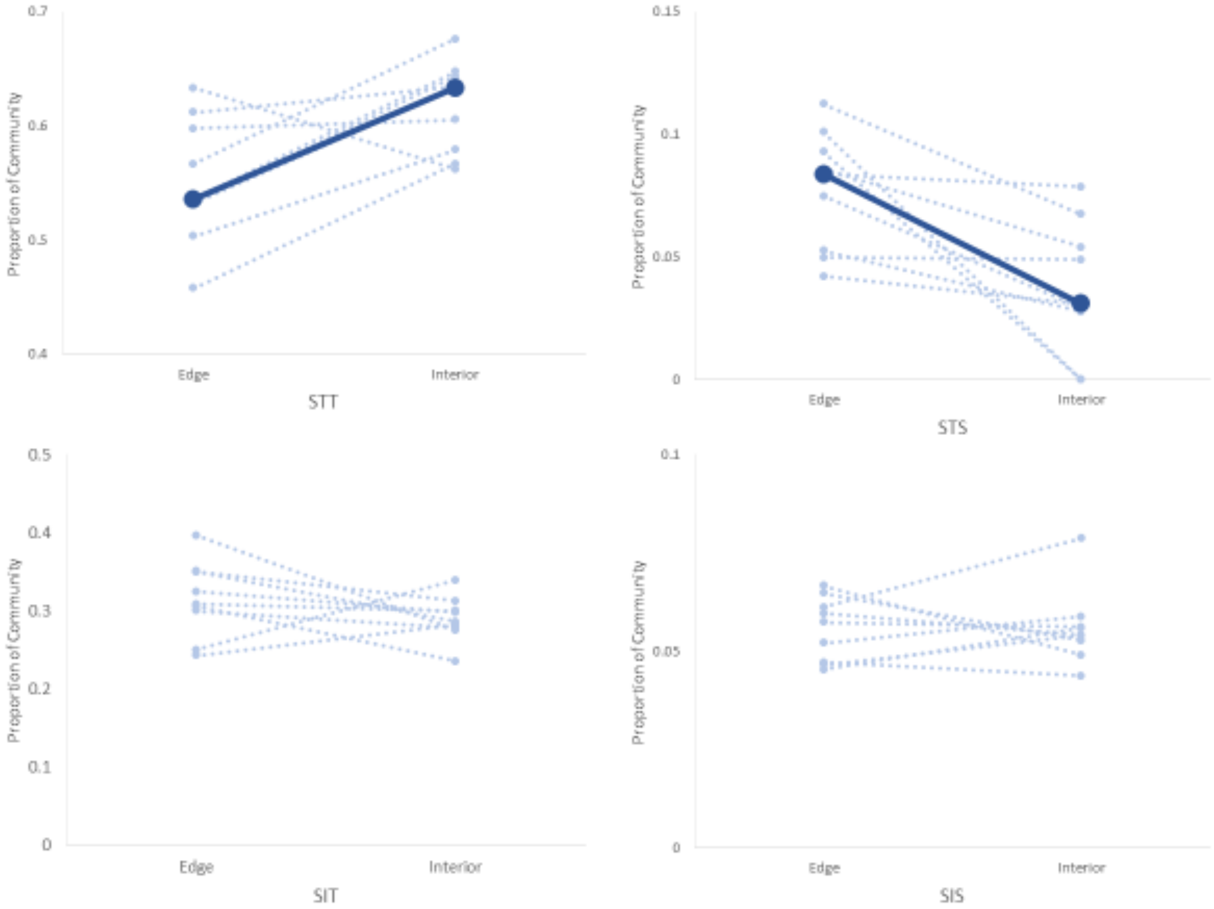


Figure 21. The proportion of each community consisting of each functional group in edge and interior plots across nine islands unweighted for abundance. Endpoints represent mean for each plot type on each island. Dotted lines denote island pairs. Solid lines denote a statistically significant relationship ($p < 0.05$) and show the median values for all nine islands. Clockwise from upper left, groups are shade-tolerant trees, shade-tolerant shrubs, shade-intolerant shrubs, shade-intolerant trees.

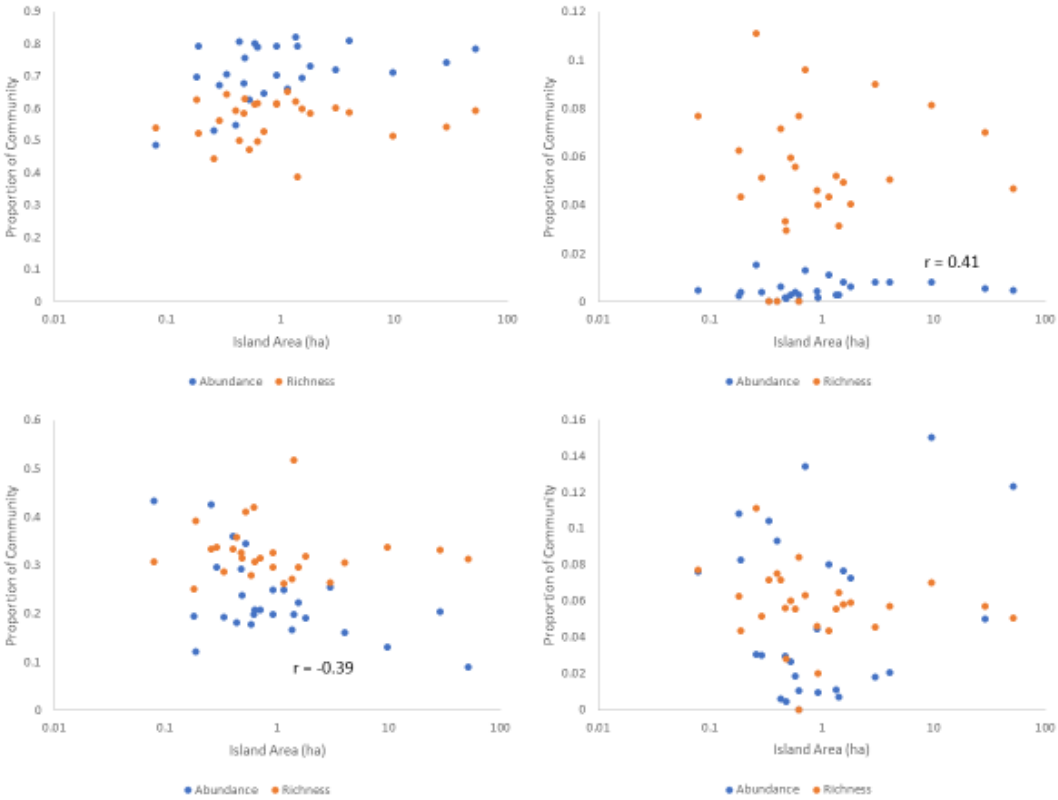


Figure 22. The relationship between island size and proportion of each community consisting of each functional group at the plot-level. Clockwise from upper left, groups are shade-tolerant trees, shade-tolerant shrubs, shade-intolerant shrubs, shade-intolerant trees. r values represent Spearman-rank correlation coefficients.

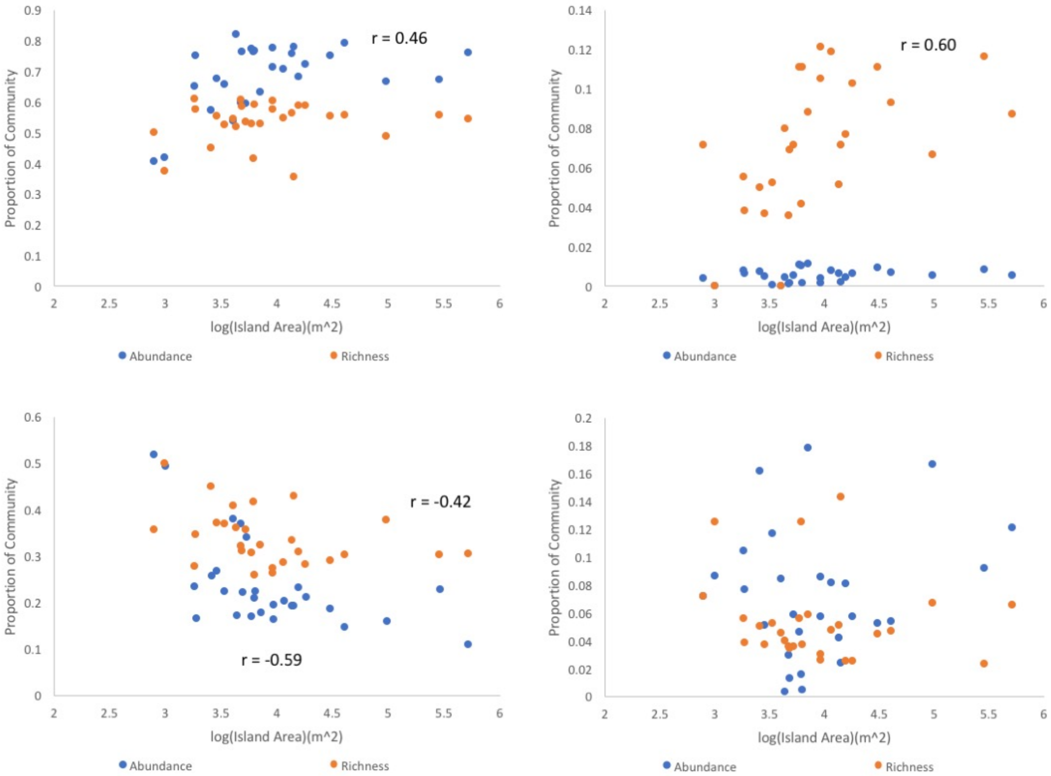


Figure 23. The relationship between island size and proportion of each community consisting of each functional group at the island-level. Clockwise from upper left, groups are shade-tolerant trees, shade-tolerant shrubs, shade-intolerant shrubs, shade-intolerant trees. r values represent Spearman-rank correlation coefficients.

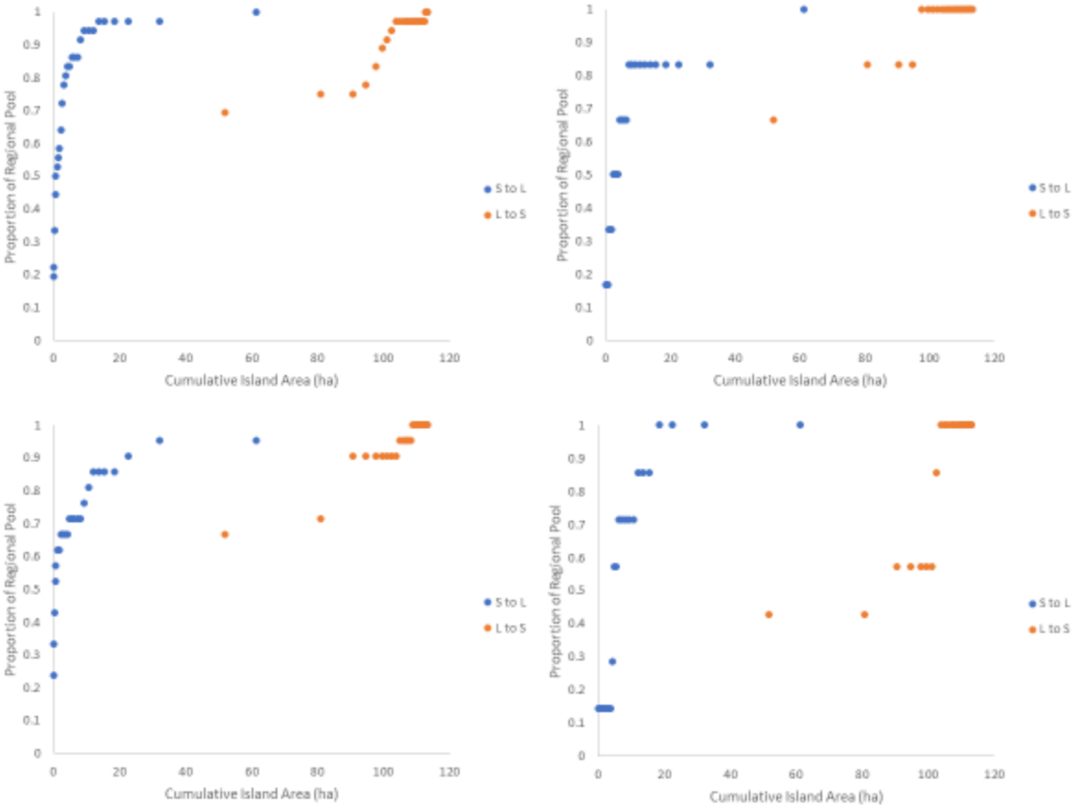


Figure 24. SLOSS analysis for each functional group. Y-axis standardized to represent the proportion of the total regional pool for each functional group to assist in ease of interpretation. Clockwise from upper left, groups are shade-tolerant trees, shade-tolerant shrubs, shade-intolerant shrubs, shade-intolerant trees.

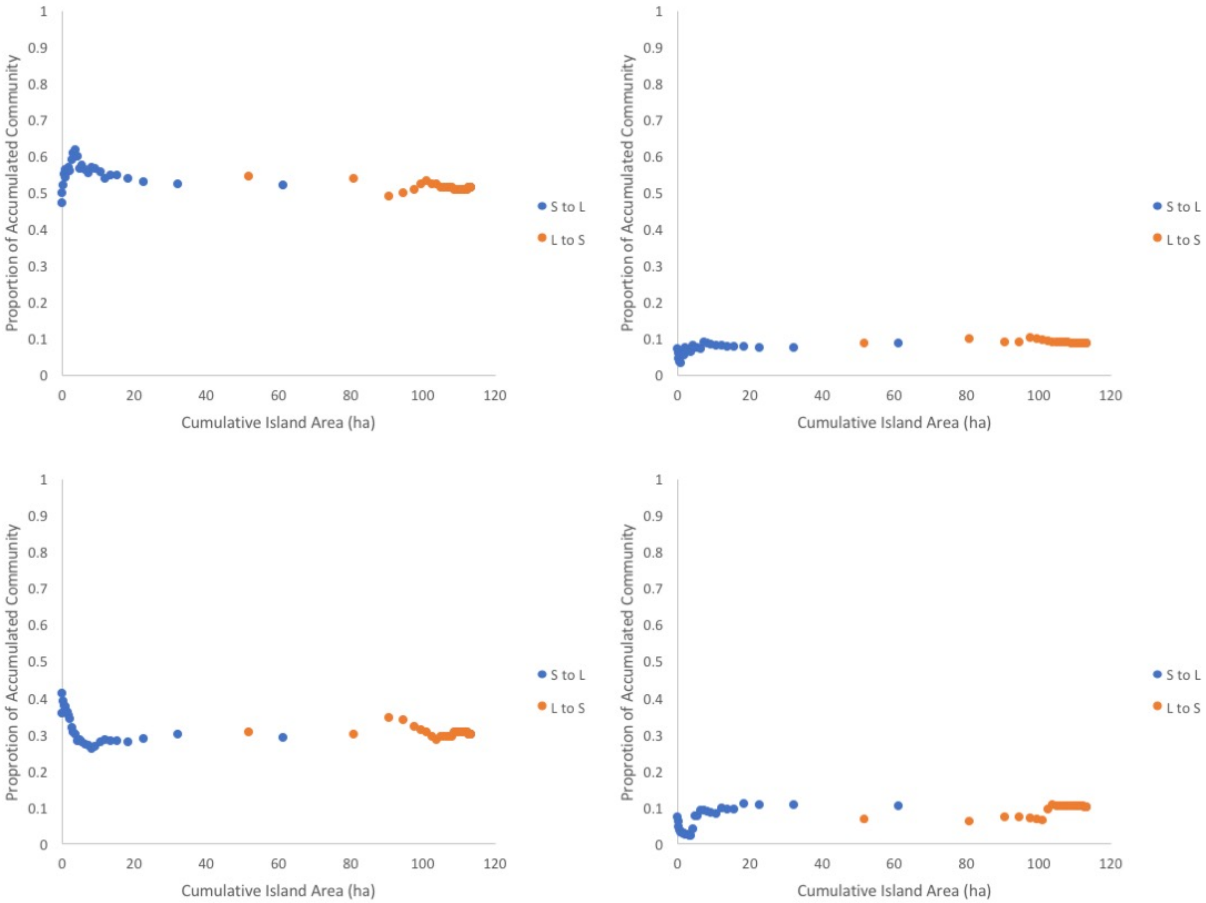


Figure 25. SLOSS analysis for each functional group comparing the relative functional compositions of each virtual community. Y-axis standardized to represent the proportion of the aggregated community for each functional group to assist in ease of interpretation. Clockwise from upper left, groups are shade-tolerant trees, shade-tolerant shrubs, shade-intolerant shrubs, shade-intolerant trees.

CHAPTER 5: SYNTHESIS

1 Major Findings

The goal of this dissertation was to test the hypothesis that habitat fragmentation impacts biological communities through creating hierarchically-nested selective pressures (Fig. 2). To test this hypothesis, I first assessed the past and present landscape context of TIL, providing the independent variables necessary for analyses which followed, and elucidating that while all fragmentation driven changes in landscape structure fundamentally arises from habitat loss, interactive effects driven by socio-economic controls can create substantially different landscape conditions, and thus it is inappropriate to ascribe all of habitat fragmentation's spatial effects directly to habitat loss. Then, I characterized the biological responses to habitat fragmentation across three scales (plot-, patch-, and landscape) at the species-level, finding significant variation in species diversity at all three levels. Finally, I replicated this analysis at the functional-level, finding much stronger evidence of species sorting than I found at the species-level. Together these findings present strong support for the hypothesis that habitat fragmentation impacts biological communities through hierarchically nested selective pressures, though the results presented here contained many interesting idiosyncrasies.

First and foremost, my analysis makes it clear that studying habitat fragmentation at species- and functional-levels can yield significantly different results. At the species-level I found that edge effects did not strongly determine diversity. However, by examining variation in the functional composition of forests, I found that edge effects were a pervasive, if not dominant, control of community composition. There are two obvious explanations for this pattern. First, though functional traits such as shade-tolerance are directly connected the ability of plants to survive in interior areas, the strength of this selective filter may vary greatly between species within each functional group. Second, the number of species within each functional group varied substantially, which would create substantial noise in a species-level analysis. Together these two factors likely interact to obscure the selective pressures caused by edge-effects when viewed at the species level.

Further, though my results cannot reject the hypothesis that habitat fragmentation creates hierarchically structured selective pressures, it is worth noting that different elements of biodiversity reacted to pressures occurring at different levels of the hierarchy. Species richness, for example, was primarily controlled at the island and landscape levels, with local species richness positively correlated with island size but not plot-type (e.g., edge vs. interior), island species richness was positively correlated with island size and isolation, precisely as predicted by IBT. Correspondingly landscape-level species richness appeared to be controlled by both the amount and configuration of habitat in the landscape. Conversely, the proportion of STT in the community appears to be a pure edge effect, while the proportion of SIT appears to be an island-level effect, likely caused by reduced successional rates in small islands (Liu et al. 2018). When aggregated these island- and plot-scale effects could have substantial impacts on the functional composition of virtual landscapes when the amount of habitat is low.

As I pointed out in Chapters 3 and 4, the responses I observed are likely specific to the communities studied here. Plants, by their nature, are highly dependent on local conditions. Assembling, sub-tropical systems are also likely more disturbance adapted than those in more specialized tropical systems. A diversity of responses to local-, patch-, and landscape-level controls between systems and taxa should be considered the rule, not the exception. For example, the only other truly hierarchical study of fragmentation I am aware of, Bowers and Dooley Jr. (1999), found that the demographic patterns of voles (genus *Microtus*) were strongly impacted by local- and landscape- but not patch-level controls. My work differs substantially from Bowers and Dooley Jr.'s (1999) in that I examined biodiversity patterns rather than the demographic dynamics of a single genus, but together our results emphasize that because the biologically relevant forces mediated by fragmentation are likely hierarchically structured, studies of fragmentation should be hierarchically structured as well.

Though not the direct goal of this dissertation, the findings of Chapter 2, which elucidated the relationship between habitat loss and the spatial configuration of the resulting landscape, should not be overlooked. One of the classical debates in fragmentation ecology is whether the spatial effects of habitat fragmentation should be considered independent of habitat loss (e.g., Fahrig 2003, 2017) or whether they should be considered a consequence of habitat loss (e.g., Didham et al. 2012). By analyzing the changes in landscape structure in the TIL region from 1980 to 2010, I found that the relationship between the spatial configuration of the landscape and habitat loss is interactive with the broader socio-economic forces impacting the region. On one hand, given that this area would likely be an intact forest in the absence of human activity, there would be little to no spatial portioning of patches if there had not been habitat loss. However, as my results showed, for a given amount of habitat loss there is a significant amount of variation in the amount of habitat fragmentation *per se* that can occur. Therefore, the spatial configuration of a fragmented landscape is not independent or directly dependent of habitat loss, but rather is the result of the interactive effects of habitat loss and other socio-economic factors, such as rural abandonment and land-use intensification (Chapter 2). While this distinction likely has little impact in studies which occur over a single time period, as habitat fragmentation *per se* cannot change unless times passes, directly ascribing all the spatial effects of habitat fragmentation to habitat loss could create causal confusion unless studies partition the variation caused by habitat loss directly with that caused by spatial variation in landscape structure caused by other factors.

2 Hierarchical Patch Dynamics

It is important to contextualize the possible mechanisms driving these patterns within the broader Hierarchical Patch Dynamics Paradigm (Wu and Loucks 1995). Hierarchy theory suggests that effects will not only be organized spatially, but also temporally, with processes that dominate at finer spatial scales occurring more rapidly than those which occur at broader spatial scales. Broadly speaking, my results support this concept. It appears that the selection toward STT occurs at very fine spatial scales, as in interior areas STT have a competitive advantage relative to shade-intolerant plants. At the island-scale, reduced immigration rates, increased extinction rates, and lower levels of inter-specific completion may reduce successional rates on smaller, more isolated islands (Liu et al. 2018), which in turn may lead to higher proportions of SIT. At the landscape-scale my SLOSS analysis shows that the relatively quick processes of island-scale extinction and immigration will have relatively little impact on the functional composition of the regional pool, provided that the amount of habitat in the landscape stays high.

To complicate matters further, though these processes occur on different time scales they also occur simultaneously. Birth and mortality occur relatively quickly and at the individual level. When aggregated individual births and deaths form the basis for the slower process of island-scale extinction. Simultaneously, island scale effects, such as area and isolation effects, control the levels of inter-specific competition within islands, subsequently altering relative fitness of individuals competing for resources within an island, and controlling birth and mortality at the individual level. Regionally, the amount and configuration of habitat in the landscape can have radical impacts on the number and type of species in the regional pool, which fundamentally constrains which niches can be filled.

3 Conclusion

In sum, these findings suggest that truly understanding the impacts of fragmentation on biological communities is no simple task. As mentioned in the conclusion of Chapter 3, habitat fragmentation is a spatially and temporally dynamic process, by which the loss of habitat in the landscape alters the regional species pool, creating increasingly smaller, increasingly more isolated patches, which sample smaller amounts of the region's biophysical space, contain fewer species to compete with one another, and are increasingly impacted by fragmentation-mediated changes in local biophysical conditions. However, despite the challenges addressing such spatially and temporally dynamic processes poses, understanding how habitat fragmentation will impact biological communities is of critical importance to conservation practitioners. Future work should embrace the complexity fragmentation poses, studying its effects on local, patch, and regional communities and ecological processes simultaneously so that scientists and conservation practitioners can fully contextualize the challenges at hand, choose between trade-offs across scales, and protect the biodiversity that remains.

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APPENDIX A

FRAGMENTATION RELEVANT PARAMETERS FOR COMMONLY STUDIED ISLANDS

PROJECT ID	AREA	PERIM	GYRATE	PARA COR	SHAPE	FRAC	ENN	DISTANCE TO MAINLAND (EDGE TO EDGE)
14	0.49	445.74	33.15	0.09	1.59	1.11	121.17	2105.77
15	0.59	432.82	35.59	0.07	1.41	1.08	77.69	2320.77
31	0.93	503.88	38.96	0.05	1.30	1.06	14.54	3043.24
32	0.34	326.23	25.44	0.10	1.40	1.08	14.54	3044.01
33	0.40	332.69	26.04	0.08	1.30	1.07	15.24	2615.06
34	0.08	142.12	11.16	0.18	1.26	1.07	15.24	2567.28
35	0.53	439.28	30.75	0.08	1.51	1.10	28.20	2362.96
36	0.19	216.41	16.78	0.11	1.24	1.06	10.83	2511.00
37	1.36	762.28	55.56	0.06	1.63	1.10	10.83	2494.14
43	4.06	1640.84	106.54	0.04	2.03	1.13	29.65	2588.23
50	0.29	271.32	22.24	0.09	1.25	1.06	89.54	3039.89
58	0.71	481.27	34.22	0.07	1.42	1.08	62.15	892.70
59	0.18	206.72	16.80	0.11	1.21	1.05	18.06	693.58
60	0.26	319.77	25.78	0.12	1.55	1.11	18.06	724.95
63	1.82	1001.30	62.98	0.06	1.85	1.13	53.30	1046.34
64	1.56	820.42	54.61	0.05	1.64	1.10	14.89	1098.86
68	0.10	148.58	12.12	0.15	1.15	1.05	14.89	1159.57
69	0.48	342.38	26.83	0.07	1.23	1.05	33.61	1227.88
72	0.63	500.65	38.36	0.08	1.57	1.10	65.58	2127.51
73	0.43	329.46	25.76	0.08	1.24	1.05	135.66	3725.02
74	0.62	510.34	41.25	0.08	1.61	1.11	26.04	3204.96
75	1.42	1052.98	63.15	0.07	2.20	1.17	22.95	3359.06
77	3.03	1595.62	98.54	0.05	2.29	1.16	16.15	2576.17
78	0.92	639.54	47.46	0.07	1.66	1.11	16.15	2470.85
113	1.16	713.83	48.49	0.06	1.65	1.11	59.56	3547.04
117	9.73	4266.83	184.56	0.04	3.41	1.21	71.30	2163.77
B6	51.89	9702.92	403.59	0.02	3.36	1.18	31.81	950.35
B7	29.05	7380.55	283.09	0.03	3.42	1.20	67.31	1938.73
JSE	1158.09	129907.37	1593.22	0.01	9.54	1.28	17.39	884.48

Table 2. Fragmentation relevant parameters for islands on which plant communities are commonly studied. Abbreviations and metric descriptions can be found in McGarigal et al. (2012).

PROJECT ID	AREA	PERIM	GYRATE	PARA	SHAPE	FRAC	ENN	DISTANCE TO MAINLAND (EDGE TO EDGE)
14	0.49	445.74	33.15	0.09	1.59	1.11	121.17	2105.77
15	0.59	432.82	35.59	0.07	1.41	1.08	77.69	2320.77
31	0.93	503.88	38.96	0.05	1.30	1.06	14.54	3043.24
32	0.34	326.23	25.44	0.10	1.40	1.08	14.54	3044.01
33	0.40	332.69	26.04	0.08	1.30	1.07	15.24	2615.06
34	0.08	142.12	11.16	0.18	1.26	1.07	15.24	2567.28
35	0.53	439.28	30.75	0.08	1.51	1.10	28.20	2362.96
36	0.19	216.41	16.78	0.11	1.24	1.06	10.83	2511.00
37	1.36	762.28	55.56	0.06	1.63	1.10	10.83	2494.14
43	4.06	1640.84	106.54	0.04	2.03	1.13	29.65	2588.23
50	0.29	271.32	22.24	0.09	1.25	1.06	89.54	3039.89
58	0.71	481.27	34.22	0.07	1.42	1.08	62.15	892.70
59	0.18	206.72	16.80	0.11	1.21	1.05	18.06	693.58
60	0.26	319.77	25.78	0.12	1.55	1.11	18.06	724.95
63	1.82	1001.30	62.98	0.06	1.85	1.13	53.30	1046.34
64	1.56	820.42	54.61	0.05	1.64	1.10	14.89	1098.86
68	0.10	148.58	12.12	0.15	1.15	1.05	14.89	1159.57
69	0.48	342.38	26.83	0.07	1.23	1.05	33.61	1227.88
72	0.63	500.65	38.36	0.08	1.57	1.10	65.58	2127.51
73	0.43	329.46	25.76	0.08	1.24	1.05	135.66	3725.02
74	0.62	510.34	41.25	0.08	1.61	1.11	26.04	3204.96
75	1.42	1052.98	63.15	0.07	2.20	1.17	22.95	3359.06
77	3.03	1595.62	98.54	0.05	2.29	1.16	16.15	2576.17
78	0.92	639.54	47.46	0.07	1.66	1.11	16.15	2470.85
113	1.16	713.83	48.49	0.06	1.65	1.11	59.56	3547.04
117	9.73	4266.83	184.56	0.04	3.41	1.21	71.30	2163.77
B6	51.89	9702.92	403.59	0.02	3.36	1.18	31.81	950.35
B7	29.05	7380.55	283.09	0.03	3.42	1.20	67.31	1938.73
JSE	1158.09	129907.37	1593.22	0.01	9.54	1.28	17.39	884.48

Table 3. Fragmentation relevant parameters for habitat areas in 100 m buffers surrounding each island.

PROJECT ID	PLAND	PD	LPI	LSI	AREA_MN	AREA_CV	FRAC_MN
14	8.5241	10.6925	5.4625	3.8486	0.7972	182.6232	1.0815
15	26.212	4.2726	25.0024	3.7801	6.1349	162.5903	1.1574
31	18.9446	11.3806	6.6568	4.3415	1.6646	138.192	1.1293
32	22.1971	6.6722	10.888	4.0162	3.3268	113.3905	1.1216
33	11.9625	14.4479	4.1345	5.0246	0.828	124.8784	1.0953
34	13.4656	14.517	3.8662	5.186	0.9276	104.5214	1.0955
35	19.1883	15.064	4.2796	6.1855	1.2738	101.7733	1.1206
36	18.6172	17.5458	4.7472	5.9535	1.0611	116.3492	1.1062
37	20.756	18.1805	9.058	6.5615	1.1417	193.672	1.1165
43	19.497	15.2142	7.0188	6.764	1.2815	198.6312	1.1259
50	21.329	6.8288	16.5598	4.3631	3.1234	165.6743	1.1145
58	11.8677	15.9295	3.6349	6.3357	0.745	123.7785	1.1118
59	12.0014	14.0837	2.7063	5.5491	0.8522	96.2192	1.1105
60	10.5714	12.314	3.3735	5.0971	0.8585	105.1129	1.0904
63	13.7231	15.3167	3.3701	6.2562	0.896	126.0317	1.1204
64	7.2567	15.3249	1.7422	5.2698	0.4735	114.8793	1.0839
68	9.0082	13.2195	2.0471	4.1559	0.6814	100.5425	1.1087
69	7.2395	11.05	1.8143	4.0442	0.6552	98.0611	1.0811
72	19.5646	4.1686	17.7546	3.8138	4.6934	151.8454	1.1159
73	2.2659	5.5399	1.5753	3.3034	0.409	124.9019	1.1026
74	2.6469	8.3456	1.4832	3.8838	0.3172	135.4291	1.0917
75	1.5543	6.4474	0.5737	3.4783	0.2411	82.6421	1.0894
77	17.2493	9.4364	7.1892	4.7315	1.828	152.9958	1.1091
78	14.3592	5.041	5.9713	3.6966	2.8485	87.1901	1.1908
113	26.277	4.9478	8.6373	4.9687	5.3108	60.6749	1.14
117	33.1873	10.7496	24.5977	6.3003	3.0873	310.2904	1.1157
B6	1.294	2.4295	0.8944	3.6083	0.5326	159.8657	1.1072
B7	0.3043	1.2789	0.2109	2.419	0.238	78.2471	1.117
JSE	22.5368	2.9292	3.0171	12.0529	7.6938	164.5282	1.128

Table 4. Fragmentation relevant parameters for habitat areas in 500 m buffers surrounding each island.

PROJECT ID	PLAND	PD	LPI	LSI	AREA_MN	AREA_CV	FRAC_MN
14	21.5677	3.8029	15.8314	5.5545	5.6713	250.6309	1.1249
15	24.3308	4.0988	20.8669	5.667	5.9361	306.109	1.1609
31	25.3445	6.6125	9.6967	8.178	3.8328	205.6972	1.1167
32	24.9703	8.3786	11.4072	8.0866	2.9802	239.7958	1.1124
33	18.0907	9.5658	4.5633	9.1442	1.8912	174.2403	1.1246
34	15.7332	9.3857	4.0951	9.0091	1.6763	170.7582	1.1106
35	15.9948	9.3977	5.7359	8.7779	1.702	217.2645	1.1133
36	19.376	9.8269	7.4359	8.9126	1.9717	224.9108	1.1347
37	25.2714	7.9746	14.8988	8.6052	3.169	310.4504	1.1163
43	29.1457	7.4445	16.9748	9.2366	3.9151	320.5026	1.106
50	25.5824	6.6593	15.4425	6.8402	3.8416	277.3321	1.0975
58	17.4274	11.0806	3.5596	10.215	1.5728	173.5495	1.126
59	19.2394	15.391	3.9829	11.2327	1.25	171.7728	1.1194
60	20.2701	15.2989	3.5037	11.0305	1.3249	174.4561	1.1271
63	25.8054	7.9761	6.7416	8.6888	3.2353	190.2707	1.1151
64	18.5294	9.0963	4.4029	9.0049	2.037	156.1626	1.1111
68	17.7676	10.8951	4.5044	8.7318	1.6308	184.0028	1.1127
69	16.0958	7.7417	3.7542	8.5093	2.0791	155.8237	1.1234
72	24.8437	4.3203	20.3686	5.5239	5.7504	303.8211	1.1538
73	0.8738	3.2826	0.4243	4.3679	0.2662	150.1902	1.0848
74	0.7909	3.1762	0.4105	4.2439	0.249	155.804	1.0797
75	0.5229	2.9646	0.1679	4.0578	0.1764	102.8749	1.0746
77	23.4088	4.4203	12.0632	7.8413	5.2957	212.0848	1.0999
78	17.9169	4.8271	8.6649	6.9024	3.7117	195.4276	1.1077
113	32.7848	2.8059	10.4435	6.8193	11.6842	110.9976	1.1409
117	29.1004	6.378	22.3367	9.3006	4.5626	424.0323	1.1227
B6	9.1005	2.372	4.0538	6.9221	3.8366	198.7953	1.1388
B7	7.0006	1.6285	6.5544	4.2229	4.2989	278.8351	1.1755
JSE	22.691	2.9213	9.0405	14.9068	7.7674	371.3217	1.1207

Table 5. Fragmentation relevant parameters for habitat areas in 1000 m buffers surrounding each island.

PPROJECT ID	PLAND	PD	LPI	LSI	AREA_MN	AREA_CV	FRAC_MN
14	25.928	1.7447	15.6096	7.4669	14.861	207.6865	1.1331
15	26.4644	2.688	18.0236	7.9827	9.8455	293.1154	1.1394
31	25.1207	4.2435	9.4129	9.8217	5.9198	275.8014	1.1115
32	25.0975	4.3621	9.6905	9.7615	5.7535	272.0051	1.1151
33	23.8809	4.9063	9.9805	10.0128	4.8674	286.5044	1.121
34	23.323	6.4662	9.3884	9.9148	3.6069	319.2701	1.1009
35	23.8222	5.2513	12.0031	10.2985	4.5364	326.6051	1.1235
36	24.9706	4.9929	12.786	10.355	5.0013	318.1624	1.1162
37	25.9965	5.1436	15.268	10.6133	5.0541	375.3441	1.1151
43	25.7167	4.6754	14.5186	10.7904	5.5004	367.0605	1.1116
50	20.0269	4.9532	11.3568	9.4769	4.0432	335.0498	1.1181
58	29.4983	7.2343	7.5661	12.0762	4.0775	234.3192	1.1192
59	32.4055	7.3715	13.4226	11.9662	4.396	309.3932	1.1221
60	35.8545	7.1035	19.0009	11.4828	5.0475	382.1112	1.1166
63	28.8322	5.9054	8.4065	11.5075	4.8823	241.1192	1.119
64	23.9407	5.8036	5.181	11.6653	4.1252	206.173	1.1164
68	21.9323	6.7223	3.7275	11.691	3.2626	184.5093	1.1199
69	19.5708	6.68	2.9809	11.8477	2.9297	183.0854	1.1216
72	27.3623	2.39	17.4599	7.7475	11.4486	263.7125	1.1325
73	0.4285	2.178	0.1935	5.1	0.1968	177.2895	1.1099
74	0.3642	1.4624	0.189	4.2439	0.249	155.804	1.0797
75	0.2461	1.3955	0.079	4.0578	0.1764	102.8749	1.0746
77	22.9976	4.2776	11.8912	10.1555	5.3762	336.4908	1.1088
78	20.9361	3.6884	10.1435	9.2087	5.6763	286.8619	1.1047
113	38.0984	2.3482	27.5914	6.9438	16.2246	297.8411	1.1386
117	26.1775	4.382	16.4526	11.0917	5.9738	409.4298	1.1134
B6	14.9586	3.3123	5.7496	8.6217	4.5161	292.2337	1.1493
B7	8.5878	1.6553	4.5206	6.8748	5.188	240.3086	1.1121
JSE	22.9994	2.6282	10.6299	17.424	8.7509	476.6387	1.1256

Table 6. Fragmentation relevant parameters for habitat areas in 1500 m buffers surrounding each island.

PROJECT ID	PLAND	PD	LPI	LSI	AREA_MN	AREA_CV	FRAC_MN
14	24.9491	1.6883	13.6514	8.8177	14.7776	260.579	1.1214
15	28.6102	1.4602	16.7419	8.687	19.5929	249.6432	1.1453
31	21.3526	3.4988	9.0287	11.3104	6.1029	362.9421	1.123
32	21.293	3.3384	8.5984	10.959	6.3782	354.8619	1.1224
33	21.8757	3.7278	9.9912	11.9981	5.8682	359.9286	1.1185
34	21.8494	3.6583	10.0472	11.8022	5.9726	353.2703	1.1288
35	22.9903	3.6168	11.4877	11.9995	6.3565	365.4072	1.1229
36	23.5797	3.3871	11.6898	11.9281	6.9617	346.9659	1.122
37	24.208	3.5645	12.066	12.2335	6.7914	362.9737	1.1224
43	23.8072	3.3109	11.3189	12.4594	7.1905	355.1825	1.1327
50	19.0739	4.1475	9.3641	10.5362	4.5989	397.0516	1.1109
58	36.2656	6.1287	20.1952	11.2475	5.9173	511.8028	1.1199
59	38.9695	6.7834	22.9008	11.5354	5.7448	549.351	1.1147
60	41.0257	6.9237	24.9881	11.2486	5.9254	579.5788	1.1128
63	26.5961	11.3838	5.4118	15.3476	2.3363	353.4854	1.134
64	24.6705	8.3443	5.4612	14.417	2.9566	301.019	1.1236
68	24.1512	8.1642	5.2947	14.1401	2.9582	293.8192	1.1309
69	22.5877	7.3821	5.0618	13.8343	3.0598	287.7298	1.1314
72	27.4341	1.6008	15.6163	8.7477	17.1378	259.727	1.1397
73	3.7381	1.9417	1.4251	7.4105	1.9252	211.5983	1.0929
74	1.0024	2.3616	0.363	6.7933	0.4245	210.5445	1.1247
75	1.3248	1.6907	0.4594	7.0114	0.7836	184.143	1.105
77	22.9272	3.5651	10.0149	12.3531	6.4311	359.5358	1.118
78	22.689	4.0149	8.7643	12.2878	5.6513	341.5009	1.1108
113	36.5489	1.8036	29.667	9.0033	20.2641	387.654	1.1141
117	24.743	3.5275	15.9224	12.3052	7.0142	490.7314	1.115
B6	20.2345	3.6844	6.3565	10.9781	5.4919	345.2953	1.1696
B7	11.221	1.579	4.0802	8.2902	7.1065	251.6843	1.1233
JSE	24.5679	3.0713	9.7574	20.5493	7.999	537.8377	1.12

Table 7. Fragmentation relevant parameters for habitat areas in 2000 m buffers surrounding each island.

PROJECT ID	PLAND	PD	LPI	LSI	AREA_MN	AREA_CV	FRAC_MN
14	23.6506	1.5379	12.564	10.0758	15.3782	304.6813	1.1293
15	26.1889	1.4416	14.7231	10.0193	18.1666	307.2182	1.1205
31	20.2526	3.4976	7.8836	13.6746	5.7904	412.0747	1.1196
32	19.8876	3.3065	7.703	13.4206	6.0147	402.367	1.1237
33	20.9305	4.0078	10.0161	13.5028	5.2225	487.4443	1.111
34	20.9885	3.7285	10.1394	13.6233	5.6292	465.2507	1.115
35	22.1945	3.8286	11.6931	13.8945	5.7971	494.2041	1.1146
36	22.2599	3.4929	11.6754	13.6126	6.3729	467.8113	1.1206
37	22.6455	3.4306	12.5505	13.7833	6.601	490.955	1.1182
43	22.2892	3.2283	12.0256	13.8235	6.9042	485.1639	1.1197
50	16.5925	4.1831	6.453	13.1664	3.9666	479.8176	1.126
58	38.4525	5.7959	23.4587	12.204	6.6345	669.5013	1.1062
59	41.6423	6.0887	25.894	12.2266	6.8393	689.3347	1.1144
60	43.0435	6.2202	27.6665	12.032	6.92	722.783	1.1121
63	27.624	16.0504	7.5897	18.698	1.7211	614.2448	1.1445
64	25.6448	10.4182	6.8349	17.1969	2.4615	492.8611	1.1357
68	25.8311	9.1654	6.4636	16.5226	2.8183	436.3784	1.1354
69	24.3808	8.8262	5.6122	16.2918	2.7623	415.877	1.1341
72	25.2914	1.6779	13.9732	10.1209	15.073	331.6835	1.1265
73	9.1742	1.7038	2.3999	9.5728	5.3847	205.4416	1.117
74	7.4599	2.663	1.6111	11.3845	2.8013	218.2476	1.1094
75	6.8548	2.3956	1.7093	10.1174	2.8615	253.2331	1.1151
77	23.2981	3.2196	9.5158	15.5337	7.2363	392.3893	1.1174
78	23.3618	3.7831	7.7906	15.6394	6.1754	366.9449	1.1205
113	34.7044	1.6104	27.9037	10.1665	21.5505	453.7395	1.1204
117	23.9293	4.7419	14.1663	15.5056	5.0464	648.9367	1.119
B6	24.5743	4.3411	7.2433	11.7293	5.6609	483.6818	1.1342
B7	14.2706	2.9857	4.9947	11.1685	4.7796	372.503	1.1435
JSE	26.2429	4.2651	8.8832	24.1002	6.1529	664.1183	1.1283

Table 8. Fragmentation relevant parameters for habitat areas in 2500 m buffers surrounding each island.

PROJECT ID	PLAND	PD	LPI	LSI	AREA_MN	AREA_CV	FRAC_MN
14	22.4149	1.8037	11.1068	11.9743	12.4274	372.9977	1.1312
15	23.6075	1.6685	12.5889	11.9582	14.1491	379.1384	1.1375
31	20.1312	3.9314	8.5965	17.2011	5.1206	511.8298	1.1125
32	19.5749	3.5677	8.3501	16.7328	5.4866	486.3527	1.115
33	20.395	4.6156	9.8281	16.8034	4.4187	605.7856	1.1174
34	20.5724	4.8351	9.8848	16.8211	4.2548	614.5434	1.1218
35	21.9666	7.5763	11.0158	17.9605	2.8994	796.2755	1.1233
36	21.8312	5.821	10.9954	17.2989	3.7504	696.0988	1.1209
37	22.4478	5.8712	11.5223	17.6606	3.8234	718.4372	1.1279
43	22.1145	5.0008	11.1065	18.0219	4.4222	666.131	1.1182
50	16.6762	4.2188	5.7203	16.897	3.9528	477.1481	1.115
58	40.2946	5.8201	25.8041	13.2637	6.9234	835.3088	1.1154
59	43.0891	6.1166	28.0688	13.3592	7.0446	860.9692	1.1183
60	44.1282	6.1593	29.3911	13.3536	7.1645	887.2346	1.1146
63	30.8784	13.105	16.1816	19.3514	2.3562	1062.3395	1.1435
64	28.7299	13.0293	12.7387	18.8283	2.205	904.5929	1.1449
68	28.6076	12.5133	12.7276	18.3276	2.2862	871.6845	1.1431
69	27.2166	11.1007	11.8503	18.2047	2.4518	812.3578	1.147
72	23.1732	1.8307	11.8821	12.1194	12.6581	386.6411	1.1254
73	15.7008	2.1333	7.6848	11.9726	7.36	386.587	1.1319
74	15.5008	2.6571	2.7204	14.3886	5.8338	242.2256	1.1235
75	13.9439	2.2903	5.479	13.7083	6.0883	338.0507	1.1153
77	23.0208	4.1302	9.216	18.7824	5.5738	496.4121	1.1146
78	23.4102	4.3013	8.5699	18.926	5.4425	463.0127	1.1198
113	33.2079	1.2658	25.5145	10.6033	26.2353	461.9139	1.1247
117	25.0322	8.8727	12.3728	19.8452	2.8213	896.5506	1.1504
B6	26.608	4.5847	6.9615	13.2405	5.8037	539.4223	1.1233
B7	18.6416	4.025	5.8639	12.9556	4.6314	458.7575	1.1337
JSE	28.1598	6.9442	7.8518	29.8123	4.0552	848.8199	1.1343

Table 9. Fragmentation relevant parameters for habitat areas in 3000 m buffers surrounding each island.

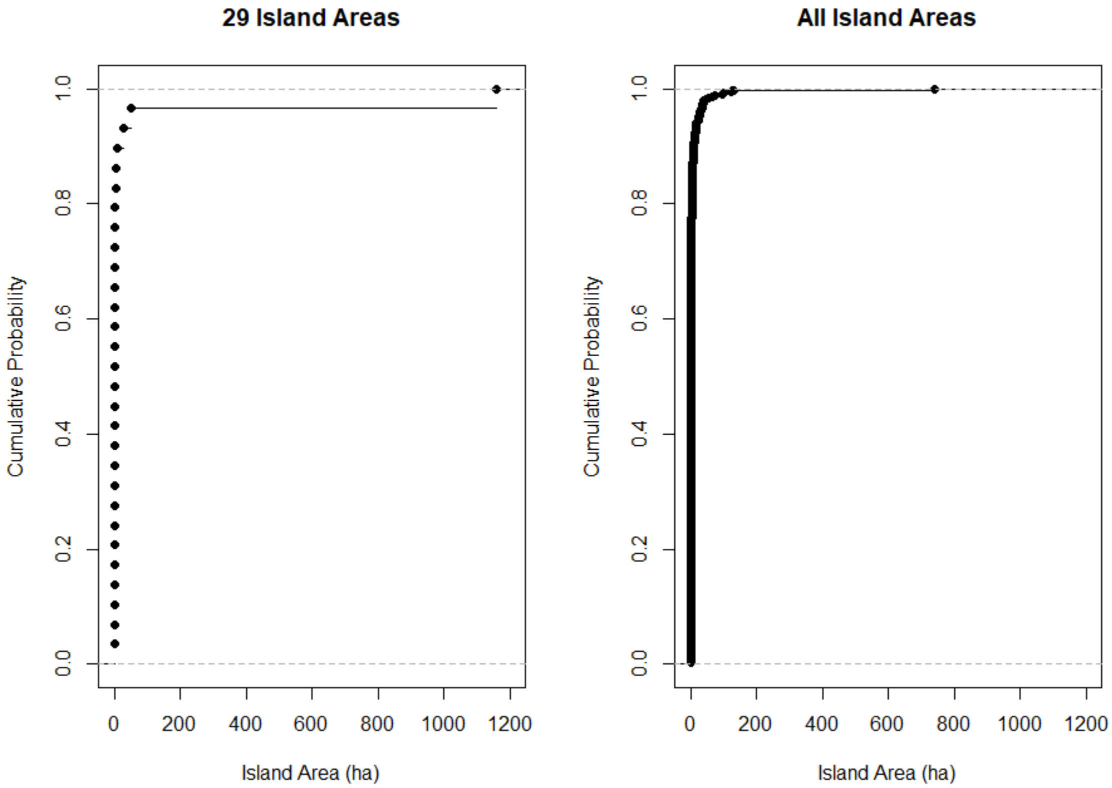

Figure 26. Empirically derived cumulative probability functions for the areas of the 29 studied islands (right) and all other islands in the landscape (left). Kolmogorov-Smirnov testing suggests that these distributions are not statistically different from one another (D = 0.20, p = 0.22)

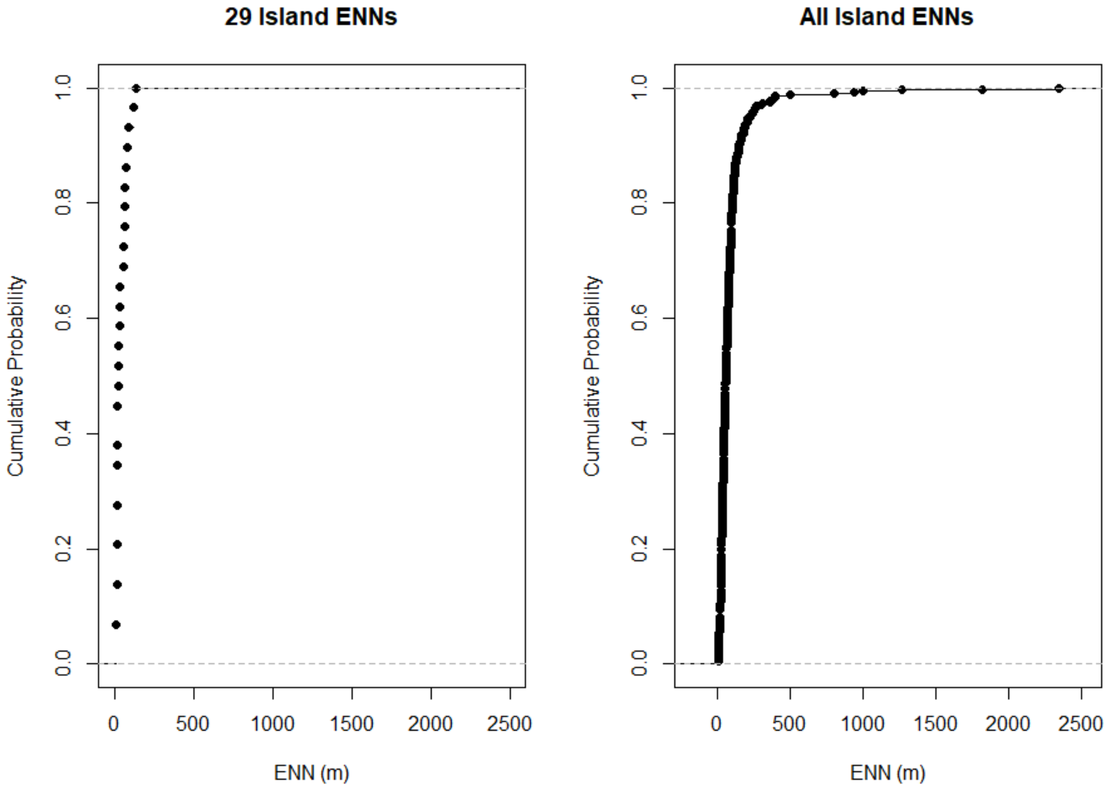

Figure 27. Empirically derived cumulative probability functions for the distance to nearest island (ENN) for the 29 studied islands (right) and all other islands in the landscape (left). Kolmogorov-Smirnov testing suggests that these distributions are statistically different from one another (D = 0.40, p < 0.001)

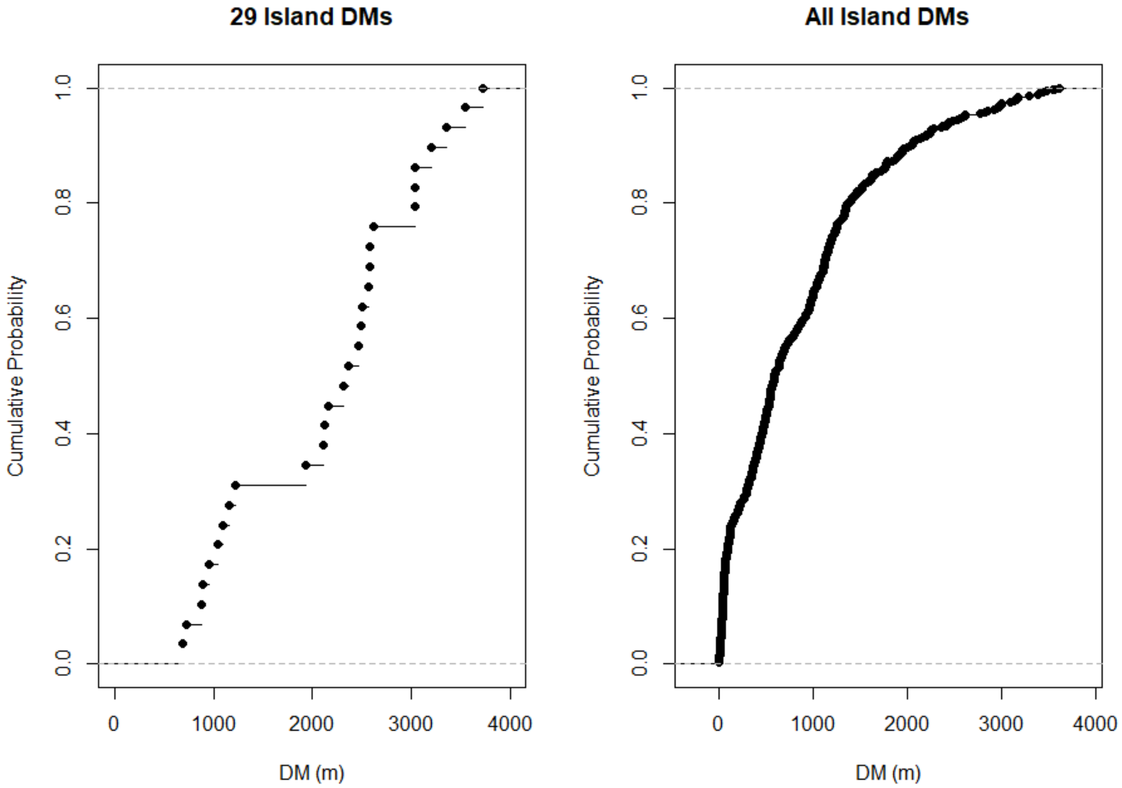

Figure 28. Empirically derived cumulative probability functions for the distance to mainland (DM) of the 29 studied islands (right) and all other islands in the landscape (left). Kolmogorov-Smirnov testing suggests that these distributions are statistically different from one another ($D = 0.58$, $p < 0.001$)

PROJECT ID	AREA	PERIM	GYRATE	PARA	SHAPE	FRAC	ENN	DISTANCE TO MAINLAND (EDGE TO EDGE)
B1	1158.09	129907.37	1593.22	0.01	9.54	1.28	17.39	884.48
B2	128.04	21256.63	575.22	0.02	4.69	1.22	27.07	1452.28
B3	31.00	8947.10	272.90	0.03	4.01	1.22	55.62	2134.78
B4	36.56	10797.89	306.01	0.03	4.46	1.23	24.01	197.01
B5	101.02	15171.31	540.82	0.02	3.77	1.19	80.90	964.61
B6	51.89	9702.92	403.59	0.02	3.36	1.18	31.81	950.35
B7	29.05	7380.55	283.09	0.03	3.42	1.20	67.31	1938.73
I1	1.03	684.76	49.73	0.07	1.68	1.11	87.27	727.55
I10	0.89	558.79	45.38	0.06	1.48	1.09	47.08	356.09
I13	0.29	377.91	32.81	0.13	1.72	1.14	54.81	1001.64
I14	1.35	700.91	51.00	0.05	1.51	1.09	52.73	984.41
I15	0.49	445.74	33.15	0.09	1.59	1.11	121.17	2105.77
I16	0.63	500.65	38.36	0.08	1.57	1.10	65.58	2127.51
I17	0.59	432.82	35.59	0.07	1.41	1.08	77.69	2320.77
I18	0.43	329.46	25.76	0.08	1.24	1.05	135.66	3725.02
I19	1.42	1052.98	63.15	0.07	2.20	1.17	22.95	3359.06
I2	2.23	1085.28	83.87	0.05	1.81	1.12	52.73	1187.39
I20	0.62	510.34	41.25	0.08	1.61	1.11	26.04	3204.96
I3	4.67	1721.59	104.04	0.04	1.99	1.13	176.81	29.75
I4	0.98	746.13	59.89	0.08	1.88	1.14	49.75	1426.71
I5	1.43	752.59	58.58	0.05	1.56	1.09	37.70	1226.33
I6	1.19	700.91	53.32	0.06	1.60	1.10	38.76	1076.74
I7	3.03	1627.92	95.88	0.05	2.33	1.16	38.76	1048.62
I9	1.25	549.10	43.76	0.04	1.22	1.04	399.72	48.64
J3	0.53	439.28	30.75	0.08	1.51	1.10	28.20	2362.96
J4	0.73	707.37	60.59	0.10	2.07	1.16	62.99	1776.70
J5	1.38	797.81	54.71	0.06	1.69	1.11	59.38	851.24
J6	1.56	820.42	54.61	0.05	1.64	1.10	14.89	1098.86
J7	1.82	1001.30	62.98	0.06	1.85	1.13	53.30	1046.34
M1	0.71	481.27	34.22	0.07	1.42	1.08	62.15	892.70
M2	0.42	368.22	28.39	0.09	1.43	1.09	90.50	665.66
M3	0.41	439.28	33.68	0.11	1.72	1.13	66.22	1184.77
M4	0.34	290.70	23.41	0.09	1.25	1.06	143.52	1529.97
N113	1.16	713.83	48.49	0.06	1.65	1.11	59.56	3547.04
N117	9.73	4266.83	184.56	0.04	3.41	1.21	71.30	2163.77
N42	0.06	109.82	9.26	0.19	1.13	1.04	82.51	2975.91
N50	0.29	271.32	22.24	0.09	1.25	1.06	89.54	3039.89
X1	1.28	665.38	47.24	0.05	1.46	1.08	75.37	928.40
X2	0.57	436.05	33.47	0.08	1.44	1.09	72.68	1129.17
X3	0.65	465.12	37.76	0.07	1.44	1.08	53.47	1370.34

X4	1.51	746.13	58.30	0.05	1.51	1.09	29.69	787.69
X5	0.17	209.95	16.78	0.12	1.27	1.07	72.68	1339.86

Table 10. Fragmentation relevant parameters for islands on which animal communities are commonly studied. Abbreviations and metric descriptions can be found in McGarigal et al. (2012).

PROJECT ID	AREA	PERIM	GYRATE	PARA	SHAPE	FRAC	ENN	DISTANCE TO MAINLAND (EDGE TO EDGE)
G1	128.04	21256.63	575.22	0.02	4.69	1.22	27.07	1452.28
G2	741.72	130731.02	1304.72	0.02	12.00	1.31	6.46	552.69
G3	101.02	15171.31	540.82	0.02	3.77	1.19	80.90	964.61
G4	74.16	15100.25	357.94	0.02	4.38	1.22	29.65	640.45
G5	3.32	1802.34	90.03	0.05	2.47	1.17	6.85	663.49
G6	3.42	2025.21	112.74	0.06	2.73	1.19	13.02	596.35

Table 11. Fragmentation relevant parameters for islands on which the genetics of communities are commonly studied. Abbreviations and metric descriptions can be found in McGarigal et al. (2012).

APPENDIX B

ABUNDANCE-BASED RESULTS RELATED TO CHAPTER 3

1. Methods

To assess whether the inclusion of abundance, rather than presence/absence metrics, altered β-diversity patters, I repeated the analysis described in the main text using Baselga's (2017) multi-site dissimilarity metrics based on the Bray-Curtis family of indices. Methods were identical to those described in the main text, except the 'beta.sample' function was replaced with 'beta.sample.abund.'

2. Results

Similar to analyses based on presence/absence data (see main text) plant communities in edge and interior plots were approximately equally dissimilar from one other ($\beta_{\text{Bray}} = 0.84$ vs 0.85 for edges and interiors, respectively, Fig 30). Nestedness became slightly more important when β-diversity was measured using abundance metrics compared to presence/absence metrics (10% vs.13% for edges, 7% vs. 11% for interiors, Fig. 30). Further, plot communities on small and large islands were equally dissimilar to one another ($\beta_{\text{Bray}} = 0.87$ vs 0.87 for plots on large vs. small island, respectively, Fig. 31) and nestedness became slightly more important when β-diversity was measured using abundance metrics compared to presence/absence metrics (7% vs. 10% for large islands, 8% vs. 11% for small islands, Fig. 31).

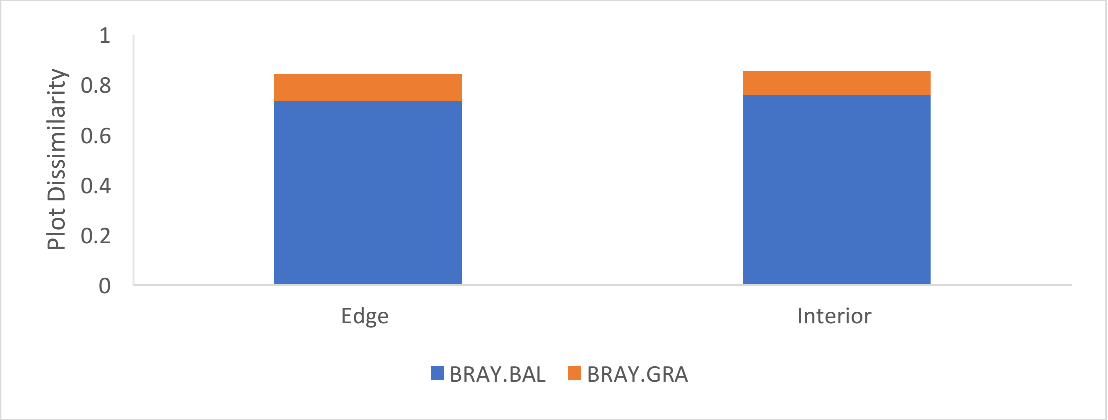

Figure 29. Plot dissimilarity of edge and interior plots measured using the multi-site Bray-Curtis family of metrics, with BRAY.BAL representing the turnover component and BRAY.GRA representing the nestedness component.

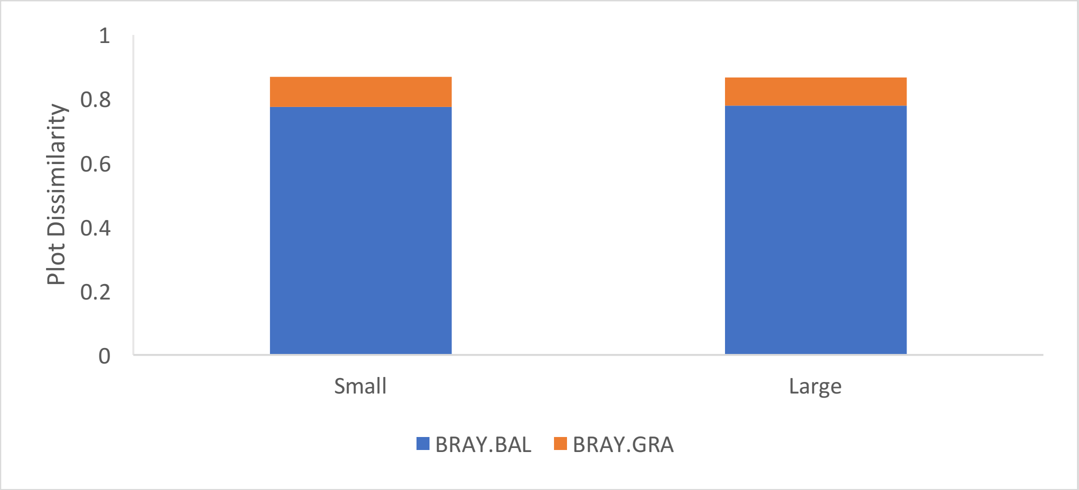

Figure 30. Plot dissimilarity from plots on large and small islands measured using the multi-site Bray-Curtis family of metrics, with BRAY.BAL representing the turnover component and BRAY.GRA representing the nestedness component.

APPENDIX C

PERMISSIONS CONCERNING PUBLISHABLE WORKS

Chapter 3 is currently in review as the following manuscript:

Wilson, M.C., Guang, H., Jiang, L., Liu, J.L., Liu, J.J., Jin, Y., Yu, M.J., and Wu, J.G. 2018. No island is and island: assessing habitat fragmentation's hierarchical effects on species diversity at multiple scales in Thousand Island Lake, China. Ecography

All co-authors have approved the use of this manuscript in this dissertation.