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Spatial scale changes the drivers of beta-diversity along land-use, environmental and geographic gradients

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In memory of Krishnaveni Redla and Raghava Rao Redla

Summary

Understanding the patterns of spatial change in community composition (beta-diversity), and the processes that structure biological communities are central themes in ecology. While the impacts of habitat change on beta-diversity are well-studied, most studies have been restricted to a single spatial scale. As a result, the effects of changing spatial scale on beta-diversity patterns across both natural and human-modified habitats are little known. My thesis targets the effect of spatial scale on tree and bird beta-diversity in the Asia-Pacific region across gradients of latitude, elevation and land-use change.

The First Chapter uses tree data (> one billion stems and > 2500 species) from 15 long-term ForestGEO plots across the Asia-Pacific region to show how spatial scale changes the relationship between beta-diversity and latitude. At small spatial scales, beta-diversity decreased with increasing latitude; but at large spatial scales, beta-diversity did not change with increasing latitude. Different relationships across spatial scales were caused by differences in species richness, which influenced β-diversity values at small spatial scales, but not at large spatial scales.

The Second Chapter uses bird data from Sri Lanka to show how horizontal (geographic) and vertical (elevation) distances can influence bird beta-diversity within three different land-use types (protected rainforests, reserve buffers and intensive agriculture). I show that bird beta-diversity within all land-use types were similar across horizontal distances. However, bird beta-diversity within land-use types were not similar across vertical distances; protected rainforests had higher beta-diversity than the other two habitats.

The Third Chapter uses bird data from the Western Ghats – Sri Lanka biodiversity hotspot to determine the drivers of bird community assembly at three different spatial scales. The geographic barrier (the Palk Strait) is the most important driver of bird beta-diversity at large spatial scale. Land-use and environment were equally important at intermediate scales and land-use was the most important driver at small scales.

In conclusion, this thesis demonstrates the importance of sampling at multiple spatial scales to better understand natural and human-influenced beta-diversity. In the First Chapter I showed that spatial scale changes the relationship between beta-diversity and latitude; and improving sampling representativeness avoids the species richness dependence of beta-diversity. In the Second Chapter I demonstrated the crucial importance of conserving rainforests across the full elevation range available. In the Third Chapter I showed that considering community assembly processes at multiple spatial scales while selecting sites for biological conservation holds great promise for preventing further species loss.

Originality statement

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Chapter 1

General introduction

Understanding the change in species composition from site-to-site (β-diversity) is a central theme in ecology and biogeography since the time of Wallace and Darwin (Terborgh 2017). In an influential paper, Whittaker (1960) coined the term 'β-diversity' and quantified it as the ratio of γ diversity (pooled diversity in a set of sampling sites) and α-diversity (average diversity of sampling sites; Tuomisto 2010a, 2010b). However, ecologists quantified β-diversity way before Whittaker (1960).

β-diversity is an important variable in ecology's oldest law, the Species-area relationship (SAR) – "you will find more species if you sample a larger area" (Rosenzweig 1995). Ecologists credit H. C. Watson with its discovery in c. 1859 when he built up plant species starting with smaller areas within Surrey (Britain's county) and expanding it to the whole island (Dony 1963; Williams 1964; Rosenzweig 1995; Fig. 1.1), and Arrhenius (1921) was the first to suggest the species-area equation ($S = c.A^Z$). The number of species 'S' scales with the sample area 'A' according to $S = c.A^z$ where 'c' and 'z' are constants. The constant 'c' is the number of species when the value of 'A' is equal to one (in any metric), and the constant 'z' is the rate of increase in species richness. Many studies have discussed the relationship between Whittaker's diversity partitioning ($\gamma = \alpha.\beta$) and species-area relationship ($S = c.A^z$; Rosenzweig 1995; Ricotta *et al.* 2002; Koleff *et al.* 2003a; Socolar *et al.* 2016). Koleff *et al.* (2003a) showed that the 'z' value is a form of β-diversity, and multiplicative diversity partitioning is similar to species-area relationship.

Another earlier form of β-diversity was described by botanist Paul Jaccard in 1901 as "*coefficient de communauté*" when he compared the species composition of plants on different mountains (Jaccard 1901). While the Whittaker's approach used the entire dataset to quantify β-diversity, Jaccard's approach used two sites at a time. Therefore, it is also called as the Jaccard's pairwise similarity index. Another botanist Thorvald Julius Sørensen described a pairwise similarity index in 1948 (Sørensen, 1948), which was similar to Jaccard's index and is called Sørensen's pairwise similarity index. These are still much used indices in the 21st century, and around fifty different β-diversity indices have been introduced since then (see Koleff et al. 2003a; Tuomisto 2010a, 2010b, Anderson *et al.* 2011; Barwell et al. 2015).

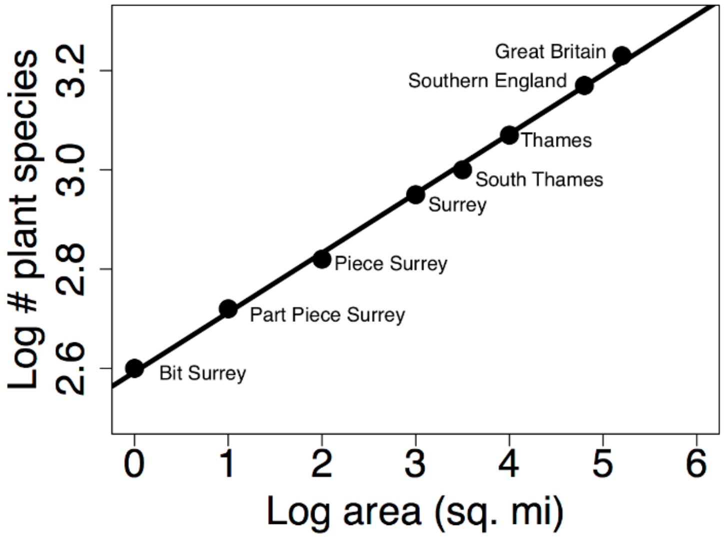

Fig 1.1. First empirical example of the species-area relationship (SAR) by H. C. Watson in 1859. This plant SAR begins with Britain's richest county – Surrey and builds up to whole Great Britain Island. Figure adapted from Rosenzweig (1995).

Quantifying β-diversity

There are two types of β-diversity: directional variation in community structure along a specified gradient and non-directional variation in community structure (Fig. 1.2). The directional variation approach is used to quantify β-diversity along a gradient (e.g. distance, environment), which produces multiple values to estimate the rate of turnover along a gradient. The non-directional variation approach is used to quantify β-diversity of the entire sampling area, which produces a single value.

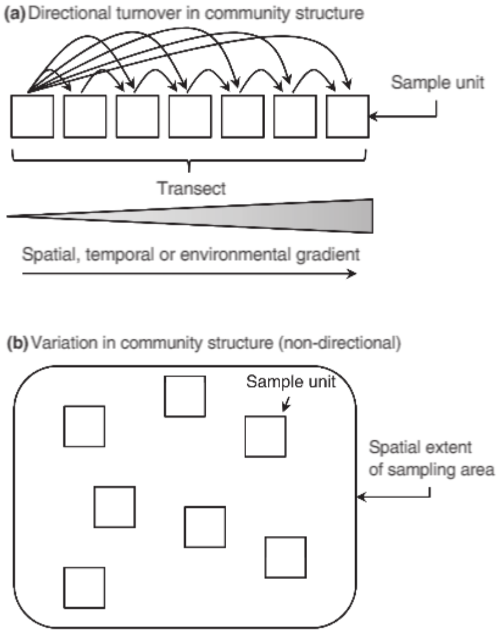

Fig 1.2. The two types of beta-diversity: directional variation along a gradient (a) and non-directional variation within a sample area (b). Directional variation is a pairwise comparison of samples that differ in space (distance), environment (climate, forest cover, soil characteristics, etc.) and time. Non-directional variation is the comparison between two scales – average species in a sample unit (alpha diversity) and total species in the spatial extent (gamma diversity). Figures from Anderson et al. (2011).

Baselga (2010) showed that β-diversity can be a result of two phenomena, loss or gain in species richness from one site to another (nestedness), and the replacement of a set of species in one site by a set of species in another site (turnover). Both turnover and nestedness can collectively reflect β-diversity, and has been widely used in β-diversity studies along gradients of climate (Hortal et al. 2011, Sreekar et al. 2017), land-use (Sreekar et al. 2017), space (Castro-Insua et al. 2016, Viana et al. 2016) and time (Beaten et al. 2012, Angeler et al. 2013). Turnover may reflect important community assembly processes like dispersal limitation and environmental filtering, whereas nestedness may reflect ordered extinction-colonization dynamics (Si et al. 2016).

Anderson et al. (2011) suggested that different measures of β-diversity may result in different conclusions because different measures can emphasize on different properties of biodiversity data – for example, presence/absence, relative abundance and inclusion of joint absences. So, they suggested that there is no single robust measure of β-diversity, and ecologists should carefully match the measure of β-diversity with the relevant question. Anderson et al. (2011) also advocated rigorous application of null models for studying β-diversity. The use of null models in β-diversity studies has stirred discussions on its use and conclusions of studies.

Null models in β-diversity

Null models in β-diversity were developed to account for random sampling effects, and its dependence on species richness (γ-diversity and/or α-diversity). Random sampling effects are caused by random assortment of species into sites caused by random community assembly in nature or by random failure to detect a species at a site (sampling errors; Socolar et al. 2016). For example, β-diversity was observed to decrease with increasing latitude (Kraft et al. 2011). However, when species are shuffled randomly between sites, the expected β-diversity also decreased with increasing latitude, suggesting that the observed latitudinal β-diversity pattern was caused by random sampling effects (Kraft et al. 2011).

Null model generated β-deviation (standardized difference between observed and expected β-diversity) attempted to account for scale-dependent and γ-dependent effects (Kraft et al. 2011). Though widely used in the recent past (Myers et al. 2013, 2015, Ashton et al. 2016), this approach has been criticized for incorporating mechanisms that generate the investigating pattern, violating the fundamental assumption of the null model (Qian *et al.* 2013). Moreover, as randomization processes force β- and γ-diversity to become interdependent, it is difficult discern whether the correlations between β- and γ-diversity are simply caused by differences in species pool or if they reflect important ecological processes (Ulrich *et al.*, 2017). Tuomisto & Ruokolainen (2012) also argued that it is mathematically invalid that β-diversity is dependent on γ-diversity. Furthermore, in contrast to our previous understanding, Bennett & Gilbert (2016) recently showed that the null model does not remove the dependence of β on γ-diversity. Therefore, it is important to identify methods that take away γ-dependence without using null models.

Dependence of β-diversity on species richness

Measures of β-diversity are often considered to be nonlinearly dependent on species richness (Anderson et al. 2011; Ulrich et al. 2018). However, as mentioned above, mathematically, this may be problematic assumption to start a study with (Tuomisto & Ruokolainen 2012). The γ-diversity (if defined as $\gamma = \alpha * \beta$) cannot be a causal factor that determines β-diversity any more than the volume of a cylinder (volume = cross section area * height) can be a causal factor that determines its height (Anonymous Reviewer, *personal communication*). However, just like volume and height, γ-diversity and β-diversity are conceptually independent phenomena that can vary independently of each other. A correlation between γ- and β-diversity emerges only because in real datasets the sampling grain (sampling unit size) is often so small that α-diversity becomes constrained and cannot increase beyond the number of individuals per sampling unit even if there are more species available in the local species pool (Tuomisto et al. 2010a, 2010b). Since γ-diversity is based on the total number of individuals sampled, it can increase with species pool size much further than α-diversity can, and when the α-diversity component cannot increase any more, the β-diversity component has to become dependent (correlated) with γ-diversity. In such cases, conclusions are dependent on γ-diversity, and not β-diversity.

How to avoid dependence of β-diversity on γ-diversity? Anderson et al. (2011) recommended the use of null models to account for the correlation between β- and γ-diversity, and many β-diversity started using them (Kraft et al. 2011, Karp et al. 2012, Myers et al. 2013, 2015, Ashton et al. 2016, Karp et

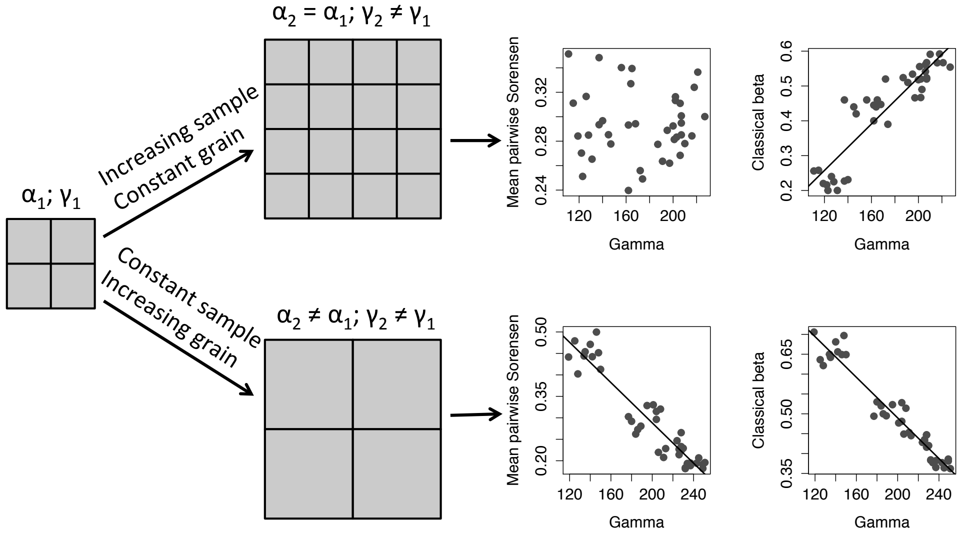

Fig 1.3. Increasing extent size by 1) increasing the number of grains and fixing grain size following Bennett and Gilbert (2016), which increases γ-diversity but keeps α-diversity constant, and by 2) maintaining the number of grains constant and increasing grain size, which increases both α- and γ-diversities. In the first scenario, mean pairwise Sorensen's distance remains constant with increasing γ-diversity, but classical proportional β-diversity increases significantly. In the second scenario, both mean pairwise Sorensen's distance and classical proportional β-diversity show similar patterns, decreasing significantly with increasing γ-diversity. Figure from Rachakonda Sreekar (*unpublished*).

al. 2018). However, many recent studies also cautioned the application of null models, which can result in high artificial rejection rates of focal patterns (type II errors; Qian et al. 2013, Bennett & Gilbert 2016, Ulrich et al. 2017). Instead, recent studies suggested the use of mean pairwise dissimilarity measures of β-diversity to account for effects of sampling intensity and γ-diversity (Bennett and Gilbert 2016, Marion et al. 2017). These studies sought to increase their extent size by fixing grain size and increasing the number of grains, therefore they assume that α-diversity does not increase with γ-diversity across richness gradients (e.g. latitudinal or altitudinal diversity gradient; see Fig. 1.3; Anderson et al. 2011, Barton et al. 2013). This is not appropriate for comparative ecology because α-diversity does not remain constant when sampling from different habitat types with varying γ-diversity (Tuomisto and Ruokolainen 2012). An ideal method is to increase both grain and extent size by varying grain size but keeping the number of grains constant (see Fig. 1.3; Tuomisto and Ruokolainen 2012). As expected, mean pairwise Sorensen's distance was independent of γ-diversity only when grain-size was not allowed to vary with extent size, but was significantly correlated with γ-diversity when both grain- and extent-size were free to vary (Fig. 1.3; Sreekar, *unpublished results*). As both null models and mean pairwise dissimilarity may not be an ideal method to use for accounting for γ-dependence on β-diversity, Ulrich et al. (2018) suggested that as a minimum, species richness (γ-diversity) should be used a statistical covariate in regression analyses.

From natural to human-driven variation

Studies often reached different conclusions as to the fundamental patterns in β-diversity, such as change across habitat types. Although niche compression hypothesis predicted higher β-diversity at lower latitudes (MacArthur 1965, Terborgh 2017), there was never a consensus (Koleff et al. 2003b, Kraft et al. 2011, Qian et al. 2013, Ashton et al. 2016; Fig. 1.4). Around half of the earlier studies have shown that β-diversity declines with increasing latitude (Fig. 1.4). But, in a seminal paper, Kraft et al. (2011) used a null model approach to show that β-deviation (standardized difference between observed and expected β-diversity) among plant communities did not change with increasing latitude. However, Qian *et al.* (2013) and Ashton *et al.* (2016) used the same approach to show increase, decrease and no change in β-deviation when using different datasets.

Studies comparing natural habitats with human-modified habitats are no different. There is also a lack of consensus about higher β-diversity in natural habitats. For example, Kitching et al. (2013) sampled moths in primary and logged forests of Danum valley, Borneo to show that β-diversity is higher in primary forests in comparison with logged forests. Contrastingly, Berry et al.

(2008) sampled trees in the same study area to show that β-diversity is higher

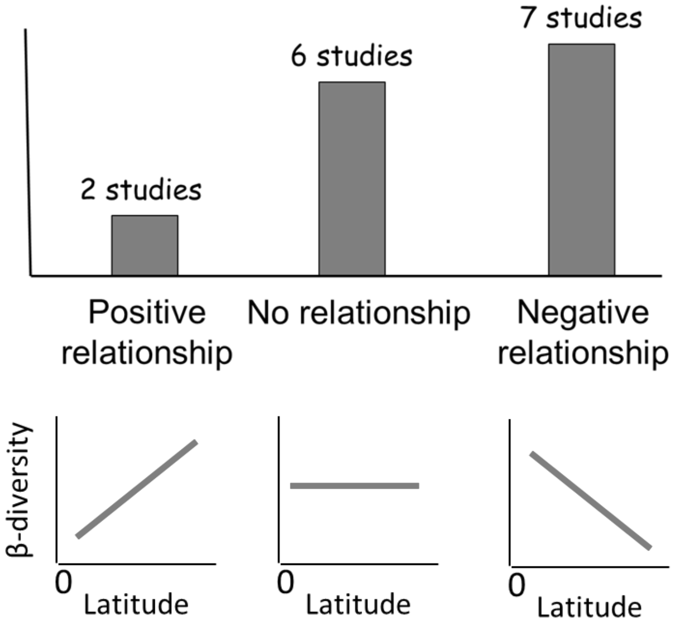

Fig 1.4. Lack of consensus on latitudinal β-diversity patterns among studies. Data from Koleff et al. (2003b).

in logged forests in comparison to primary forests. The results of these two studies were completely different from the results of a recent quantitative synthesis (Newbold et al. 2016), which showed that β-diversity in primary forest is similar to β-diversity in all types of human-modified habitats (secondary forests, plantations, pasture and urban).

Karp et al. (2012) showed that the observed bird β-diversity in high intensity agriculture is higher than forests due to random community assembly. They found out that as bird abundance is generally low in high-intensity agriculture, birds occurred randomly in sample sites. When null models were used to remove random sampling effects (randomly sample individuals while retaining α-diversity), the β-diversity in high intensity agriculture became smaller than primary forests. Terborgh et al. (1990) showed that, in contrast to expectations, bird β-diversity in forests is generally small. When territories of territorial birds were superimposed in an Amazonian lowland forest, as many as 150 species were found to overlap at a single point. Thus, showing that most forest birds are generalists with high α-diversity and low β-diversity (Terborgh et al. 1990, Terborgh 2015). Therefore, within habitat β-diversity should not be used for conservation decision making, and natural habitats with low β-diversity can also have high conservation value.

β-diversity reflects community assembly mechanisms

The prevailing theory for community assembly suggests that environmental filtering in conjunction with dispersal limitation and stochasticity drive β-diversity patterns (Audino et al. 2017). However, the relative importance of community assembly mechanisms change with latitude. (Myers et al. 2013). Dispersal limitation is the main driver for tree β-diversity at lower latitudes, while environmental filtering was the main driver for tree β-diversity at higher latitudes (Myers et al. 2013).

Legendre et al. (2009), Cáceres et al. (2012) and Spasojevic et al. (2016) showed that spatial scale can change the importance of drivers that influence tree community assembly. Increasing spatial scale may result in larger variation in environment like soil and topography; and distinct soil and topography types can shape tree community structure (Davies et al. 2005, Katabuchi et al. 2012). Biotic processes causing conspecific negative density dependence (CNDD) results in lower species aggregation, lower β-diversity and higher species diversity (LaManna et al. 2017a, 2017b). Therefore, if CNDD is higher at lower latitudes (LaManna et al. 2017a), we should expect higher species diversity and lower β-diversity. In contrast, many studies report higher β-diversity at the equator (Fig. 1.4). It has been more than 50 years since Whitaker (1960) coined the term β-diversity, and we still do not understand the basic patterns and drivers of β-diversity.

Quantitative synthesis of β-diversity within different land-use types suggested that all land-use types have similar β-diversity (Newbold et al. 2016). Similarly, the relative importance of community assembly mechanisms appears to remain unchanged with land-use change. For example, Myers et al. (2015)

showed that the relative importance of community assembly mechanisms that drove woody-plant assembly in unburned and burned forests in Missouri, USA was similar to each other. Unfortunately, there aren't many studies that compared community assembly within multiple land-use types. More comparative studies will provide important insights into the mechanisms of community assembly.

β-diversity in biodiversity conservation

Increasing anthropogenic activities is decreasing the biodiversity on our planet, and reducing biodiversity loss is an important aspect of conservation biology. While most field-based studies and quantitative synthesis of biodiversity change are focused on analysis of α-diversity, most biodiversity change is happening through β-diversity (Catano et al. 2017, Hillebrand et al. 2018). However, there are two faces of β-diversity, and both lower and higher β-diversity can be important for biodiversity conservation. It depends on the question and context (Anderson et al. 2011, Socolar et al. 2016; Fig. 1.2).

First, I will introduce within habitat β-diversity. In general, this is a categorical comparison. For example, a comparison of β-diversity values between primary and secondary forests. When a primary forest is degraded into a secondary forest – ranges of specialist species contract, which results in species replacement by generalist species. As generalist species tend to have higher habitat breadth, local communities tend to be similar or homogenized (McKinney et al. 2006). Therefore, hypothetically, primary forests should have higher β-diversity. In most cases, habitats with higher β-diversity is good for biodiversity conservation, as it helps conservation of distinct communities in the landscape. However, the overall richness of species in the community, and especially threatened species should also be considered while using higher β-diversity as an index for biodiversity conservation. A primary forest might harbor multiple threatened species with high α-diversity and low β-diversity (Terborgh 1990), but a secondary forest might harbor no threatened species, low α-diversity, but high β-diversity. Neutral sampling effects can cause high β-diversity in modified landscapes due to low community size (Catano et al.

2017). For example, Karp et al. (2012) showed that high intensive agricultural landscapes had higher β-diversity than forests. Communities in high intensive agricultural landscapes are generally small in both species richness and the number of individuals in a community. Sampling small communities from a meta-community can increase the chances that the two communities are different from one another due to random community assembly in nature. After controlling for such stochastic effects using null models, Karp et al. (2012) showed that forests had higher β-diversity than high intensive agricultural landscapes. Terborgh (2017) suggested that β-diversity in tropical rainforests are generally small, especially for birds. Therefore, comparing between habitat types can be futile, unless conducted at large spatial scales with variation in environment and in presence of major biogeographic barriers.

Second, I will introduce the across habitat β-diversity. In general, this is a continuous comparison (Fig. 1.2). For example, a comparison of pairwise β-diversity values along any gradient. For example, along gradients of rainfall, land-use change, geographic distance, elevation, etc. Multiple community assembly mechanisms like environmental filtering and dispersal limitation can restrict the distribution of species causing species aggregations (Myers et al. 2013, Catano et al. 2017). In the context of biodiversity conservation, lower β-diversity along a disturbance gradient is good, in most cases. For example, lower β-diversity between primary and secondary forests (land-use gradient) is a good indicator of biodiversity maintenance by the secondary forest. Higher β-diversity along the same gradient suggests a loss of forest specialist species and replacement of generalist species that prefer human-modified habitats. Similarly, higher β-diversity due to climate change indicates that communities are vulnerable, but a lower β-diversity suggest that communities are comparatively resilient. Analysing the importance of land-use, elevation and spatial gradients together can have important implications for protected area and restoration planning (Socolar et al. 2016). For example, equal importance of land-use and elevation on variation in β-diversity suggests that natural habitats should be protected along the complete elevation range (Sreekar et al.

2017). However, most studies that determined the importance of multiple gradients on β-diversity usually sampled at small spatial scales. At small spatial scales, previous studies have suggested that land-use change is the most important variable for explaining β-diversity (Becca et al. 2017, Audino et al 2017). Future studies should determine the drivers of community assembly at multiple spatial scales.

Thesis outline

This thesis is comprised of four chapters motivated by research questions that are crucial for advancing our understanding of β-diversity within and among land-use types across multiple spatial scales.

1. Why is there a lack of consensus on basic β-diversity patterns?
2. Can intensive agriculture erase β-diversity in natural habitats?
3. Are the drivers of community assembly affected by spatial scale?

In Chapter Two, I collate a large tree dataset to answer the first question. I will determine the relationship between latitude and β-diversity at different spatial scales. The relationship between latitude and β-diversity is highly variable (Fig. 1.4). In many studies, the relationship is negative, where β-diversity peaks at lower latitudes. In other studies, there is no significant relationship, where β-diversity is similar across all latitudes (see Fig. 1.4). A possible reason for this lack of consensus among studies is data are often collected at different spatial scales (sampling effects). As β-diversity has a non-linear relationship with spatial scale (Rosindell et al. 2011), we can expect the relationship between β-diversity and latitude to depend on the spatial scale at which the data was collected.

I used a large tree dataset of around one million individual trees belonging to around 3000 species across 15 permanent ForestGEO plots in the Asia-Pacific region (Anderson-Teixeira et al. 2015). Each ForestGEO plot was ≥15 ha. This allowed me to sample at different spatial scales and test the alternative hypothesis – spatial scale changes the relationship between beta-diversity and latitude. The main aim of Chapter Two is to determine the drivers of β-diversity patterns along latitudinal gradients. This could help better understand the importance of spatial scale in β-diversity studies across all fields of study.

The change in species composition (β-diversity) from the base of a mountain to its peak is a well-known and a striking biodiversity pattern. It is relatively unknown, if such patterns can persist in human-modified environments. In Chapter Three, I focus on the effects of horizontal (geographic) and vertical (elevation) distance on β-diversity in natural and human-modified environments. I use a large bird dataset of around 30,000 observations and 120 species along an elevation gradient with steep climatic changes. Using this dataset, I test the alternative hypothesis by comparing the β-diversity along an elevation gradient in three different habitats: protected rainforests, reserve buffer and intensive agriculture. This could help us understand if β-diversity patterns can persist in human-modified landscapes.

Niche-based processes are known to structure biotic communities along gradients of land-use change (Audino et al. 2017, Becca et al. 2017). But, studies are often restricted to small spatial scales with limited to no variation in environment and space (dispersal barriers). In Chapter Four, I estimate the relative importance of community assembly mechanisms that structure communities at multiple spatial scales. The community assembly theory states that species composition is influenced by niche-based processes in conjunction with dispersal limitation and stochasticity (Hubbell 2001, Rosindell et al. 2011, Audino et al. 2017). Niche theory suggests that local scale environmental factors like habitat and soil type; and landscape scale environmental factors like elevation, temperature and precipitation determine biotic species composition change – environment limits or enables dispersal of organisms (Leite et al. 2013, Audino et al. 2017). However, dispersal limitation can also be important due to spatial attributes like geographic barriers that limit dispersal of organisms even in the presence of favorable environmental conditions (Ricklefs 1987, Hubbell 2001). Partitioning the variation explained by environmental and spatial variables will help us understand the relative importance of community assembly mechanisms in structuring communities at multiple spatial scales.

I use a large bird dataset of around 37,000 observations belonging to 190 species across 32 two km transects along land-use (natural rainforest to intensive agriculture), elevation (45–1295 m) and spatial (5-500 km) gradients in the Western Ghats–Sri Lanka biodiversity hotspot. This allowed me to sample at two different spatial scales within the biodiversity hotspot. The large spatial scale included all transects in the variation partitioning analysis and the intermediate spatial scale analyzed transects in the Western Ghats and Sri Lanka, separately. The main aim of Chapter Four is to determine the relative importance of different community assembly mechanisms in the biodiversity hotspot. This could help understand the importance of considering natural variation along with human impacts in a biodiversity conservation context.

In the final part of the thesis, I synthesize the findings of the next four chapters and expand our knowledge on the patterns and processes that shape biodiversity in the Anthropocene.

References

Anderson MJ, *et al.* (2011) Navigating the multiple meanings of β-diversity: a roadmap for the practicing ecologist. *Ecol. Lett.* 14:19–28.

Anderson-Teixeira KJ, *et al.* (2015) CTFS-ForestGEO: a worldwide network monitoring forests in an era of global change. *Glob. Chang. Biol.* 21:528–549.

Angeler DG, Drakare S (2013) Tracing alpha, beta, and gamma diversity responses to environmental change in boreal lakes. *Oecologia,* 172:1191–1202.

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

Ashton LA, *et. al*. (2016) Vertical stratification of moths across elevation and latitude. *J. Biogeogr.* 43:59-69.

Audino LD, Murphy SJ, Zambaldi L, Louzada J, Comita LS (2017) Drivers of community assembly in tropical forest restoration sites: role of local environment, landscape and space. *Ecol. Appl.* 20:1469–1478.

Bagchi R, *et al.* (2011). Spatial patterns reveal negative density dependence and habitat association in tropical trees. *Ecology* 92:1723–1729.

Barton PS, Cunningham SA, Manning AD, Gibb H, Lindenmayer DB, Didham RK (2013) The spatial scaling of beta diversity. *Glob. Ecol. Biogeogr.* 22:639-647.

Barwell LJ, Isaac NJ, Kunin WE (2015) Measuring beta diversity with species abundance data. *J. Anim. Ecol.* 84:1112–1122.

Baselga A (2010) Partitioning the turnover and nestedness components of beta diversity. *Glob. Ecol. Biogeogr.* 19:134–143.

Becca G, *et. al.* (2017) High mammal turnover in forest patches immersed in biofuel plantations. *Biol. Conserv.* 210:352–359.

Bennett JR, Gilbert B (2016) Contrasting beta diversity among regions: how do classical and multivariate approaches compare? *Glob. Ecol. Biogeogr.* 25:368–377.

Berry NJ, Phillips OL, Ong RC, Hamer KC (2008) Impacts of selective logging on tree diversity across a rainforest landscape: the importance of spatial scale. *Landsc. Ecol.* 23:915-929.

Burivalova Z, Sekercioglu CH, Koh LP (2014) Thresholds of logging intensity to maintain tropical forest biodiversity. *Curr. Biol.* 24:1–6.

Cáceres MD, *et al.* (2012) The variation of tree beta diversity across a global network of forest plots. *Glob. Ecol. Biogeogr.* 21:1191–1202.

Castro-Insua A, Gomez-Rodriguez C, Baselga A (2016) Break the pattern: breakpoints in beta diversity of vertebrates are general across clades and suggest common historical causes. *Glob. Ecol. Biogeogr.* 25:1279–1283.

Catano CP, Dickson TL, Myers JA (2017) Dispersal and neutral sampling mediate contingent effects of disturbance on plant beta-diversity: a meta-analysis. *Ecol. Lett.* 20:347–356.

Davies SJ, Tan S, Lafrankie JV, Potts MD (2005) *Soil-related floristic variation in the hyperdiverse dipterocarp forest in Lambir Hills, Sarawak.* Pollination

Ecology and Rain forest Diversity, Sarawak Studies (eds: D. Roubik, S. Sakai and A. Hamid), pp. 22–34. Springer-Verlag, New York, USA.

Dony JG (1963) The expectation of plant records from prescribed areas. *Watsonia* 5: 377-385.

Gibson L, *et al.* (2011) Primary forests are irreplaceable for sustaining tropical biodiversity. *Nature* 478:378-381.

Hillebrand H, *et al.* (2018) Biodiversity change is uncoupled from species richness trends: consequences for conservation and monitoring. *J. Appl. Ecol.* 55:169-184.

Hubbell SP (2001) *The unified neutral theory of biodiversity and biogeography*. Princeton University Press, Princeton, NJ.

Hortal J, *et al.* (2011) Ice age climate, evolutionary constraints and diversity patterns of European dung beetles. *Ecol. Lett.* 14:741-748.

Jaccard P (1901) Étude comparative de la distribution florale dans une portion des Alpes et des jura. *Bulletin de la Société Vaudoise des Sciences Naturelles* 37:547–579.

Leite MDS, Tambosi LR, Romitelli I, Metzger JP (2013) Landscape ecology perspective in restoration projects for biodiversity conservation: a review. Natureza & Conservacao 11:108–118.

Karp DS, Frishkoff LO, Echeverri A, Zook J, Juarez P, Chan KMA (2018) Agriculture erases climate-driven β-diversity in neotropical bird communities. *Glob. Chan. Biol.* 24:338–349.

Karp DS, Rominger AJ, Zook J, Ranganathan J, Ehrlich PR, Daily GC (2012) Intensive agriculture erodes beta-diversity at large scales. *Ecol. Lett.* 15:963-970.

Kitching RL, Ashton LA, Nakamura A, Whitaker T, Khen CV (2013) Distance-driven species turnover in Bornean rainforests: homogeneity and heterogeneity in primary and post-logging forests. *Ecography* 36:675-682.

Koleff P, Gaston KJ, Lennon JJ (2003) Measuring beta diversity for presence-absence data. *J. Anim. Ecol.* 72:367-382.

Koleff P, Lennon JJ, Gaston KJ (2003) Are there latitudinal gradients in species turnover? *Glob. Ecol. Biogeogr.* 12:483-498.

Kraft NJB, *et al.* (2011) Disentangling the drivers of β diversity along latitudinal and elevational gradients. *Science* 333:1755-1758.

Katabuchi M, Kurokawa H, Davies SJ, Tan S, Nakashizuka T (2012) Soil resource availability shapes community trait structure in a species-rich dipterocarp forest. *J. Ecol.* 100:643–651.

LaManna JA, *et al.* (2017a) Negative density dependence mediates biodiversity-productivity relationships across scales. *Nature Ecol. Evol.*, 1:1107–1115.

LaManna JA, *et al.* (2017b) Plant diversity increases with the strength of negative density dependence at the global scale. *Science* 356:1389–1392.

Legendre P, Mi X, Ren H, Ma K, Yu M, Sun I, He F (2009) Partitioning beta diversity in a subtropical broad-leaved forest of China. *Ecology* 90:663–674.

MacArthur RH (1965) Patterns of species diversity. *Biol. Rev. Camb. Philos. Soc.* 40:510-533.

Marion ZH, Fordyce JA, Fitzpatrick BM (2017) Pairwise beta diversity resolves an underappreciated source of confusion in calculating species turnover. *Ecology* 98:933–939.

McKinney ML (2006) Urbanization as a major cause of biotic homogenization. *Biol. Conserv.* 127:247-260.

Myers JA, Chase JM, Jimenez I, Jorgensen PM, Murakami AA, Zambrana NP, Seidel R (2013) Beta-diversity in temperate and tropical forests reflect dissimilar mechanisms of community assembly. *Ecol. Lett.* 16:151-157.

Myers JA, Chase JM, Crandall, RM, Jimenez I (2015) Disturbance alters beta-diversity but not relative importance of community assembly mechanisms. *J. Ecol.* 103:1291–1299.

Newbold T, *et.al.* (2016) Global patterns of terrestrial assemblage turnover within and among land uses. *Ecography* 39:1151-1163.

Qian H, Chen S, Mao L, Ouyang Z (2013) Drivers of β-diversity along latitudinal gradients revisited. *Glob. Ecol. Biogeogr.* 22:659-670.

Ricklefs RE (1987) Community diversity – relative roles of local and regional processes. *Science* 235:167–171.

Ricotta C, Carranza ML, Avena G (2002) Computing β-diversity from species-area curves. *Basic Appl. Ecol.* 3:15-18.

Rosenzweig ML (1995) *Species diversity in space and time*. Cambridge University Press, U.K.

Rosindell J, Hubbell SP, Etienne RS (2011) The unified neutral theory of biodiversity and biogeography at age ten. *Trends Ecol. Evol.*, 26:340–348.

Si X, Baselga A, Leprieur F, Song X, Ding P (2016) Selective extinction drives taxonomic and functional alpha and beta diversities in island bird assemblages. *J. Anim. Ecol.* 85:409-418.

Spasojevic MJ, Turner BL, Myers JA (2016) When does intraspecific trait variation contribute to functional beta-diversity? *J. Ecol.* 104:487–496.

Socolar JB, Gilroy JJ, Kunin WE, Edwards DP (2016) How should beta-diversity inform biodiversity conservation. *Trends Ecol. Evol.* 31:67-80.

Sørensen T (1948) A method of establishing groups of equal amplitude in plant sociology based on similarity of species and its application to the analyses of the vegetation on Danish commons. *Biologiske Skrifter* 5:1-34.

Sreekar R, *et al*. (2015). The effect of land use on the diversity and mass-abundance relationships of understory insectivores in Sri Lanka and southern India. *Sci. Rep. 5,* 11569.

Sreekar R, *et al.* (2017) Horizontal and vertical species turnover in tropical birds in habitats with differing land use. *Biol. Lett.* 13: 2017.0186.

Terborgh J, Robinson SK, Parker TA, Munn CA, Pierpont N (1990) Structure and orgonisation of an Amazonian forest bird community. *Ecol. Monogr.* 60:213-238.

Terborgh JW (2015) Toward a trophic theory of species diversity. *Proc. Natl. Acad. Sci. USA* 37:11415-11422.

Tuomisto H (2010a) A diversity of beta diversities: straightening up a concept gone awry. Part 1. Defining beta diversity as a function of alpha and gamma diversity. *Ecography* 33:2-22.

Tuomisto H (2010b) A diversity of beta diversities: straightening up a concept gone awry. Part 2. Quantifying beta diversity and related phenomena. *Ecography* 33:2-22.

Tuomisto H, Ruokolainen K (2012) Comment on “Disentangling the drivers of β diversity along latitudinal and elevational gradients”. *Science* 335:1573.

Ulrich W, Baselga A, Kusumoto B, Shiono T, Tuomisto H, Kubota Y (2017) The tangled link between β- and γ-diversity: a Narcissus effect weakens statistical influences in null model analyses of diversity patterns. *Glob. Ecol. Biogeogr.* 26:1–5.

Viana DS, *et al.* (2016) Assembly mechanisms determining high species turnover in aquatic communities over regional and continental scales. *Ecography* 39:281-288.

Whittaker RH (1960) Vegetation of Siskiyou Mountains, Oregon and California. *Ecol. Monogr*. 30:279–338.

Williams CB (1964) *Patterns in the balance of nature.* Academic Press, U.K.

Chapter 2

Spatial scale changes the relationship between beta diversity, species richness and latitude

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2.1 Summary

The relationship between β-diversity and latitude still remains to be a core question in ecology because of the lack of consensus between studies. One hypothesis for the lack of consensus between studies is that spatial scale changes the relationship between latitude and β-diversity. Here, we test this hypothesis using tree data from 15 large-scale forest plots (≥15 ha, dbh ≥1 cm) across a latitudinal gradient (3-30°) in the Asia-Pacific region. We found that the observed β-diversity decreased with increasing latitude when sampling local tree communities at small spatial scale (grain size ≤0.1 ha), but the observed β-diversity did not change with latitude when sampling at large spatial scales (≥0.25 ha). Differences in latitudinal β-diversity gradients across spatial scales were caused by pooled species richness (γ-diversity), which influenced observed β-diversity values at small spatial scales, but not at large spatial scales. Therefore, spatial scale changes the relationship between β-diversity, γ-diversity and latitude, and improving sample representativeness avoids the γ-dependence of β-diversity.

2.2 Introduction

Decreasing species richness from the equator to the poles is one of the best-recognized patterns in ecology [1,2]. This latitudinal pattern in species richness is consistent across different spatial scales, habitats, and taxonomic groups [3]. However, latitudinal differences in species co-occurrence still remain a core question in ecology because of the lack of consensus on the patterns of site-to-site variability in species composition (β-diversity) across latitudinal gradients [4-7]. Difficulties in disentangling the variation caused by pooled species richness (γ-diversity) and site-to-site variation in species composition (β-diversity), as well as in the estimation of β-diversity itself, pose challenges to understanding the latitudinal β-diversity patterns.

Null model approaches have been proposed to account for variation caused by γ-diversity, by calculating the rate of deviation of observed β-diversity from a null-model generated stochastic expectation (hereafter β-deviation), and have been widely used in studies on β-diversity [4,6,8-10]. Although recent studies have criticized the use of null models (see discussion) [7,11,12], they still provide heuristic values that may help understand how non-random (biological) processes structure local communities. A β-deviation of zero indicates that the observed β-diversity is similar to random sampling, while positive β-deviation values reflect species aggregation [6,8] As the degree of species aggregation is known to increase with grain size [13], we should expect spatial-scale effects on β-deviation as well [10,11].

The majority of previous studies that examined latitudinal tree β-diversity patterns used small grain sizes to measure α-diversity (≤0.1 ha) [5-7,14]. However, studies have demonstrated that β-diversity metrics may risk false conclusions when data is collected using such small grains [15,16], primarily because biodiversity patterns measured at small grains are weaker and more variable [17,18]. Observations show that β-diversity decreases exponentially with increasing spatial scale [19], and can be divided into two segments (figure 2.1): the first segment where the grain sizes are small and its influence on β-diversity is high, and the second segment where grain sizes are comparatively large and its influence on β-diversity is low (figure 2.1). Steeper slopes in the first segment can be caused by sampling at small grains that result in artificially lower local (α) diversity and higher γ:αratios (β-diversity; statistical Type I errors). A lower influence of α-diversity results in the correlation between β- and γ-diversity [20]. This potentially prevents accurate estimation of β-diversity, especially when γ-diversity varies with environmental gradients such as elevation and latitude [6,21]. Previous studies have shown that the influence of γ-diversity on β-diversity decreases with increasing grain size [6,22] and changes β-diversity patterns across broad-scale ecological gradients [22]. The largest grain size in the previous studies was 0.1 ha [22].

In this study, we compare the relationship between β-diversity, γ-diversity and latitude at multiple spatial scales. First, we use tree census data from two 50 ha plots to determine: i) the sensitivity of β-diversity to grain size; and ii) if the null-model generated β-deviation is also sensitive to grain size.

Second, we use tree census data from 15 plots (≥15 ha) along a latitudinal gradient in the Asia-Pacific region to assess: iii) if the relationship between β-diversity and latitude changes with increasing grain size; and iv) if the relationship between the null model generated β-deviation and latitude remains similar at all grain sizes.

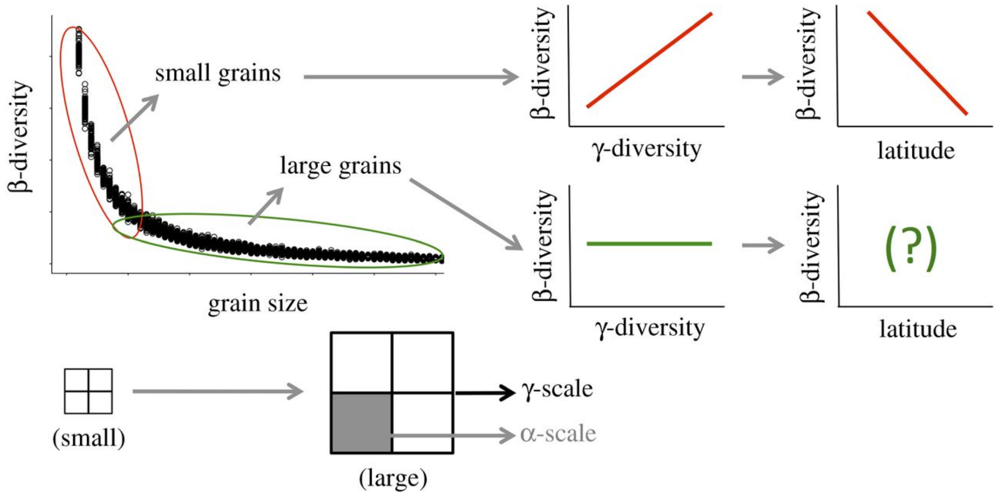


Figure 2.1. Illustration of the relationship between observed β-diversity and spatial scale (grain size) showing a bi-phasic curve: 1) large variation at small spatial scales, and 2) small variation at large spatial scales. Decreasing γ-diversity with increasing latitude is well known [3], and if β-diversity is correlated with γ-diversity at small spatial scales, we should also expect β-diversity to decline with increasing latitude. However, reliance of β-diversity on γ-diversity is mathematically invalid as long as α-diversity is large and allowed to vary freely with γ-diversity [15]. Therefore, at large spatial scales, we should expect β-diversity not to be reliant on γ-diversity, and the latitudinal β-diversity patterns in such scenarios remain unknown.

2.3 Methods

Sensitivity of β-diversity

We compared the effects of grain size on classical multiplicative β-diversity and null-model generated β-deviation using woody-plant data from a 52-ha (1040 m x 500 m) forest plot in Lambir Hills National Park, Sarawak, Malaysia (4°186' N, 114°017' E; elevation: 104-244 m) and a 50-ha forest plot on Barro

Colorado Island (BCI), Panama (9°154' N, 79°846’ W; elevation: 120-160 m). All stems with diameter at breast height (DBH) 1 cm or greater were identified to species and precisely mapped across the entire area. The Lambir and BCI plots contain more than 350,000 and 200,000 mapped trees ($\geq$1 cm DBH) belonging to c. 1200 and c. 300 species, respectively [23-27]. All stems that are $\geq$1 cm were identified to species and precisely mapped across the entire area. Nothing is omitted and nearly all individuals are assigned to distinct taxa. The Lambir and BCI plots have been censused approximately every five years since 1991 and 1981, respectively. Our analysis of Lambir and BCI plots is based on the 2007-08 census and 2010 census, respectively. The 52 ha (1040 m X 500 m) Lambir plot was trimmed to 50 ha (1000 m X 500 m) to evenly fit multiple non-overlapping grains ranging from 10 m X 10 m to 150 m X 150 m.

A grain is a sample at local scale (α) and an extent (γ) is a set of multiple grains. In this study, each extent had a set of nine grains of varying sizes (10 m x 10 m to 150 m x 150 m), all contained within one of the two 50-ha plots (Lambir and BCI). We chose the first sampling grain randomly and the remaining eight were chosen alongside this in a 3 x 3 matrix design. We then repeated the sampling 25 times for each grain size. We measured α-diversity as the mean species richness of each grain and γ-diversity as the species richness of an extent.

We calculated three classical measures of β-diversity (multiplicative β-diversity, proportional β-diversity and z-value of the species-area relationship) and two multivariate distance measures of β-diversity (mean pairwise Sørensen distance and Hellinger’s distance). We calculated:

(i) Classical multiplicative β-diversity as γ/α.

(ii) Classical proportional β-diversity as $1-(\alpha/\gamma)$.

(iii) z-value [28] of the species-area relationship as $\log(\gamma)-\log(\alpha)/\log(\text{grain number})$.

(iv) Mean pairwise Sørensen distance using ‘beta.pair’ function in *betapart* package in R (http://www.r-project.org/).

(v) Hellinger’s distance using ‘beta.div’ function in *adespatial* package in R.

In this paper we only present the results of classical multiplicative β-diversity because all metrics were highly correlated with each other (Pearson $r > 0.95$).

To determine if β-diversity deviated from the null expectations of random sampling (standardized β-deviation, which we refer to as β-deviation), we compared β-diversity of observed and randomized datasets [4,6]. Specifically, we generated randomized datasets by randomizing trees (≥1 cm DBH) across all nine grains, while retaining the relative species abundance across the extent and the total number of individuals in each grain. This accounts for variation in γ-diversity [4,6]. We generated 1000 randomized datasets for each sampling design. We calculated β-deviation = $(\beta_{obs} - \beta_{rand})/SD_{rand}$, where β_{obs} is the observed β-diversity, and β_{rand} and SD_{rand} are the mean and standard deviation, respectively, of the expected β-diversity. Under the null hypothesis of equal values for the observed and expected β-diversity, the distribution of β-deviation is approximately standard normal [29], which we assumed when calculating P-values (i.e., 95% of β-deviation values are expected to fall in the range of -1.96 to 1.96) [6].

Latitudinal β-diversity patterns

We used tree data from 15 long-term, large-scale forest dynamics plots along a latitudinal gradient from Papua New Guinea to northern China. The Center for Tropical Forest Science/Smithsonian Institution Global Earth Observatories (CTFS/SIGEO; http://www.sigeo.si.edu/) and the Chinese Forest Biodiversity Network (CForBio; http://cfbiodiv.org/) coordinated data collections in all plots: Badagongshan, Fushan, Gutianshan, Hainan, Heishiding, Lambir, Lienhuachih, Mo Singto, Nonggang, Palanan, Pasoh, Sinharaja, Tiantongshan, Wanang, Xishuangbanna (electronic supplementary material, figure S2.1). Each of the 15 plots covers 15 ha to 52 ha of forest in which all stems with diameter at breast height (DBH) 1 cm or greater were identified and precisely mapped across the entire area.

For analyses of latitudinal β-diversity patterns, we use 20 grains of varying sizes: 10 m x 10 m (0.01 ha), 20 m x 20 m (0.04 ha), 30 m x 30 m (0.09 ha), 50 m x 50 m (0.25 ha), 70 m x 70 m (0.49 ha) and 100 m x 100 m (1 ha).

We used a nested design, where we chose the first grain randomly and the remaining 19 next to each other in a 4 x 5 matrix design. We did not fit 100 m x 100 m grains into Palanan and Nonggang plots due to their small size (<20 ha). Extent size represents the combination of 20 grains, and therefore extent size (γ-scale) varies with grain size (α-scale). We measured α-diversity as the mean species richness of each grain and γ-diversity as the species richness of an extent (electronic supplementary material, figure S2.2, figure S2.3). We used the two most widely used metrics of β-diversity, classical multiplicative β-diversity ($\beta = \gamma/\alpha$) [30] and mean pairwise Sørensen dissimilarity distance as measures of β-diversity [31]. These two metrics were highly correlated with proportional beta, z-value and Hellinger's distance (Pearson $r > 0.89$; electronic supplementary material, figure S2.4). A randomized null-model approach was used to measure the deviation of observed β-diversity from the null expectations of random sampling (β-deviation; see above for details). We also calculated the rate of deviation of observed mean pairwise Sørensen from a null-model generated stochastic expectation (hereafter pairwise Sørensen deviation). We extracted mean monthly temperature and mean annual precipitation data for each plot from the WORLDCLIM database version 1.4 [32].

Data analysis

Tree β-diversity often shows a non-linear bi-phasic curve with spatial scale, with faster change in β-diversity values at small spatial scales, and slower change at comparatively larger spatial scales (figure 2.1) [19]. We therefore fitted a regression model with segmented relationships between β-diversity and spatial scale to estimate a threshold between small and large spatial scale (see figure 2.1). Segmented-regression is a method where two regression lines are fitted onto an independent variable (grain size in our analysis), which are joined together at a break point [33]. It can be used to detect changes in model fits and can be important in decision-making.

We used general linear models with normal error structure to determine the change in β-diversity and β-deviation of different grain sizes with γ-diversity and latitude. We did not include temperature in the models as it was highly correlated with latitude (Pearson $r = 0.9$, $p < 0.001$), but precipitation was included as a covariate. We used backward elimination technique to simplify the models. We $\log_e$ transformed γ-diversity prior to analysis and used absolute values of latitude. We removed the Lambir site from the models determining the change in β-deviation with varying γ-diversity and latitude because of high heteroscedasticity. Lambir had β-deviation (spatial aggregation) values up to two times higher than any other site, which may be caused by the presence of distinct soil types and strong habitat associations within this particular plot [34,35]. All analyses were conducted in the statistical program R (R Core Team, v. 3.3.1). The data are available in supplementary information (electronic supplementary material, table S2.1) and on request from ForestGEO (http://forestgeo.si.edu) and CForBio (http://cfbiodiv.org). The R-codes for the analyses of the sensitivity of β-diversity and latitudinal β-diversity patterns are available in the electronic supplementary material, appendix S2.1 and appendix S.2.2, respectively.

2.4 Results

Sensitivity of β-diversity

Grain size significantly influenced classical multiplicative β-diversity at both tropical forest sites with a sharp decrease in values at very small grains (Lambir: $R^2 = 0.94$, $P < 0.001$; BCI: $R^2 = 0.97$, $P < 0.001$; figure 2.2). The slope of the first segment (10 m x 10 m to 35 m x 35 m; Lambir: -0.110 ± 0.005 [SE]; BCI: -0.066 ± 0.003) was c. 16 times higher than that of the second (Lambir: -0.007 ± 0.0006; BCI: -0.004 ± 0.0003) at both sites (figure 2.2). Grain size had a very strong relationship with both number of individuals sampled and γ-diversity ($R^2 > 0.95$). For both Lambir and BCI sites, β-deviation did not differ from stochastic expectation at small grain sizes ($|\beta\text{-deviation}| < 1.96$), but increased with grain size (Lambir: $R^2 = 0.28$, $P < 0.001$; BCI: $R^2 = 0.63$, $P < 0.001$; figure 2.2).

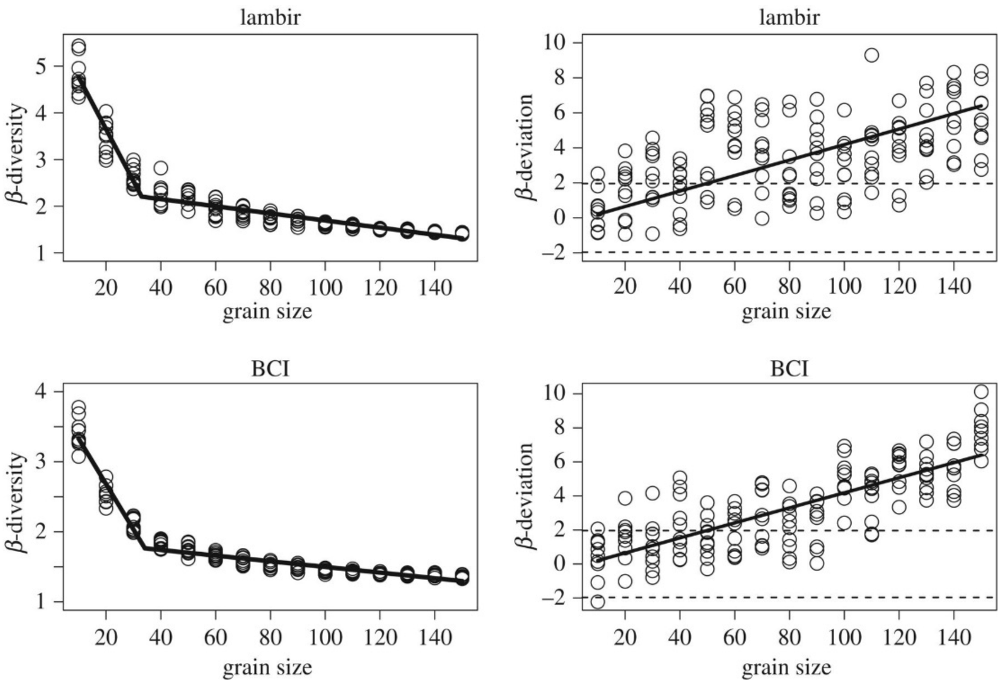


Figure 2.2. Variation in classical multiplicative β-diversity and β-deviation with increasing grain size in Lambir, Malaysia and BCI, Panama. β-deviation of zero indicates that the observed pattern does not differ from random sampling. The dashed lines in β-deviation plots represent the criterion (±1.96 standard deviations) for assessing the statistical significance. The x-axis represents grain size at α-scale (e.g. 50 = 50 m x 50 m).

Latitudinal β-diversity patterns

Changes in precipitation did not affect either of the β-diversity metrics (classical multiplicative and mean pairwise Sørensen) at any grain size (electronic supplementary material, table S2.2), and precipitation was therefore eliminated from all models. Both the β-diversity metrics increased significantly with γ-diversity at small grains (10 m x 10 m to 30 m x 30 m), but showed no relationship with γ-diversity at larger grains (50 m x 50 m to 100 m x 100 m; figure 2.3; electronic supplementary material, figure S2.5). Latitudinal β-diversity patterns were similar. Both the measured β-diversity indices decreased significantly with increasing latitude while sampling at small grains (10 m x 10 m to 30 m x 30 m), but showed no relationship with latitude at relatively larger grains (50 m x 50 m to 100 m x 100 m; figure 2.4; electronic supplementary material, figure S2.5). The γ-diversity was highly correlated with α-diversity at all grain sizes ($R^2 > 0.84$, $p < 0.01$), and the number of individuals in each grain did not change with latitude ($R^2 = 0.001$; $P = 0.85$).

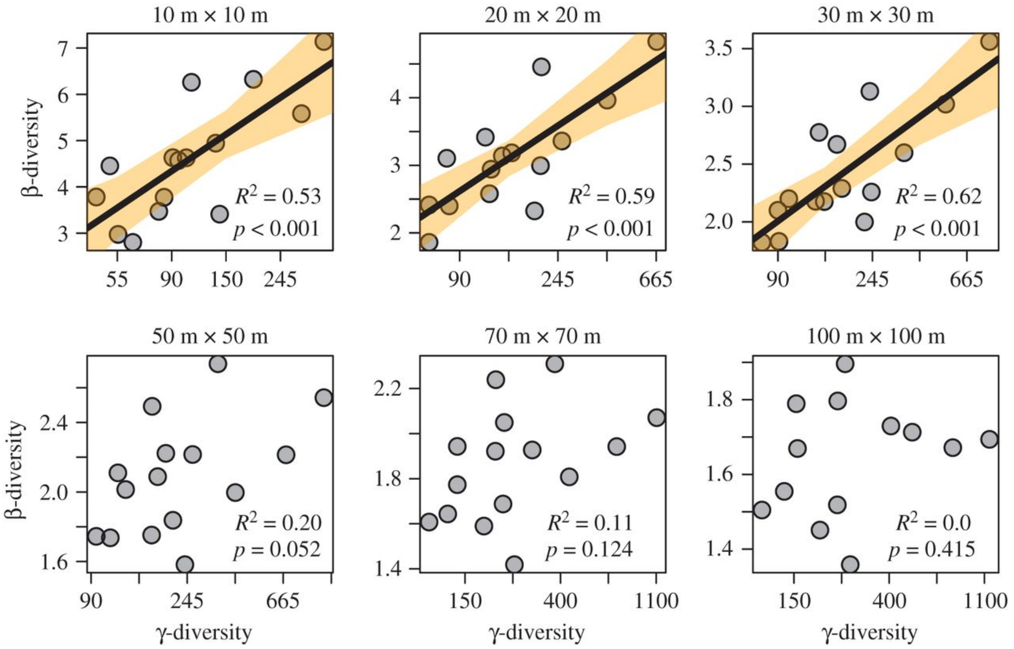


Figure 2.3. Classical multiplicative β-diversity increased with γ-diversity when sampling at small grains (10 m x 10 m to 30 m x 30 m) within each ForestGEO plot, but showed no relationship with γ-diversity at larger grains (50 m x 50 m to 100 m x 100 m).

Changes in precipitation did not affect either β-deviation or Sørensen-deviation at any grain size, and so precipitation was eliminated from all models (electronic supplementary material, table S2.3). Standardized β-deviation did not vary with either γ-diversity or latitude at all grain sizes (figure 2.5; electronic supplementary material, table S2.4). The pairwise Sørensen deviation was similar to β-deviation. The values of pairwise Sørensen deviation also did not vary with either γ-diversity or latitude at all grain sizes (electronic supplementary material, figure S2.6).

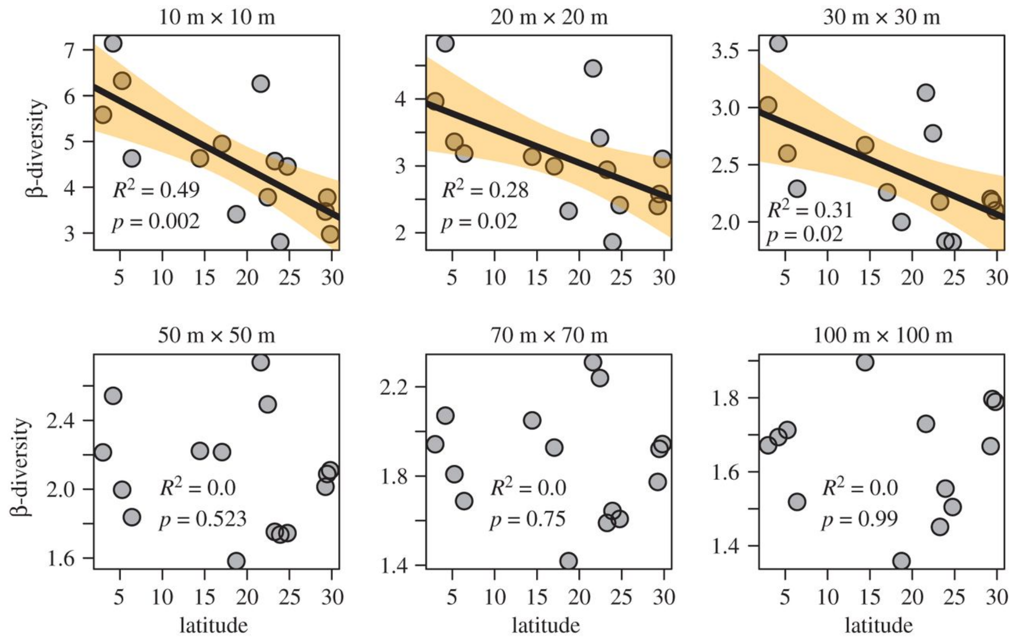


Figure 2.4. Classical multiplicative β-diversity decreased with increasing latitude when sampling at small grains (10 m x 10 m to 30 m x 30 m) within each ForestGEO plot, but showed no relationship with latitude at larger grains (50 m x 50 m to 100 m x 100 m).

2.5 Discussion

Our results demonstrate that latitudinal β-diversity gradients are strongly dependent on spatial scale (grain size). We found that β-diversity was highly dependent on γ-diversity at small grains, but not at large grains (figure 2.3; electronic supplementary material, figure S2.4). Our study therefore confirms that the use of large grains still remains to be the best-known method for measuring γ-independent β-diversity [15, 36, 37], unless questions specific to β-diversity at smaller spatial scales are being addressed. Their correlation is problematic because variation in γ-diversity alone can account for gradients in β-diversity [6]. At relatively large grains (≥0.25 ha), where β-diversity is not influenced by γ-diversity, β-diversity remained similar across the latitudinal gradient (figure 2.4; electronic supplementary material, figure S2.4).

It should be noted that the grain size is relative and will vary with sampling method and taxon. Our study sampled all trees ≥ 1 cm DBH, but when sampling trees ≥ 10 cm DBH even a grain size of 100 m x 100 m can be considered small [38]. Sampling using small grains could explain the correlation between β- and γ-diversity. For example, let us assume a homogeneous community with 100 species and a β-diversity (β = γ/α) of one, i.e. α-diversity is equal to γ-diversity. But, if only 40 individuals are sampled at α-scale, the probability of β-diversity being one is zero, simply caused by constraining α-diversity that makes β-diversity dependent on γ-diversity [15]. Therefore, β-diversity at small grains is higher at the equator because of sampling inadequacy, which makes it dependent on γ-diversity [6,15,20].

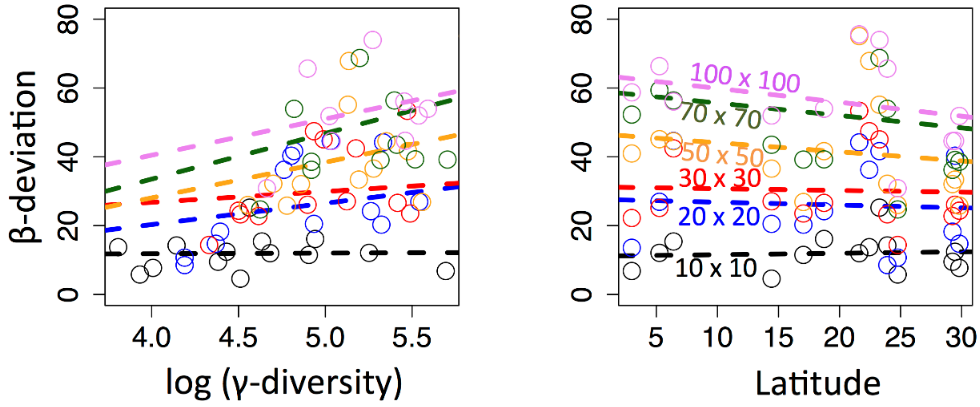


Figure 2.5. Standardized β-deviation did not vary significantly with γ-diversity and latitude at any grain size. However, β-deviation values increased significantly with grain size, indicating stronger intraspecific aggregation at larger spatial scales. Dashed lines indicate non-significant relationships.

Methods to account for γ-dependence of β-diversity have received strong scientific attention and stirred discussions [6,7,10-12]. Previous studies used null-model generated β-deviation to account for γ-dependent effects [4,6,10]. But recent studies have challenged the use of β-deviation for comparing between habitat types [11,12], as studies that used β-deviation have resulted in contrasting conclusions within and across studies [4,6,7]. Recently, Ulrich *et al.* [12] has showed that the use of null models can result in high artificial rejection rates of focal patterns (Type II statistical errors). Our case study, along with several previous studies, suggests that the use of large grains is the best available method to avoid γ-dependence of β-diversity [15, 36, 37].

Our data was limited to forests in the tropics and subtropics and we did not have data from permanent plots in the temperate region (>30° latitude). Recently, Castro-Insua *et al.* [39] investigated if there were any latitudinal thresholds in β-diversity, and showed that different β-diversity patterns exist on either side of a threshold at c. 30° latitude. Although we found no relationship between β-diversity and latitude, this relationship might change in the temperate region. Our plots also have a broader longitudinal spread that is ideal in a study of latitudinal effects, and seven of 15 plots are on islands. Future studies should examine latitudinal β-diversity patterns using large spatial scales in a different regions that includes temperate plots. Studies using more sites, across American and African latitudinal gradients, and using multiple growth forms and larger distances between grains, will be useful to determine spatial scale effects on β-diversity patterns and differences in the mechanisms that drive community assembly.

Our results suggest that sampling at large sampling grains can remove the influences of γ- on β-diversity. Specifically, we show that observed β-diversity does not change with increasing latitude (3-30° latitude; figure 2.3). Therefore, our results support the idea that β-diversity in the tropics is similar to β-diversity in the sub-tropics. These results have important implications for community ecology and demonstrate that the general β-diversity patterns and the processes structuring communities are still open for discussion.

2.6 References

[1] Wallace AR. 1878 *Tropical Nature and other essays*. Macmillan and Company, London.

[2] Rosenzweig ML. 1995 *Species diversity in space and time*. Cambridge University Press, U.K.

[3] Hillebrand H. 2004 On the generality of the latitudinal diversity gradient.

Am. Nat. **163**, 192–211.

[4] Ashton LA *et al.* 2016 Vertical stratification of moths across elevation and latitude. *J. Biogeogr.* **43**, 59–69.

[5] Koleff P, Lennon JJ, Gaston, KJ. 2003 Are there latitudinal gradients in species turnover? *Glob. Ecol. Biogeogr.* **12**, 483–498.

[6] Kraft NJB *et al.* 2011 Disentangling the drivers of β diversity along latitudinal and elevational gradients. *Science* **333**, 1755–1758.

[7] Qian H, Chen S, Mao L, Ouyang Z. 2013 Drivers of β-diversity along latitudinal gradients revisited. *Glob. Ecol. Biogeogr.* **22**, 659–670.

[8] Myers JA *et al.* 2013 Beta-diversity in temperate and tropical forests reflects dissimilar mechanisms of community assembly. *Ecol. Lett.* **16**, 151–157.

[9] Catano CP, Dickson TL, Myers JA. 2017 Dispersal and neutral sampling mediate contingent effects of disturbance on plant beta-diversity: a meta-analysis. *Ecol. Lett.* **20**, 347–356.

[10] Mori AS, Fujii S, Kitagawa R, Koide D. 2015 Null model approaches to evaluating the relative role of different assembly processes in shaping ecological communities. *Oecologia* **178**, 261–273.

[11] Bennett JR, Gilbert B. 2016 Contrasting beta diversity among regions: how do classical and multivariate approaches compare? *Glob. Ecol. Biogeogr.* **25**, 368–377.

[12] Ulrich W, Baselga A, Kusumoto B, Shiono T, Tuomisto H, Kubota Y. 2017 The tangled link between β- and γ-diversity: a Narcissus effect weakens statistical influences in null model analyses of diversity patterns. *Glob. Ecol. Biogeogr.* **26**, 1–5.

[13] Clark AT *et al.* 2017 Functional traits of tropical trees and lianas explain spatial structure across multiple scales. *J. Ecol.* **106**, 795–806.

[14] Xu W, Chen G, Liu C, Ma K. 2015 Latitudinal differences in species abundance distributions, rather than spatial aggregation, explain beta-diversity along latitudinal gradients. *Glob. Ecol. Biogeogr.* **24**, 1170–1180.

[15] Beck J, Holloway JD, Schwanghart W. 2013 Undersampling and the

measurement of beta diversity. *Methods Ecol. Evol.* **4**, 370–382.

[16] Pitman NCA, Terborgh J, Silman MR, Nunez P. 1999 Tree species distributions in an upper Amazonian forest. *Ecology* **80**, 2651-–2661.

[17] Field R *et al.* 2009 Spatial species richness gradients across scales: a meta-analysis. *J. Biogeogr.* **36**, 132–147.

[18] Mittelbach GG *et al.* 2001 What is the observed relationship between species richness and productivity? *Ecology* **82**, 2381–2396.

[19] Rosindell J, Hubbell SP, Etienne RS. 2011 The unified neutral theory of biodiversity and biogeography at age ten. *Trend. Ecol. Evol*. **26**, 340–348.

[20] Tuomisto H, Ruokolainen K. 2012 Comment on "Disentangling the drivers of β diversity along latitudinal and elevational gradients". *Science* **335**, 1573.

[21] Sreekar R *et al.* 2017 Horizontal and vertical species turnover in tropical birds with differing land use. *Biol. Lett.,* 13, 20170186.

[22] Tello JS *et al.* 2015 Elevational gradients in β-diversity reflect variation in the strength of local community assembly mechanisms across spatial scales. *PLOS ONE* **10**, e0121458.

[23] Condit R. 1998 *Tropical forest census plots.* Springer-Verlag and R. G. Landes Company, Germany and USA.

[24] Condit R, Lao S, Perez R, Dolins SB, Foster RB, Hubbell SP. 2012 Barro Colorado forest census data, 2012 version. DOI: http://dx.doi.org/10.5479/data.bci.20130603.

[25] Lee H, Davies SJ, LaFrankie JV, Tan S, Itoh A. 2002 Floristic and structural diversity of 52 hectares of mixed dipterocarp forest in Lambir Hills National Park, Sarawak, Malaysia. *J. Trop. For. Sci.* **14**, 379–400.

[26] Lee HS *et al*. 2005 *The 52-hectare Forest Research Plot at Lambir Hills, Sarawak, Malaysia: Tree distribution maps, diameter tables and species documentation*. Forest Department Sarawak, Arnold Arboretum-CTFS Program, Smithsonian Tropical Research Institute, Sarawak, Malaysia.

[27] Hubbell SP *et al*. 1999 Light gap disturbances, recruitment limitation, and tree diversity in a Neotropical forest. *Science* **283**, 554–557.

[28] Koleff, P., Gaston, K.J. & Lennon, J.J. (2003b). Measuring beta diversity for presence-absence data. *J. Anim. Ecol.,* 72, 367–382.

[29] Gotelli NJ, Rohde K. 2002 Co-occurrence of ectoparasites of marine fishes: a null model analysis. *Ecol. Lett.* **5**, 86–94.

[30] Whittaker RH. 1960 Vegetation of Siskiyou Mountains, Oregon and California. *Ecol. Monogr*. **30**, 279–338.

[31] Santini L *et al.* 2017 Assessing the suitability of diversity metrics to detect biodiversity change. *Biol. Conserv.* **213**, 341-350.

[32] Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A. 2005 Very high resolution interpolated climate surfaces for global land areas. *Int. J. Climatol.* **25**, 1965–1978.

[33] Muggeo V 2010 Package "segmented". *Biometrika* **58**, 525–534.

[34] Davies SJ, Tan S, Lafrankie JV, Potts MD. 2005 *Soil-related floristic variation in the hyperdiverse dipterocarp forest in Lambir Hills, Sarawak.* Pollination Ecology and Rain forest Diversity, Sarawak Studies (eds: D. Roubik, S. Sakai and A. Hamid), pp. 22–34. Springer-Verlag, New York, USA.

[35] Katabuchi M, Kurokawa H, Davies SJ, Tan S, Nakashizuka T. 2012 Soil resource availability shapes community trait structure in a species-rich dipterocarp forest. *J. Ecol.* **100**, 643–651.

[36] Chao A, Jost L. 2012 Coverage based rarefaction and extrapolation: standardizing samples by completeness rather than size. *Ecology* **93**, 2533–2547.

[37] Tuomisto H. 2010. A diversity of beta diversities: straightening up a concept gone awry. Part 2. Quantifying beta diversity and related phenomena. *Ecography* **33**, 23–45

[38] Condit R, Hubbell SP, LaFrankie JV, Sukumar R, Manokaran N, Foster RB, Ashton PS. 1996 Species-area and species-individual relationships of tropical trees: a comparison of three 50 ha plots. *J. Ecol.* 84: 549–562.

[39] Castro-Insua A, Gomez-Rodriguez C, Baselga A. 2016 Break the pattern: breakpoints in beta diversity of vertebrates are general across clades and suggest common historical causes. *Glob. Ecol. Biogeogr.* **25**, 1279–1283.

2.7 Supporting information

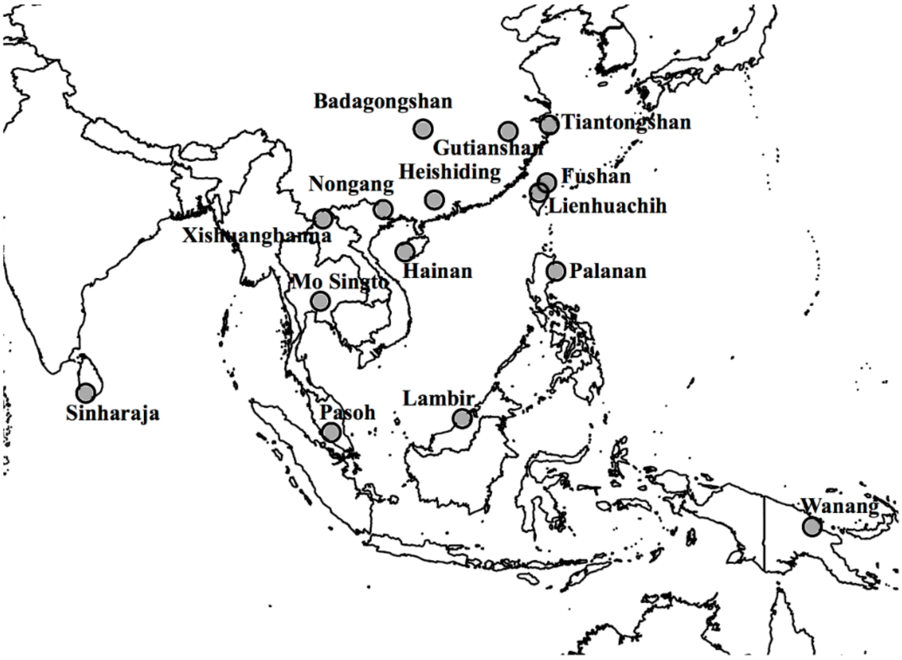


Figure S2.1. Asia-Pacific map showing the locations of the 15 large forest dynamics plots studied in this paper.

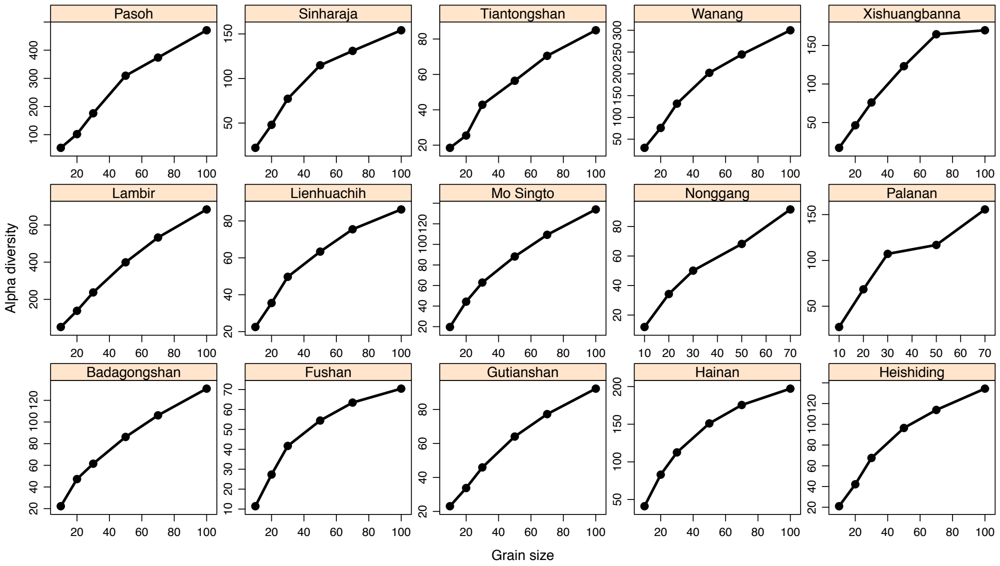


Figure S2.2. Relationship between α-diversity and grain size at all the 15 sampled sites.

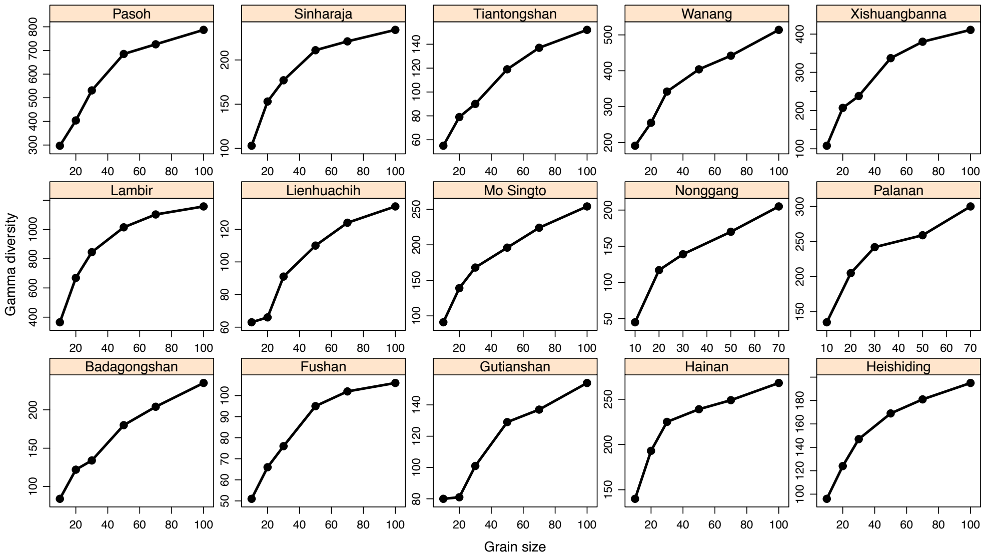
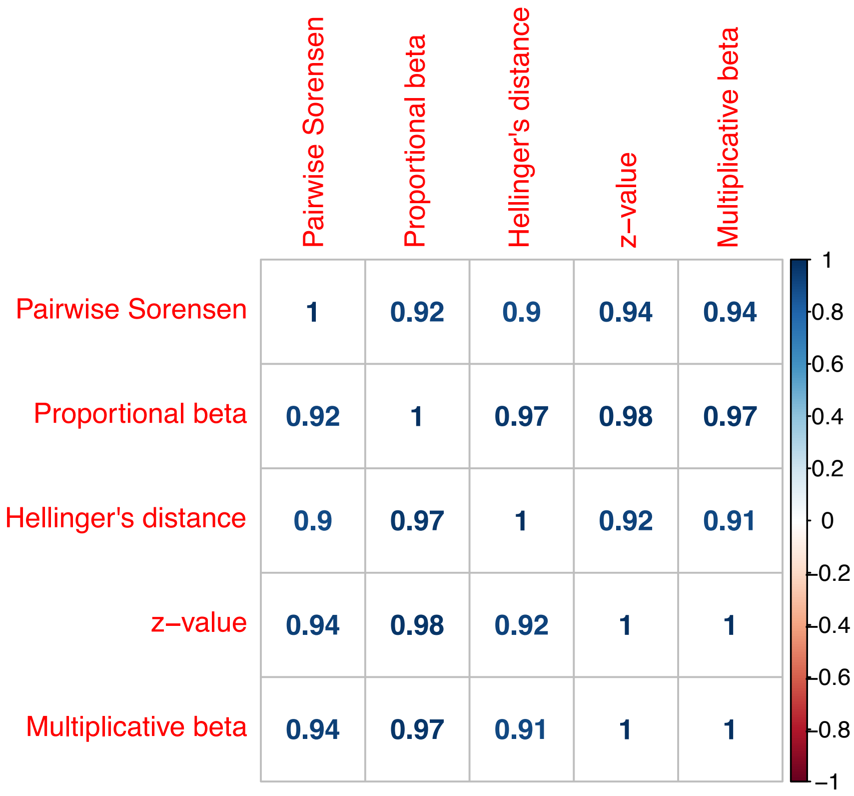


Figure S2.3. Relationship between γ-diversity and grain size at all the 15 sampled sites.



	Pairwise Sorensen	Proportional beta	Hellinger's distance	z–value	Multiplicative beta
Pairwise Sorensen	1	0.92	0.9	0.94	0.94
Proportional beta	0.92	1	0.97	0.98	0.97
Hellinger's distance	0.9	0.97	1	0.92	0.91
z–value	0.94	0.98	0.92	1	1
Multiplicative beta	0.94	0.97	0.91	1	1

Figure S2.4. Pearson’s Correlation matrix of all the measured beta-diversity metrics. All measured metrics were highly correlated with each other.

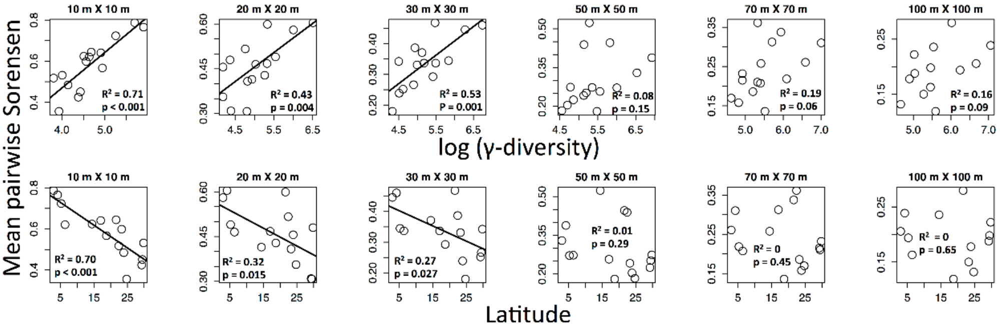


Figure S2.5. Mean pairwise Sørensen increased with γ-diversity and decreased with latitude when sampling used small grains (10 m x 10 m to 30 m x 30 m), but showed no relationship with γ-diversity and latitude at larger grains (50 m x 50 m to 100 m x 100 m).

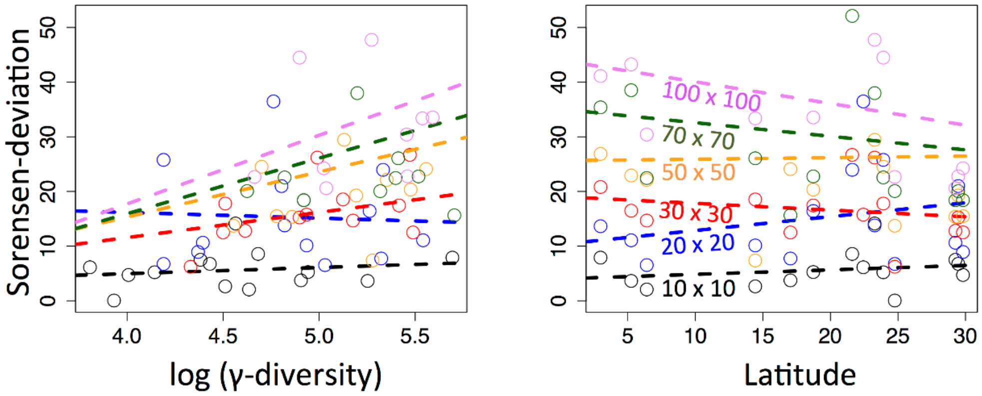


Figure S2.6. Standardized pairwise Sørensen-deviation did not vary significantly with γ-diversity and latitude at any grain size. However, pairwise Sørensen-deviation values increased significantly with grain size, indicating stronger intraspecific aggregation at larger spatial scales. Dashed lines indicate non-significant relationships.

Table S2.1. Classical beta-diversity and mean pairwise Sørensen for each site at different grain sizes.

Site	Grain size	Gamma	Multiplicative Beta	Mean pairwise Sørensen
Xishuangbanna	100 x 100	411	1.72967291	0.279756841
Xishuangbanna	70 x 70	380	2.310030395	0.337580068
Xishuangbanna	50 x 50	337	2.737611698	0.446970732
Xishuangbanna	30 x 30	238	3.129520053	0.468792946
Xishuangbanna	20 x 20	207	4.456404736	0.599185204
Xishuangbanna	10 x 10	108	6.260869565	0.644315211
Heishiding	100 x 100	195	1.450892857	0.150193897
Heishiding	70 x 70	181	1.589811155	0.185963876
Heishiding	50 x 50	169	1.752203214	0.241376744
Heishiding	30 x 30	147	2.176165803	0.33123569
Heishiding	20 x 20	124	2.941874259	0.408301589
Heishiding	10 x 10	96	4.571428571	0.598697089
Lienhuachih	100 x 100	134	1.554524362	0.177924443
Lienhuachih	70 x 70	124	1.643472498	0.157798053
Lienhuachih	50 x 50	110	1.736385162	0.204017254
Lienhuachih	30 x 30	91	1.830985915	0.238748017
Lienhuachih	20 x 20	66	1.85915493	0.455909136
Lienhuachih	10 x 10	63	2.8	0.484524719
Fushan	100 x 100	106	1.504613201	0.131889597
Fushan	70 x 70	102	1.607565012	0.169612458
Fushan	50 x 50	95	1.744719927	0.182727001
Fushan	30 x 30	76	1.822541966	0.179610377
Fushan	20 x 20	66	2.413162706	0.356053547
Fushan	10 x 10	51	4.454148472	0.356111165

Mo Singto	100 x 100	254	1.896229937	0.235795013
Mo Singto	70 x 70	224	2.049405306	0.257739984
Mo Singto	50 x 50	196	2.222222222	0.52345062
Mo Singto	30 x 30	168	2.6709062	0.371354948
Mo Singto	20 x 20	139	3.137697517	0.414527201
Mo Singto	10 x 10	91	4.631043257	0.624008621
Sinharaja	100 x 100	234	1.518494484	0.163015453
Sinharaja	70 x 70	221	1.687667048	0.207391863
Sinharaja	50 x 50	211	1.837178929	0.272509511
Sinharaja	30 x 30	177	2.289780078	0.336959426
Sinharaja	20 x 20	153	3.184183143	0.4650329
Sinharaja	10 x 10	103	4.629213483	0.6207393
Wanang	100 x 100	514	1.713047825	0.193909383
Wanang	70 x 70	442	1.808140724	0.218555945
Wanang	50 x 50	404	1.996540647	0.2712884
Wanang	30 x 30	342	2.598784195	0.345037468
Wanang	20 x 20	255	3.359683794	0.489905646
Wanang	10 x 10	191	6.324503311	0.723726086
Pasoh	100 x 100	787	1.67162277	0.205738183
Pasoh	70 x 70	726	1.942474916	0.260867424
Pasoh	50 x 50	685	2.213962508	0.329341807
Pasoh	30 x 30	531	3.019618993	0.446205209
Pasoh	20 x 20	404	3.964671246	0.580326571
Pasoh	10 x 10	297	5.582706767	0.787044323
Nonggang	70 x 70	205	2.239213545	0.361573519
Nonggang	50 x 50	170	2.492668622	0.43880577
Nonggang	30 x 30	139	2.774451098	0.387116167
Nonggang	20 x 20	117	3.416058394	0.516521123

Nonggang	10 x 10	45	3.781512605	0.517819378
Tiantongshan	100 x 100	152	1.789287816	0.222135883
Tiantongshan	70 x 70	137	1.943262411	0.232017585
Tiantongshan	50 x 50	119	2.109929078	0.273843341
Tiantongshan	30 x 30	90	2.100350058	0.342641601
Tiantongshan	20 x 20	79	3.104125737	0.47995031
Tiantongshan	10 x 10	55	2.972972973	0.531874913
Gutianshan	100 x 100	154	1.669376694	0.187920091
Gutianshan	70 x 70	137	1.773462783	0.214863285
Gutianshan	50 x 50	129	2.014051522	0.224637054
Gutianshan	30 x 30	101	2.20043573	0.251872352
Gutianshan	20 x 20	81	2.4	0.309096547
Gutianshan	10 x 10	80	3.470715835	0.42459787
Badagongshan	100 x 100	235	1.796636086	0.198170391
Badagongshan	70 x 70	204	1.921808761	0.210354704
Badagongshan	50 x 50	180	2.088167053	0.251628457
Badagongshan	30 x 30	134	2.178861789	0.266323984
Badagongshan	20 x 20	122	2.579281184	0.307577534
Badagongshan	10 x 10	84	3.775280899	0.451209741
Palanan	70 x 70	300	1.927401221	0.312620514
Palanan	50 x 50	259	2.215568862	0.256934098
Palanan	30 x 30	242	2.258516099	0.336983674
Palanan	20 x 20	205	2.994886779	0.467565575
Palanan	10 x 10	135	4.945054945	0.6409486
Hainan	100 x 100	268	1.358337557	0.11916625
Hainan	70 x 70	249	1.418399316	0.135884149
Hainan	50 x 50	239	1.581733951	0.180078049
Hainan	30 x 30	225	1.999111506	0.292777268

Hainan	20 x 20	193	2.325301205	0.428409055
Hainan	10 x 10	140	3.41047503	0.567101074
Lambir	100 x 100	1158	1.693849192	0.238724561
Lambir	70 x 70	1103	2.070778185	0.310339439
Lambir	50 x 50	1015	2.54258517	0.387883059
Lambir	30 x 30	845	3.561643836	0.460911384
Lambir	20 x 20	669	4.832069339	0.604341535
Lambir	10 x 10	365	7.142857143	0.76565142

Table S2.2. Relationship between precipitation and observed β-diversity metrics (classical multiplicative β-diversity and mean pairwise Sørensen)

Multiplicative β-diversity		
Grain size	**Estimate ± SE**	***P*-value**
10 m x 10 m	0.00065 ± 0.00036	0.096
20 m x 20 m	0.00008 ± 0.00025	0.736
30 m x 30 m	0.00000 ± 0.00016	0.962
50 m x 50 m	-0.00007 ± 0.0001	0.5
70 m x 70 m	-0.00007 ± 0.00007	0.352
100 m x 100 m	-0.00004 ± 0.00005	0.421
Mean pairwise Sørensen		
Grain size	**Estimate ± SE**	***P*-value**
10 m x 10 m	0.00003 ± 0.00004	0.44
20 m x 20 m	0.00001 ± 0.00003	0.594
30 m x 30 m	-0.00001 ± 0.00002	0.658
50 m x 50 m	-0.00004 ± 0.0003	0.247
70 m x 70 m	-0.00001 ± 0.00002	0.468
100 m x 100 m	-0.00001 ± 0.00001	0.46

Table S2.3. Relationship between precipitation and null-model generated β-deviation and Sørensen-deviation

β-deviation		
Grain size	**Estimate ± SE**	***P*-value**
10 m x 10 m	-0.00021 ± 0.00172	0.901
20 m x 20 m	-0.00125 ± 0.00423	0.772
30 m x 30 m	-0.00306 ± 0.00372	0.425
50 m x 50 m	-0.00366 ± 0.00468	0.467
70 m x 70 m	-0.00362 ± 0.00638	0.581
100 m x 100 m	-0.00106 ± 0.00446	0.817
Sørensen-deviation		
Grain size	**Estimate ± SE**	***P*-value**
10 m x 10 m	-0.00206 ± 0.00095	0.052
20 m x 20 m	-0.00434 ± 0.00256	0.116
30 m x 30 m	-0.00246 ± 0.00162	0.156
50 m x 50 m	-0.00349 ± 0.00528	0.52
70 m x 70 m	-0.00395 ± 0.00518	0.46
100 m x 100 m	-0.00098 ± 0.00512	0.851

Table S2.4. Latitude and γ-diversity did not affect standardized β-deviation across all sampling scales (quadrat sizes).

	γ-diversity		Latitude	
Quadrat size	R^2	*p*	R^2	*p*
10 m x 10 m	0.001	0.95	0.004	0.81
20 m x 20 m	0.03	0.53	0.009	0.75
30 m x 30 m	0.002	0.87	0.01	0.74
50 m x 50 m	0.07	0.37	0.07	0.38
70 m x 70 m	0.06	0.40	0.06	0.41
100 m x 100 m	0.16	0.21	0.15	0.23

Appendix S2.1. Sensitivity of β-diversity analyses. The R-code used for extracting and analyzing data from the 50-ha plots in Lambir, Borneo and BCI, Republic of Panama.

```
 rm(list = ls()) ### This clears everything from memory
library(dplyr)
d<-read.csv("~data.csv") ### read the plot data

### function to make names of local communites
Quad.func <- function(data, size = 20){

  data2 <- data %>% mutate(temp.x = as.integer(gx / size) +
1) %>%
    mutate(temp.y = as.integer(gy / size) + 1) %>%
    mutate(temp.quad = paste(temp.x, temp.y, sep = "_"))

  temp.name <- names(data2)
  temp.name[temp.name == "temp.x"] <- paste("gx", size, sep =
"")
  temp.name[temp.name == "temp.y"] <- paste("gy", size, sep =
"")
  temp.name[temp.name == "temp.quad"] <- paste("quadrat", size,
sep = "")

  names(data2) <- temp.name
  data2
}

#### making quadrats
D <- d %>%
  filter(gx < 1000) %>%
  Quad.func(5) %>%
  Quad.func(10) %>%
  Quad.func(20) %>%
  Quad.func(50) %>%
  Quad.func(100)

head(D)
```

```
### Making tables accordingly
m1.5 <- table(D$quadrat5, D$sp)
m1.10 <- table(D$quadrat10, D$sp)
m1.20 <- table(D$quadrat20, D$sp)
m1.50 <- table(D$quadrat50, D$sp)
m1.100 <- table(D$quadrat100, D$sp)

library(vegan)
library(segmented)


### FUNCTIONS ###

#### Large quadrats
Large.quad <- function(data, n.sample, size = 120){
  if (n.sample > 4) stop("Maximum sample size is 4 by 4")
  lim.size <- n.sample * 0.5

  sp.data <- data %>%
    select(sp) %>%
    distinct

  temp.dat <- data %>%
    filter((gx >= lim.size * size) & (gx < max(gx) - lim.size *
size)) %>% filter((gy >= lim.size * size) & (gy < max(gy) -
lim.size * size))

  if (nrow(temp.dat) == 0) stop("Quadrat size or sample size are
too large")

  x.mid <- sample(temp.dat$gx, 1)
  y.mid <- sample(temp.dat$gy, 1)

  temp.dat2 <- data %>%
    filter((gx >= x.mid - lim.size * size) & (gx < x.mid +
lim.size * size)) %>%
    filter((gy >= y.mid - lim.size * size) & (gy < y.mid +
```

```
lim.size * size)) %>%
    mutate(gx.new = gx - min(gx)) %>%
    mutate(gy.new = gy - min(gy)) %>%
    mutate(x.site = as.integer(gx.new / size) + 1) %>%
    mutate(y.site = as.integer(gy.new / size) + 1) %>%
    mutate(temp.quad = paste(x.site, y.site, sep = "_")) %>%
    full_join(., sp.data, by = "sp")

  com.mat <- table(temp.dat2$temp.quad, temp.dat2$sp)

  com.mat
}

### Null model

My.shuffle <- function(samp){
  samp.n <- r2dtable(1, rowSums(samp), colSums(samp))[[1]]
  rownames(samp.n) <- rownames(samp)
  colnames(samp.n) <- colnames(samp)
  samp.n
}

SES.func <- function(res.list, runs){
  obs.alpha <- sapply(res.list, specnumber) %>% apply(2, mean)
  obs.ind <- sapply(res.list,sum)
  obs.gamma <- res.list %>%
    lapply(function(x) apply(x, 2, sum)) %>%
    sapply(specnumber)

  obs.beta <- obs.gamma / obs.alpha
  obs.z <- (log(obs.gamma)-log(obs.alpha))/log(9)
  rand.alpha <- matrix(NA, nrow = runs, ncol = length(res.list))
  rand.beta <- rand.alpha
  rand.gamma <- rand.alpha

  for (i in 1:runs){
    rand.dat <- lapply(res.list, My.shuffle)
    rand.alpha[i, ] <- sapply(rand.dat, specnumber) %>% apply(2,
mean)
```

```
    rand.beta <- obs.gamma / rand.alpha
  }

  mean.rand.beta <- apply(rand.beta, 2, mean)
  sd.rand.beta <- apply(rand.beta, 2, sd)

  ses.beta <- (obs.beta - mean.rand.beta) / sd.rand.beta

  data.frame(site = 1:length(res.list), obs.ind, obs.alpha,
obs.gamma, obs.beta, obs.z,mean.rand.beta, sd.rand.beta,
ses.beta, runs)
}

### Sampling function
Samp.func<-function(data.matrix, n.sample, n.gap) {
  x.vec <- data.matrix %>%
    rownames() %>%
    strsplit("_") %>%
    sapply("[",1) %>%
    as.numeric()

  x.n <- x.vec[x.vec <= (max(x.vec) -
                            (n.sample * (n.gap + 1) - n.gap -
1))] %>%
    sample(1)

  y.vec <- data.matrix %>%
    rownames() %>%
    strsplit("_") %>%
    sapply("[",2) %>%
    as.numeric()

  y.n <- y.vec[y.vec <= (max(y.vec) -
                            (n.sample * (n.gap + 1) - n.gap -
1))] %>%
    sample(1)

  x.n2 <- seq(x.n, (x.n + n.sample * (n.gap + 1)) - n.gap - 1)
```

```
  y.n2 <- seq(y.n, (y.n + n.sample * (n.gap + 1)) - n.gap - 1)

  if (n.gap != 0) {
    x.n2 <- (n.gap + 1) * c(1:n.sample) - n.gap + x.n - 1
    y.n2 <- (n.gap + 1) * c(1:n.sample) - n.gap + y.n - 1
  }

  temp <- expand.grid(x.n2, y.n2)
  site.name <- paste(temp$Var1, temp$Var2, sep = "_")
  data.matrix[site.name, ]
}

### Analysis ###
### Quadrat size
size.vec <- seq(10, 150, by = 10)

obs.alpha <- NULL
before <- proc.time()
for (i in 1:length(size.vec)){
  temp <- lapply(1:10, function(x) Large.quad(D1, n.sample = 3,
size = size.vec[i]))
  obs.alpha <- c(obs.alpha, SES.func(temp, runs = 1)$obs.alpha)
}

obs.beta <- NULL
before <- proc.time()
for (i in 1:length(size.vec)){
  temp <- lapply(1:10, function(x) Large.quad(D1, n.sample = 3,
size = size.vec[i]))
  obs.beta <- c(obs.beta, SES.func(temp, runs = 1)$obs.beta)
}

obs.gamma <- NULL
before <- proc.time()
for (i in 1:length(size.vec)){
  temp <- lapply(1:10, function(x) Large.quad(D1, n.sample = 3,
size = size.vec[i]))
  obs.gamma <- c(obs.gamma, SES.func(temp, runs = 1)$obs.gamma)
}
```

```
ses.beta <- NULL
before <- proc.time()
for (i in 1:length(size.vec)){
  temp <- lapply(1:10, function(x) Large.quad(D1, n.sample = 3,
size = size.vec[i]))
  ses.beta <- c(ses.beta, SES.func(temp, runs = 99)$ses.beta)
}

(L.Divers<-data.frame(obs.alpha, obs.beta,
obs.z,obs.gamma,obs.ind, ses.beta, size = rep(size.vec, each =
10)))



### Figure
par(mfrow=c(1,2))
plot(obs.beta ~ size ,L.Divers,cex=2,xlab='Quadrat
size',ylab='Beta',cex.lab=1.5,
     cex.axis=1.5)
lm_b2<-lm(obs.beta ~ size ,L.Divers)
L.o.seg_b2<-segmented(lm_b2,seg.Z=~size)
plot(L.o.seg_b2, add=T, lwd=4, rug=F,
conf.interval=0.95,shade=T)

plot(ses.beta ~ size ,L.Divers,cex=2,xlab='Quadrat
size',ylab='Beta deviation',
      cex.lab=1.5, cex.axis=1.3)
lm_ses2<-lm(ses.beta ~ size  ,L.Divers)
L.o.seg_ses2<-segmented(lm_ses2,seg.Z=~size)
plot(L.o.seg_ses2, add=T, lwd=4, rug=F,
conf.interval=0.95,shade=T)
```

Appendix S2.2. Latitudinal β-diversity pattern analyses. The R-code used for extracting measuring β-diversity and β-deviation at multiple grainsizes.

```
rm(list = ls()) # This clears everything from memory.
library(dplyr)
library(vegan)
library(adespatial)
library(betapart)

dat <- read.csv("~sp_abun.csv") ## read the dataset
summary(dat)
d<-dat ## if plot is only sampled once
#d <- subset(dat, status == 'A') ## Select only 'alive'
individuals
#d<-subset(dat, status=='Alive')

## function to make names of local communites
Quad.func <- function(data, size = 20){
  data2 <- data %>% mutate(temp.x = as.integer(gx / size) + 1)
%>%
    mutate(temp.y = as.integer(gy / size) + 1) %>%
    mutate(temp.quad = paste(temp.x, temp.y, sep = "_"))
  temp.name <- names(data2)
  temp.name[temp.name == "temp.x"] <- paste("gx", size, sep =
"")
  temp.name[temp.name == "temp.y"] <- paste("gy", size, sep =
"")
```

```
  temp.name[temp.name == "temp.quad"] <- paste("quadrat", size,
sep = "")

  names(data2) <- temp.name

  data2

}


####making 20 one ha (100 m X 100 m) quadrats and trim the plot
to 20 ha (500 m X 400 m)

D <- d %>%

  filter(gx < 500) %>% ##Check gx range for Banna

  ## filter(gx < 800)  %>%   ## for Mo Singto

  ## filter(gx > 300)  %>%    ## for Mo Singto

  filter(gy < 400) %>%

  Quad.func(70)

head(D)


## Making table

m1.70 <- table(D$quadrat70, D$sp)

head(m1.70)


####### Simulation


My.shuffle <- function(samp){

  samp.n <- r2dtable(1, rowSums(samp), colSums(samp))[[1]]

  rownames(samp.n) <- rownames(samp)

  colnames(samp.n) <- colnames(samp)

  samp.n
```

```
}


div.func <- function(samp){
  alpha <- specnumber(samp) %>% mean
  gamma <- apply(samp, 2, sum) %>% specnumber
  beta <- gamma/alpha
  betaP <- (gamma-alpha)/gamma
  y <- samp
  y[y>0]=1
  betaT <- mean(beta.pair(y)$beta.sor)
  betaP <- mean(bray.part(samp)$bray)
  c(alpha = alpha, beta = beta, betaP = betaP, betaT = betaT,
gamma = gamma)
}


SES.func <- function(samp, runs){
  obs <- div.func(samp)
  obs.alpha <- obs["alpha"]
  obs.gamma <- obs["gamma"]
  obs.beta <- obs["beta"]
  obs.betaP <- obs["betaP"]
  obs.betaT <- obs["betaT"]

  rand.res <- replicate(runs, div.func(My.shuffle(samp)))
  mean.rand.beta <- rand.res["beta", ] %>% mean
  sd.rand.beta <- rand.res["beta", ] %>% sd
  mean.rand.betaP <- rand.res["betaP", ] %>% mean
```

```
  sd.rand.betaP <- rand.res["betaP", ] %>% sd

  mean.rand.betaT <- rand.res["betaT", ] %>% mean

  sd.rand.betaT <- rand.res["betaT", ] %>% sd


  ses.beta <- (obs.beta - mean.rand.beta) / sd.rand.beta

  ses.betaP <- (obs.betaP - mean.rand.betaP) / sd.rand.betaP

  ses.betaT <- (obs.betaT - mean.rand.betaT) / sd.rand.betaT


  data.frame (ses.beta, ses.betaP, ses.betaT)

}


#######################

#### plot sizes    ####


Large.quad <- function(data, n.sample, size = 120){

  if (n.sample > 5) stop("Maximum sample size is 5 by 5")

  lim.size <- n.sample * 0.5

  sp.data <- data %>%

    select(sp) %>%

    distinct

  temp.dat <- data %>%

    filter((gx >= lim.size * size) & (gx < max(gx) - lim.size *
size)) %>%

    filter((gy >= (lim.size-0.5) * size) & (gy < max(gy) -
(lim.size-0.5) * size))

  if (nrow(temp.dat) == 0) stop("Quadrat size or sample size are
too large")
```

```
  x.mid <- sample(temp.dat$gx, 1)
  y.mid <- sample(temp.dat$gy, 1)
  temp.dat2 <- data %>%
    filter((gx >= x.mid - lim.size * size) & (gx < x.mid + lim.size * size)) %>%
    filter((gy >= y.mid - (lim.size-0.5) * size) & (gy < y.mid + (lim.size-0.5) * size)) %>%
    mutate(gx.new = gx - min(gx)) %>%
    mutate(gy.new = gy - min(gy)) %>%
    mutate(x.site = as.integer(gx.new / size) + 1) %>%
    mutate(y.site = as.integer(gy.new / size) + 1) %>%
    mutate(temp.quad = paste(x.site, y.site, sep = "_")) %>%
    full_join(., sp.data, by = "sp")
  com.mat <- table(temp.dat2$temp.quad, temp.dat2$sp)
  com.mat
}

##################################
###          Analysis         ####
##################################

## Generating 20 70 X 70 m quadrats from the plots
m1.70 <- Large.quad(D, n.sample = 5, size = 70)
(Gamma.70 <- specnumber(apply(m1.70, 2, sum)))
(Alpha.70 <- mean(specnumber(m1.70)))
(Beta.70 <- Gamma.70/Alpha.70)
m1.70X<-m1.70
```

```
m1.70X[m1.70X>0]=1
(BetaP.70 <- mean(beta.pair(m1.70X)$beta.sor))
(BetaB.70 <- mean(bray.part(m1.70)$bray))
(BetaSES.70 <-SES.func(m1.70,1000))
(PL.70<-data.frame(Gamma.70, Alpha.70, Beta.70, BetaP.70, BetaB.70, BetaSES.70))

#### Generating 20 50 x 50 m plots
m1.50 <- Large.quad(D, n.sample = 5, size = 50)
(Gamma.50 <- specnumber(apply(m1.50, 2, sum)))
(Alpha.50 <- mean(specnumber(m1.50)))
(Beta.50 <- Gamma.50/Alpha.50)
m1.50X<-m1.50
m1.50X[m1.50X>0]=1
(BetaP.50 <- mean(beta.pair(m1.50X)$beta.sor))
(BetaB.50 <- mean(bray.part(m1.50)$bray))
(BetaSES.50 <-SES.func(m1.50,1000))
(PL.50<-data.frame(Gamma.50, Alpha.50, Beta.50, BetaP.50, BetaB.50, BetaSES.50))

## Generating 20 30 X 30 m quadrats from the plots
m1.30 <- Large.quad(D, n.sample = 5, size = 30)
(Gamma.30 <- specnumber(apply(m1.30, 2, sum)))
(Alpha.30 <- mean(specnumber(m1.30)))
(Beta.30 <- Gamma.30/Alpha.30)
m1.30X<-m1.30
m1.30X[m1.30X>0]=1
```

```
(BetaP.30 <- mean(beta.pair(m1.30X)$beta.sor))

(BetaB.30 <- mean(bray.part(m1.30)$bray))

(BetaSES.30 <-SES.func(m1.30,1000))

(PL.30<-data.frame(Gamma.30,   Alpha.30,   Beta.30,   BetaP.30,
BetaB.30, BetaSES.30))

## Generating 20 20 X 20 m quadrats from the plots

m1.20 <- Large.quad(D, n.sample = 5, size = 20)

(Gamma.20 <- specnumber(apply(m1.20, 2, sum)))

(Alpha.20 <- mean(specnumber(m1.20)))

(Beta.20 <- Gamma.20/Alpha.20)

m1.20X<-m1.20

m1.20X[m1.20X>0]=1

(BetaP.20 <- mean(beta.pair(m1.20X)$beta.sor))

(BetaB.20 <- mean(bray.part(m1.20)$bray))

(BetaSES.20 <-SES.func(m1.20,1000))

(PL.20<-data.frame(Gamma.20,   Alpha.20,   Beta.20,   BetaP.20,
BetaB.20, BetaSES.20))


## Generating 20 10 X 10 m quadrats from the plots

m1.10 <- Large.quad(D, n.sample = 5, size = 10)

(Gamma.10 <- specnumber(apply(m1.10, 2, sum)))

(Alpha.10 <- mean(specnumber(m1.10)))

(Beta.10 <- Gamma.10/Alpha.10)

m1.10X<-m1.10

m1.10X[m1.10X>0]=1

(BetaP.10 <- mean(beta.pair(m1.10X)$beta.sor))

(BetaB.10 <- mean(bray.part(m1.10)$bray))
```

```
(BetaSES.10 <-SES.func(m1.10,1000))

(PL.10<-data.frame(Gamma.10,   Alpha.10,   Beta.10,   BetaP.10,
BetaB.10, BetaSES.10))




pl.n<-data.frame(PL.70,PL.50,PL.30,PL.20,PL.10)

pl.n2<-matrix(pl.n, nrow=5, byrow=TRUE)

colnames(pl.n2)<-c('Gamma', 'Alpha', 'Beta', 'BetaP', 'BetaB',
'SES_Beta', 'SES_Bray', 'SES_Sor')

pl.n2

write.csv(pl.n2,'plot_xxxx.csv') ## Results in .csv file
```

Chapter 3

Horizontal and vertical species turnover in tropical birds in habitats with differing land-use

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Principal Author

Name of Principal Author (Candidate)	Sreekar Rachakonda		
Contribution to the Paper	Designed the study, analysed the data, interpreted the results, wrote the paper and acted as corresponding author.		
Overall percentage (%)	85%		
Certification:	This paper reports on original research I conducted during the period of my Higher Degree by Research candidature and is not subject to any obligations or contractual agreements with a third party that would constrain its inclusion in this thesis. I am the primary author of this paper.		
Signature		Date	30/08/2018

Co-Author Contributions

By signing the Statement of Authorship, each author certifies that:

i. the candidate’s stated contribution to the publication is accurate (as detailed above);

ii. permission is granted for the candidate in include the publication in the thesis; and

iii. the sum of all co-author contributions is equal to 100% less the candidate's stated contribution.

Name of Co-Author	Richard T. Corlett		
Contribution to the Paper	Helped with writing and discussing the manuscript.		
Signature		Date	30/08/2018

Name of Co-Author	Salindra Dayananda		
Contribution to the Paper	Helped with classifying Sri Lankan birds into feeding guilds. Also discussed the results and commented on the manuscript.		
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Name of Co-Author	Uromi M. Goodale		
Contribution to the Paper	Selected sites and acquired bird data. Helped with writing and discussing the manuscript.		
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Contribution to the Paper	Helped with preparing maps and discussing the manuscript.		
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Contribution to the Paper	Selected sites and acquired bird data. Helped with discussing the manuscript.		
Signature		Date	30/08/2018

Name of Co-Author	Lian Pin Koh		
Contribution to the Paper	Helped with writing and discussing the manuscript.		
Signature		Date	30/08/2018

Name of Co-Author	Eben Goodale		
Contribution to the Paper	Selected sites and acquired bird data. Helped with study design, writing and discussing the manuscript.		
Signature		Date	30/08/2018

3.1 Summary

Large tracts of tropical rainforests are being converted into intensive agricultural lands. Such anthropogenic disturbances are known to reduce species turnover across horizontal distances. But it is not known if they can also reduce species turnover across vertical distances (elevation), which have steeper climatic differences. We measured turnover in birds across horizontal and vertical sampling transects in three land-use types of Sri Lanka: protected forest, reserve buffer, and intensive-agriculture, from 90 to 2100 m a.s.l. Bird turnover rates across horizontal distances were similar across all habitats, and much less than vertical turnover rates. Vertical turnover rates were not similar across habitats. Forest had higher turnover rates than the other two habitats for all bird species. Buffer and intensive-agriculture had similar turnover rates, even though buffer habitats were situated at the forest edge. Therefore, our results demonstrate the crucial importance of conserving primary forest across the full elevational range available.

3.2 Introduction

One of the most documented patterns in ecology is that species richness generally declines with increasing anthropogenic activities. Species composition homogenization is considered to be the underlying mechanism governing such patterns [1-3], with generalist species expanding their ranges, while specialist species ranges contract, leading to specialists being replaced by generalists, and increasing similarities among communities in space and time [4]. Climate change is likely to increase the severity of homogenization, as climate change and land-use change favour the same generalist species, which expand their ranges tracking the climate, while ranges of specialists contract [5]. Studies have repeatedly shown reduced horizontal turnover indicating greater homogenization within human-modified landscapes compared with forests [1-3], but changes in vertical turnover remain unknown. Vertical distances show high variation in temperature (6°C per km), yet all previous studies that measured turnover rates across vertical distances have mainly used natural habitats [6-7]. Human-modified habitats are known to have simplified communities with generalist species that can use multiple habitats [8], leading to the testable hypothesis that vertical turnover in human-modified habitats would be lower compared to less disturbed, proximal habitats.

Here we compare species turnover within bird guilds with horizontal and vertical distances across a tropical mountain range in three different land-use types: within relatively undisturbed and protected forest, at the edges of those protected reserves, and in intensive agriculture. We hypothesized that species turnover will be: 1) highest in forest and lowest in intensive-agriculture habitats, because forest species are more specialized, and 2) higher vertically than horizontally, because the climatic gradient is steeper; and highest in forest because the vertical gradient in vegetation structure and composition is steeper in natural than anthropogenic habitats. Understanding these patterns is important both for efficient conservation planning and for predicting—and hopefully mitigating—the impacts of on-going climate change.

3.3 Methods

Study site

We conducted this study in wet-evergreen regions of Sri Lanka (figure S3.1). Forty-one 2-km transects were spaced along an elevational gradient between 90 and 2180 m, in three different land-use types: 1) Interior forest transects were inside mature evergreen rainforests within protected areas, 2) Buffer transects were along the boundaries of protected areas, within degraded forests and timber plantations, and 3) intensive-agriculture transects were in open habitats with intensive agriculture. Mean monthly temperature (range: 14.7 - 27.1°C) and mean annual precipitation (1972 - 4273 mm) for each transect were extracted from the WORLDCLIM database (30 arc-seconds resolution; version 1.4; [9]). For every one-kilometer increase in elevation, temperature decreased by c. 5°C and annual precipitation decreased by c. 1000 mm (see results; figure S3.1). Some amount of caution is required while interpreting the climate data because WORLDCLIM is modeled data and may not exactly represent true climatic parameters. Tree canopy cover for the entire island of Sri Lanka was extracted from the global forest change dataset [10].

Bird data

A team of two walked along the transects at one km/hr, identified all the individual birds seen and heard, and recorded their distances from the transect line. Each transect was visited 7.2 ± 4.0 (SD) times in one year, in both the breeding and non-breeding seasons. The data consists of 27234 observations of 125 bird species. Transects were horizontal with little variation in elevation and transect co-ordinates were extracted from the center of transect. We used DISTANCE software (http://www.distancesampling.org) to estimate relative densities by accounting for detectability of species (see Appendix S3.1 for details). We recorded all 27 endemic diurnal birds of Sri Lanka, of which 14—all predominantly forest birds—are threatened with extinction (http://www.iucnredlist.org). We divided the birds into three non-exclusive guilds: 1) All birds, 2) Insectivores, with arthropods as their primary diet, and 3) Understorey insectivores, which primarily used the understorey. See previous studies for details [11,12]. All analyses were conducted in the statistical program R (R Core Team, v. 3.3.1). We partitioned Bray-Curtis dissimilarity into nestedness and turnover components, and used the turnover component as a response variable to determine the turnover across horizontal and vertical distances in each habitat and across all three guilds. We used coefficients of each model to estimate the turnover rate (turnover per km) and compared coefficients between habitats and between horizontal and vertical distances.

Data analysis

We partitioned abundance-based Bray-Curtis dissimilarity to measure nestedness and turnover between sites using *bray.part* function in 'betapart' package [13]. Nestedness is defined as biological subsets where species remain constant, but individuals are lost from richer sites to poorer sites. Turnover is defined as the balanced variation where individuals remain constant, but species are swapped between sites [14]. In this study, we used turnover as a response variable.

We measured the horizontal distance as the shortest distance (in kms) between two transects (as the crow flies) according to the haversine method (*distm* function in 'geosphere' package) [15-16], and the vertical distance as the difference in elevation (in kms) between two transects. We used multivariate regression of distance matrices (*MRM* function in 'ecodist' package) to investigate the turnover of bird guilds across horizontal and vertical distances in each land-use type [17-18]. MRM is more flexible than the mantel test and more than one predictor can be used. Significance of coefficients was tested with 1000 permutations. We measured the turnover rate (turnover per km) in a habitat type as the estimated coefficient in the model. To generate confidence intervals of estimated coefficients, we sampled communities with replacement, generated turnover distance matrix with resampled data, ran the model to generate coefficient of interest and repeated the process 1000 times to generate 1000 coefficient values. To compare turnover rates (coefficients) between habitats, we calculated an approximate two-tailed p value as

$$p = 1 - 2 \,.\left|\frac{x}{1000} - 0.5\right|$$

where 'x' is the mean coefficient value of the intercept [19]. The forest habitat was used as an intercept to compare differences with buffer and intensive-agriculture habitats, and buffer was used as an intercept to compare differences between buffer and intensive-agriculture habitats. We used Bonferroni correction to adjust significance levels for multiple comparisons using the *p.adjust* function.

Many recent studies have suggested the use of a null model approach to account for variation in gamma-diversity on turnover [20], but turnover was not correlated with pairwise gamma-diversity in our study (mantel tests: $p > 0.05$), except for all birds guild in forests (table S3), so we did not do this. Pairwise gamma-diversity was measured as the total number of species in a plot-pair. Horizontal and vertical trends in pairwise gamma diversity did not influence turnover rates (figure S3.4). Furthermore, many other studies have challenged the use of the null-modeling approach [21].

We used generalized linear models with Poisson error structure to determine the elevation effects on the relative densities of 14 threatened forest endemic species. We used a multivariate generalized linear model (MGLM; *manyglm* function in 'mvabund' package) to determine the influence of both land-use and elevation on Sri Lankan bird community (response variable). MGLMs were shown to have better power properties than distance-based methods [22]. We obtained estimated *p*-values from monte-carlo resampling (999 random permutations), and used non-metric multi-dimensional scaling (NMDS) to visualize results.

To better meet the assumptions of DISTANCE, we used half normal models with cosine adjustments selected by Akaike Information Criterion (AIC) and 100 m truncation. If a species had more than 40 observations outside of flocks, we estimated its detectability, and if a species had more than 40 such observations in each of the three land-uses, we estimated its detectability stratified by land-use. Species with less than 40 observations in total were given the detectability of the average species.

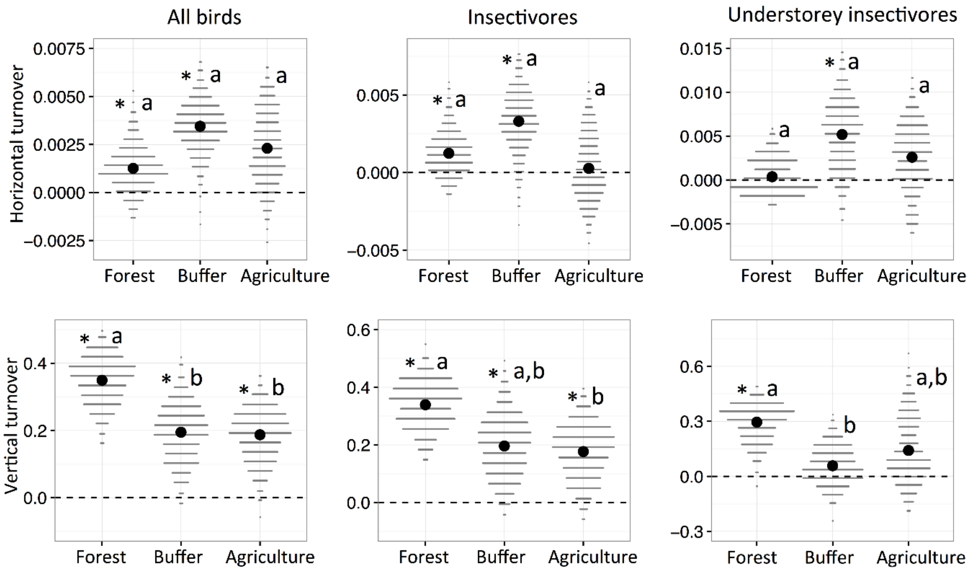

Figure 3.1. Species turnover per kilometer across horizontal and vertical distances between transects for all birds (n = 125 species), insectivores (n = 70 species) and understorey insectivores (n = 23 species) in forest, buffer and intensive-agriculture habitats. The figure represents mean of 1000 coefficient values (in grey) generated by multiple regression on distance matrices (MRM) after resampling the response with replacement. The black dashed line indicates no turnover (see table 3.1), * indicates significant turnover with distance, and habitats with different letters have significantly different turnover rates.

3.4 Results

Annual precipitation changed significantly with only vertical (estimate = 1093.35 mm/km; p = 0.001) distance, but not with horizontal distance (estimate = 4.52 mm/km; p = 0.087). Mean monthly temperature changed significantly with both vertical (estimate = 4.73°C/km, p = 0.001) and horizontal distances (estimate = 0.01°C/km, p = 0.013), but much more rapidly vertically than horizontally.

Analyzing across increasing horizontal distance, bird turnover in forest habitats increased significantly for all bird and insectivore guilds, though not for the understorey insectivore group (figure 3.1; asterisk indicates significant turnover). In buffer habitats, bird turnover increased with horizontal distance across all guilds. In contrast, birds in intensive-agriculture habitats remained similar with horizontal distance across all guilds. Analyzing across increasing vertical distance, bird turnover increased across all guilds in forest habitats. Bird turnover in buffer and intensive-agriculture habitats increased with vertical distance for all birds and insectivores, though not for the understorey insectivore group (figure 3.1).

The horizontal turnover rates were similar among habitats for all guilds ($p > 0.05$; figure 3.1; same letters indicate similar turnover rates). The vertical turnover rates in intensive-agriculture habitats were similar to buffer habitats for all guilds ($p > 0.05$, table S3.1). However, intensive-agriculture habitats had lower vertical turnover rates than forests for all birds ($p = 0.001$) and insectivore guilds ($p = 0.012$). Similarly, buffer habitats had lower turnover rates than forests for all birds ($p = 0.03$) and understorey insectivore guilds ($p = 0.001$). Vertical turnover of all birds in forest, buffer and intensive agriculture habitats was 287, 60 and 91 times greater than horizontal turnover (table 3.1).

Among the 14 threatened endemic forest species, seven preferred low elevations, one preferred middle elevations, five preferred high elevations, and one did not show any elevation preference (figure 3.2, table S3.2). Both elevation ($p < 0.001$) and land-use ($p < 0.001$) had a significant influence on Sri Lankan bird community composition (figure S3.2).

3.5 Discussion

Previous studies on land-use intensification have looked at turnover rates in different types of human disturbance across horizontal gradients but not vertical gradients [1-3]. To our knowledge, our results show for the first time that, buffer and intensive-agriculture habitats show significant vertical turnover rates, but

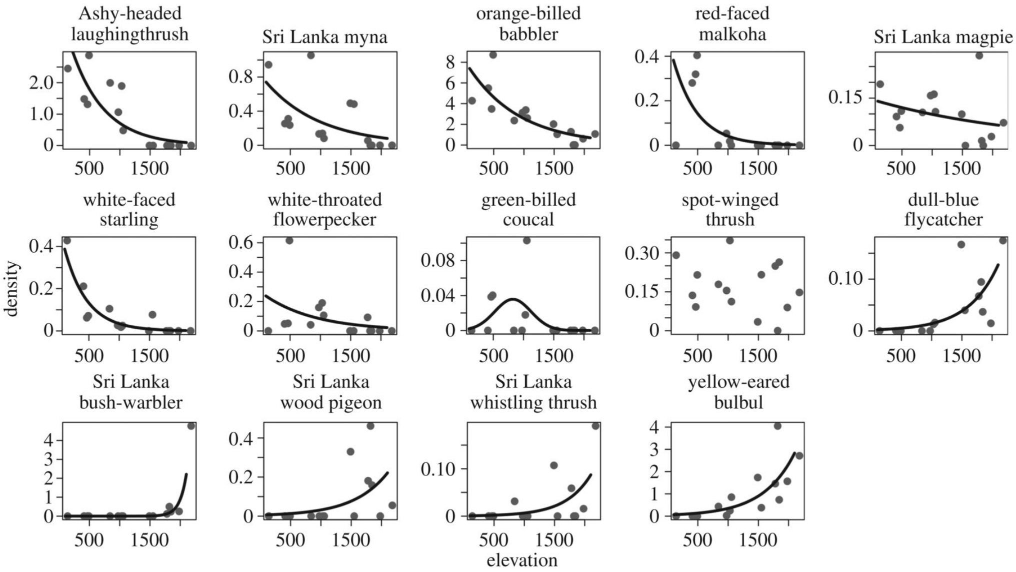

Figure 3.2. Relative density of threatened Sri Lankan endemic species across an elevation gradient in Sri Lanka showing differences in elevational preferences. See table S3.2 for details.

not as high as forests. Low and high elevation forests harbor markedly different bird communities, but the bird communities in low and high elevation buffer and agriculture are only moderately different. Within forests, although bothvertical and horizontal distances influenced forest bird turnover, small vertical distances (c. 2 km; 0.373 per km) had a much bigger effect than large horizontal distances (c. 75 km; 0.0013 per km). Both these results are consistent with a dominant influence of vertical distance on bird turnover in all habitats at regional scales. Recent studies suggest that biotic factors (habitat, diet and interspecific competition) that are indirectly related to temperature may be driving high turnover rates across vertical gradients [23-24].

Among forest birds, 14 threatened endemic diurnal forest species showed high turnover with elevation (figure 3.2). Five preferred high elevation forests (> 1500 m), increasing their extinction risk due to climate change, especially in islands like Sri Lanka where opportunities for dispersal are limited. Rapid upward shifts in tropical organisms have already been observed

Table 3.1. Results of multiple regression of distance matrices with turnover as response variable and horizontal distance and vertical distance as predictor variables.

	Estimate	*p* value
All birds		
Forest ($R^2 = 0.86$)		
Horizontal	0.0013	0.022
Vertical	0.373	0.001
Buffer ($R^2 = 0.62$)		
Horizontal	0.0034	0.002
Vertical	0.203	0.001
Agriculture ($R^2 = 0.60$)		
Horizontal	0.0022	0.061
Vertical	0.200	0.001
Insectivores		
Forest ($R^2 = 0.85$)		
Horizontal	0.0012	0.037
Vertical	0.376	0.001
Buffer ($R^2 = 0.50$)		
Horizontal	0.0032	0.006
Vertical	0.215	0.001
Agriculture ($R^2 = 0.27$)		
Horizontal	-0.0001	0.958
Vertical	0.1964	0.005
Understorey insectivores		
Forest ($R^2 = 0.63$)		
Horizontal	-0.0005	0.554
Vertical	0.3493	0.001
Buffer ($R^2 = 0.30$)		
Horizontal	0.0053	0.003
Vertical	0.048	0.382
Agriculture ($R^2 = 0.27$)		
Horizontal	0.0037	0.061
Vertical	0. 107	0.142

with warming of c. 0.5°C in tropical land areas over the last 50 years [25]. A recent study predicted that a 2°C rise in temperature would shift the bird communities upwards by 400 m [15]. For the whole of Sri Lanka, the forested area (> 75% tree cover) at elevations > 1500 m and > 1900 m is 583 km^2 and 152 km^2, respectively. So, a 400 m shift upwards would reduce the potential habitat for high elevation threatened endemic species by 74%. Similar shifts might extirpate entire populations of these species in the isolated Knuckles mountain range where the highest peak is 1863 m (figure S3.3).

In conclusion, our study shows that the turnover rate in tropical birds is very sensitive to vertical distance in all land-use types, and especially high in forests; while turnover with horizontal distance is much smaller. Land-use intensity was also important for turnover in bird communities (figure S3.2). These results suggest a need to prioritize the protection of sufficient forest area across the full elevational range over protecting additional forest areas at similar elevations, as long as enough habitat is protected at any one elevation to sustain populations. Even though established reserves are relatively well protected in Sri Lanka, the extraordinary level of endemicity, both of fauna and flora [26-27], call for restoration of degraded areas and expansion of the relatively small size of the existing protected area to cover endemic hotspots. The results also highlight the vulnerability of high-elevation specialists to even moderate global warming and thus emphasize the critical importance of achieving the targets included in the 2015 Paris Agreement.

3.6 References

1. Karp DS, Rominger AJ, Zook J, Ranganathan J, Ehrlich PR, Daily GC. 2012 Intensive agriculture erodes β-diversity at large scales. *Ecol. Lett.* **15**, 963-970.
2. Kitching RL, Ashton LA, Nakamura A, Whitaker T, Khen CV. 2013. Distance-driven species turnover in Bornean rainforests: homogeneity and heterogeneity in primary and post-logging forests. *Ecography* **36**, 675-682.

3. Solar RRD, Barlow J, Ferriera J, Berenguer E, Lees AC, Thomson JR. 2015 How pervasive is biotic homogenization in human modified tropical forest landscapes? *Ecol. Lett.* **18**, 1108-1118.
4. McKinney ML. 2006 Urbanization as a major cause of biotic homogenization. *Biol. Conserv.* **127**, 247-260.
5. Frishkoff LO, Karp DS, Flanders JR, Zook J, Hadly EA, Daily GC, M'Gonigle LK. 2016 Climate change and habitat conversion favor the same species. *Ecol. Lett.* **19**, 1081-1090
6. La Sorte FA, Butchart SHM, Jetz W, Bohning-Gaese K. 2014 Range-wide latitudinal and elevational temperature gradients for the world's terrestrial birds: implications under global climate change. *PLOS ONE* **9**, e98361.
7. Jankowski JE, Ciecka AL, Meyer NY, Rabenold KN. 2009 Beta diversity along environmental gradients: implications of habitat specialization in tropical montane landscapes. *J. Anim. Ecol.* **78**, 315-327.
8. Sekercioglu, CH. 2012 Bird functional diversity and ecosystem services in tropical forests, agroforests and agricultural areas. *J. Ornithol.* **153**, 153-161.
9. Hijmans RJ, Cameron, SE, Parra JL, Jones PG, Jarvis A. 2005 Very high resolution interpolated climate surfaces for global land areas. *Int. J. Climatol.* **25**, 1965-1978.
10. Hansen MC, Potapov PV, Moore R, Hancher M, Turubanova A, Tyukavina A, Thau D, Stehman SV, Goetz SJ, Loveland TR *et al.* 2013 High resolution global maps of the 21st century forest cover change. *Science* **342**, 850-853.
11. Sreekar R, Srinivasan U, Mammides C, Chen J, Goodale UM, Kotagama SW, Sidhu S, Goodale E (2015) The effect of land-use on the diversity and mass-abundance relationships of understory avian insectivores in Sri Lanka and southern India. *Sci. Rep.* **5**, 11569.
12. Mammides C, Chen J, Goodale UM, Kotagama SW, Sidhu S, Goodale

E. 2015 Data from: Does mixed-species flocking influence how birds respond to a gradient of land-use intensity? Dryad Digital Repository. http://dx.doi.org/10.5061/dryad.vk070.

13. Baselga A, Orme CDL. 2012 betapart: an R package for the study of beta diversity. *Methods Ecol. Evol.* **3**, 808-812.
14. Baselga A. 2013 Separating the two components of abundance-based dissimilarity: balanced changes in abundance vs. abundance gradients. *Methods Ecol. Evol.* **4**, 552-557.
15. Sinnott RW. 1984 Virtues of the Haversine. *Sky and Telescope* **68,** 159.
16. Hijmans RJ, Williams E, Vennes C. 2011 Package 'geosphere'. Available: https://cran.r-project.org/web/packages/geosphere. Accessed: 10 March 2017.
17. Lichstein J. 2007 Multiple regression on distance matrices: A multivariate spatial analysis tool. *Plant Ecol.* **188**, 117-131.
18. Goslee SC, Urban DL. 2007 The ecodist package for dissimilarity-based analysis of ecological data. *J. Stat. Softw.* **22**, 1-19.
19. Bagchi R, Philipson CD, Slade EM, Hector A, Phillips S, Villanueva JF, Lewis OT, Lyal CHC, Nilus R, Madran A, Scholes JD, Press MC. 2011 Impacts of logging on density-dependent predation of dipterocarp seeds in a South East Asian rainforest. *Phil. Trans. R. Soc. B* **366**, 3246-3255.
20. Socolar JB, Gilroy JJ, Kunin WE, Edwards DP. 2016 How should beta-diversity inform biodiversity conservation? *Trends Ecol. Evol.* **31**, 67-80.
21. Ulrich W, Baselga A, Kusumoto B, Shiono T, Tuomisto H, Kubota Y. 2016 The tangled link between *β*- and γ-diversity: a Narcissus effect weakens statistical inferences in null model analyses of diversity patterns. *Glob. Ecol. Biogeo.* DOI: 10.1111/geb.12527.
22. Wang Y, Naumann U, Wright ST, Warton DI. 2012 mvabund – an R package for model-based analysis of multivariate abundance data. *Methods Ecol. Evol.* **3**, 471-474.
23. Londono GA, Chappell MA, Jankowski JE, Robinson SK. 2017 Do

thermoregulatory costs limit altitude distribution of Andean forest birds? *Func. Ecol.* **31**, 204-215.

24. Freeman BG. 2016 Thermal tolerances to cold do not predict elevational limits in New Guinean montane birds. *Diversity Distrib.* **22**, 309-317.
25. Freeman BG, Freeman AMC. 2014 Rapid upslope shifts in New Guinean birds illustrate strong distributional responses of tropical montane species to global warming. *Proc. Nat. Acad. Sci. USA* **111**, 4490-4494.
26. Bossuyt F, Meegaskumbura M, Beenaerts N, Gower DJ, Petiyagoda R, Roelants K, Mannaert A, Wilkinson M, Bahir MM, Manamendra-Arachchi K, *et al.* 2004 Local endemism within the Western Ghats – Sri Lanka biodiversity hotspot. *Science* **306**, 479-481.
27. Gunatilleke IAUN, Gunatilleke CVS. 1991 Threated woody endemics of the wet lowlands of Sri Lanka and their conservation. *Biol. Conserv.* **55**, 17-36.

3.7 Supporting information

Table S3.1. Differences in turnover rates of multiple bird guilds between habitats across horizontal and vertical distances. The p values were adjusted using Bonferroni correction, and bold values indicate significance ($p < 0.05$).

	p value
All birds	
Horizontal	
Forest vs. buffer	0.357
Forest vs. agriculture	0.758
Buffer vs. agriculture	0.822
Vertical	
Forest vs. buffer	**0.026**
Forest vs. agriculture	**0.001**
Buffer vs. agriculture	0.995
Insectivores	
Horizontal	
Forest vs. buffer	0.484
Forest vs. agriculture	0.667
Buffer vs. agriculture	0.249
Vertical	
Forest vs. buffer	0.114
Forest vs. agriculture	**0.012**
Buffer vs. agriculture	0.952
Understorey insectivores	
Horizontal	
Forest vs. buffer	0.387
Forest vs. agriculture	0.950
Buffer vs. agriculture	0.966
Vertical	
Forest vs. buffer	**0.006**
Forest vs. agriculture	0.623
Buffer vs. agriculture	0.829

Table S3.2. Results of generalised linear models with relative densities of threatened endemic forest species as response variables and elevation as predictor variable. We sampled 15 forest transects along the elevational gradient. IUCN threatened status of each is specified in parentheses next to the common name, VU: vulnerable, NT: near threatened and EN: endangered.

Species	**Estimate ± SE**	**z value**	***p* value**
Ashy-headed laughingthrush (VU)	-0.0018 ± 0.00006	-31.17	<0.0001
Sri Lanka myna (NT)	-0.0011 ± 0.00008	-12.64	<0.0001
Orange-billed babbler (NT)	-0.0012 ± 0.00003	-40.82	<0.0001
Red-faced malkoha (VU)	-0.0024 ± 0.00025	-9.636	<0.0001
Sri Lanka magpie (VU)	-0.00039 ± 0.00013	-2.893	0.00382
White-faced starling (VU)	-0.00269 ± 0.00028	-9.493	<0.0001
White-throated flowerpecker (NT)	-0.00117 ± 0.00016	-7.315	<0.0001
Green-billed coucal (VU)	0.0092 ± 0.00359	2.562	0.0104
Spot-winged thrush (NT)	-0.00022 ± 0.0002	-1.164	0.104
Dull-blue flycatcher (NT)	0.00199 ± 0.00009	20.01	<0.0001
Sri Lanka bush-warbler (NT)	0.00905 ± 0.00034	26.63	<0.0001
Sri Lanka wood pigeon (VU)	0.00177 ± 0.00021	8.225	<0.0001
Sri Lanka whistling thrush (EN)	0.00236 ± 0.00045	5.233	<0.0001
Yellow-eared bulbul (NT)	0.0019 ± 0.00006	29.73	<0.0001

Table S3.3. Relationship between turnover and pairwise gamma-diversity in different habitats and for multiple guilds show no correlation except for all birds guild in forest habitats. Mantel tests were used to determine the correlation between the two distance matrices.

	mantel-r	*p* value
All birds		
Forest	-0.246	0.022
Buffer	-0.029	0.805
Agriculture	-0.264	0.153
Insectivores		
Forest	-0.219	0.055
Buffer	0.048	0.700
Agriculture	-0.298	0.061
Understorey insectivores		
Forest	-0.238	0.065
Buffer	-0.126	0.320
Agriculture	-0.225	0.144

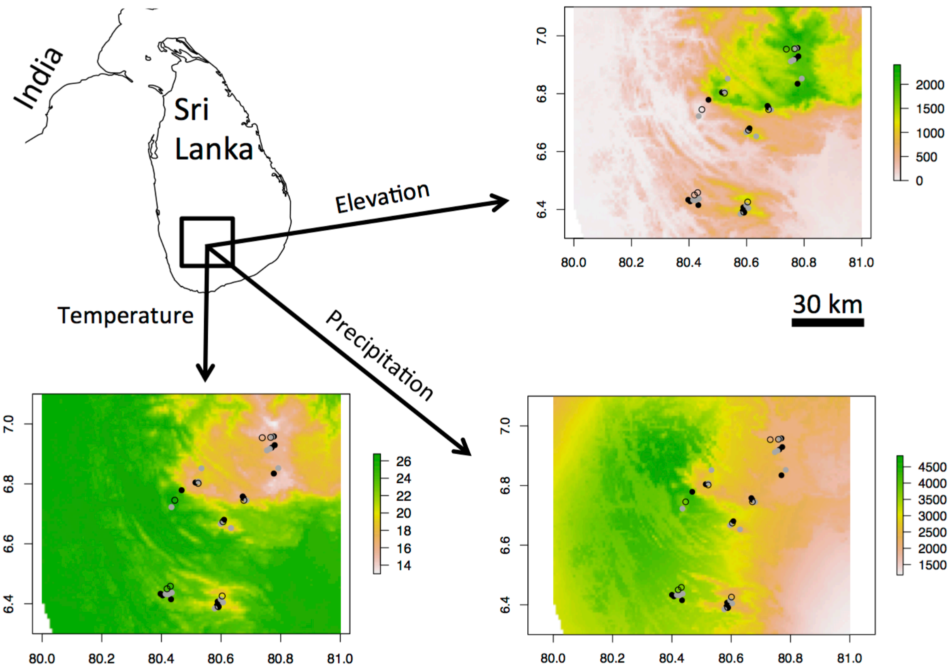

Figure S3.1. Map showing forest (filled black circles), buffer (filled grey circles), and intensive-agriculture (open circles) transects across gradients of elevation, temperature and precipitation in Sri Lanka.

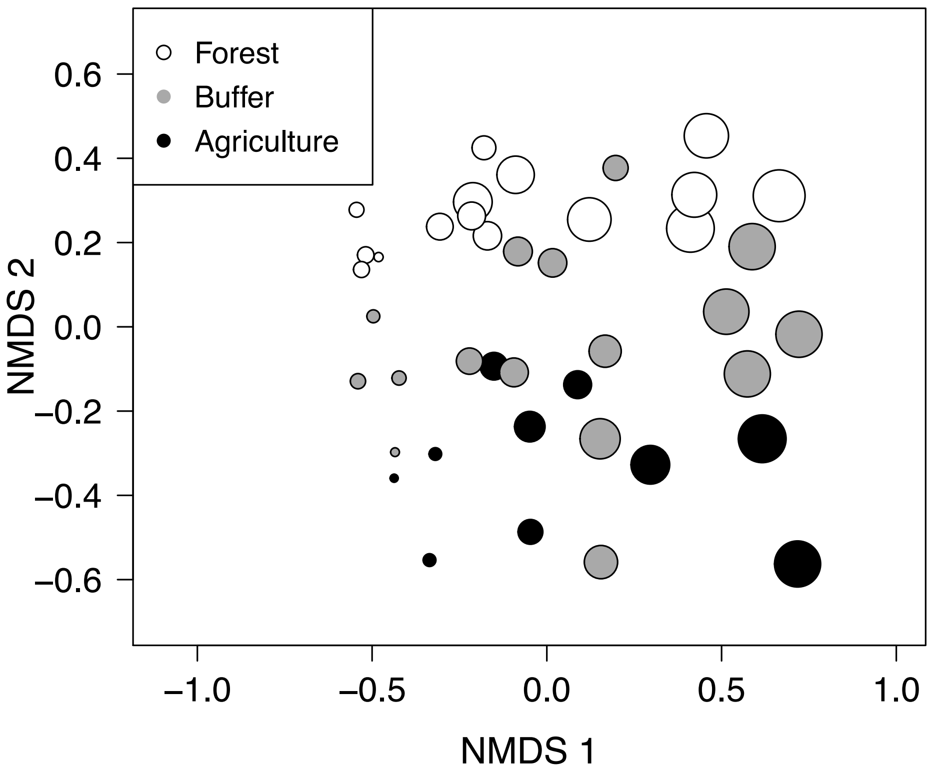

Figure S3.2. A non-metric dimensional scaling (NMDS) plot showing differences across land-use types and elevation. The size of the circle is proportion to the elevation. The first and second axes show the influence of elevation and land-use type on bird communities, respectively.

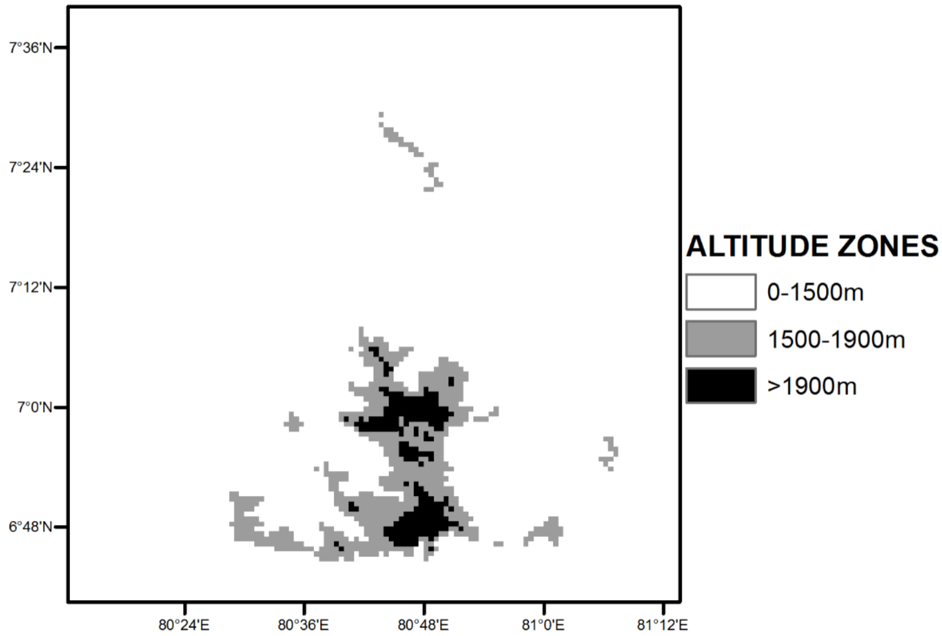

Figure S3.3. Map showing high elevation (>1500 m) regions in Sri Lanka. The isolated light-grey patch on the top (7.24 N) is the Knuckles mountain range.

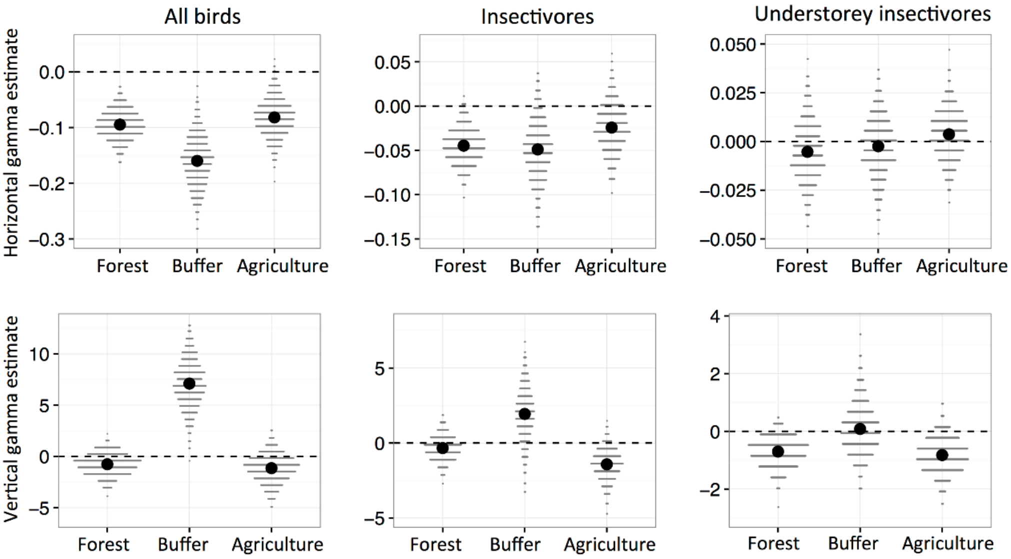

Figure S3.4. Change in pairwise gamma diversity (per km) across horizontal and vertical distances between transects for all birds, insectivores and understorey insectivores in forest, buffer and intensive-agriculture habitats. The figure represents mean of 1000 coefficient values (in grey) generated by multiple regression on distance matrices (MRM) after resampling the communities with replacement. The black dashed line indicates no change.

Chapter 4

Bird community assembly at multiple spatial scales in the Western Ghats – Sri Lanka biodiversity hotspot: role of land-use, environment and space

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Overall percentage (%)	85%		
Certification:	This paper reports on original research I conducted during the period of my Higher Degree by Research candidature and is not subject to any obligations or contractual agreements with a third party that would constrain its inclusion in this thesis. I am the primary author of this paper.		
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Co-Author Contributions

By signing the Statement of Authorship, each author certifies that:

i. the candidate's stated contribution to the publication is accurate (as detailed above);

ii. permission is granted for the candidate in include the publication in the thesis; and

iii. the sum of all co-author contributions is equal to 100% less the candidate's stated contribution.

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Signature		Date	30/08/2018

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Contribution to the Paper	Selected sites and acquired bird data. Helped with study design, writing and discussing the manuscript.		
Signature		Date	30/08/2018

4.1 Summary

Context The importance of community assembly theory for biodiversity conservation is increasingly being recognized. Conservation policies aimed at improving forest cover can benefit by better understanding the relative importance of different ecological mechanisms in structuring ecological communities.

Objectives While the importance of niche-based processes that restrict species to a specific land-use type is known to drive species composition change at small spatial scales, the relative importance of land-use change on species composition at larger scales remain poorly known. In this study, we evaluated the drivers of species composition change at larger spatial scales with significant variation in environment and space.

Methods We used a variation-partitioning approach to evaluate the relative importance of land-use (ranked value of forest loss), environment (temperature and precipitation) and space (geographic position and barriers) on bird species composition across 32 two-km line transects in the Western Ghats–Sri Lanka biodiversity hotspot.

Results Space was the most important variable to explain species composition change in the biodiversity hotspot, suggesting that assembly was predominantly driven by dispersal limitation over the Palk Strait, which separates Western Ghats and Sri Lanka. Land-use and environment variables were equally important to explain species composition change on either side of the Palk Strait, suggesting that assembly was predominantly driven by niche-based processes at intermediate scales.

Conclusions Therefore, to conserve distinct communities in a biodiversity hotspot, it may be important to consider geographic barriers and environmental variation along with land-use change.

4.2 Introduction

Understanding the patterns of change in community composition (beta-diversity) in space and time, and the processes that structure communities is a central theme in ecology (Hubbell, 2001; Chase & Myers, 2011). While the impacts of land-use change on beta-diversity are widely known (see Newbold et al., 2016), most studies have been restricted to small spatial scales, with minimal differences in environmental conditions and space (geographic distance). A better understanding of the mechanisms that alter beta-diversity at multiple spatial scales would not only help expand community assembly theory, but also expand our knowledge on how to manage and restore biodiversity in the Anthropocene (Myers et al., 2015, Audino et al., 2017). For example, while forest loss and climate change may increase dispersal of birds into favourable landscapes (Davey et al. 2013, Karp et al. 2018), environment and space can restrict their dispersal patterns (Ramachandran et al., 2017; Sreekar et al., 2017). Therefore, policies aimed at improving forest cover in a biodiversity hotspot will benefit by better understanding the relative importance of different ecological mechanisms in structuring ecological communities.

Partitioning the variation of observed beta-diversity into components explained by land-use intensity, environment, and space provides insights into mechanisms of community assembly (Legendre et al., 2009; Myers et al., 2015). For example, in a changing landscape with increasing forest loss, beta-diversity is expected to increase with land-use change because of the spatial aggregation of habitat-specialist species (Audino et al., 2017; Becca et al., 2017). Similarly, large differences in environment (temperature and precipitation) and space can also cause spatial aggregations of species due to environmental filtering and dispersal limitation, respectively (Ricklefs, 1987; Hubbell, 2001; Kraft et al., 2011). Unmeasured environmental variables and stochastic processes may influence the unexplained variance in beta-diversity (Legendre et al., 2009; Myers et al., 2013, 2015). Here, we use the variation-partitioning approach to determine the relative importance of land-use change, environment, and space in explaining the variation in bird beta-diversity at multiple spatial scales in a biodiversity hotspot.

In this study, we determined the drivers of variation in bird beta-diversity across multiple spatial scales in Western Ghats – Sri Lanka biodiversity hotspot. Specifically, we ask two questions:

i. At a large spatial scale, differences in environment and space have been shown to drive bird beta-diversity in the Western Ghats – Sri Lanka biodiversity hotspot (Ramachandran et al., 2017). Space is influenced by geographic barrier effects (the Palk Strait). However, Ramachandran et al. (2017) did not incorporate land-use in their study, and therefore the relative importance of land-use change to drive bird beta-diversity at large spatial scale remains unknown. Is spatial variation in land-use the most important driver of bird beta-diversity in the biodiversity hotspot, more important than environmental differences and spatial separation (the Palk Strait)?
ii. At intermediate scales, changes in environment due to differences in elevation have been shown to drive bird beta-diversity (Sreekar et al., 2017). Compared to environment, what is the relative importance of land-use and space (geographic distance)?

4.3 Methods

Study area

We used bird data collected along 32 two-km transects across a gradient of land-use, environment and space to determine the drivers of the bird community assembly at multiple spatial scales in the Western Ghats–Sri Lanka biodiversity hotspot (Goodale et al. 2014; Mammides et al. 2015). We divided the dataset into three spatial scales – (i) large spatial scale: it includes all 32 transects, some of which are separated by a physical geographic barrier (the Palk Strait; Fig.

4.1), altitude of c. 1200 m and across various land-use types (protected primary forest, reserve border areas -"buffer", and intensive agriculture); (ii) intermediate spatial scale: transects in Western Ghats (n =16) and Sri Lanka (n = 16) were divided into different datasets. Therefore, transects are separated by comparatively small distances (< 50 km), but are varied by elevation and land-use (Fig. 4.1).

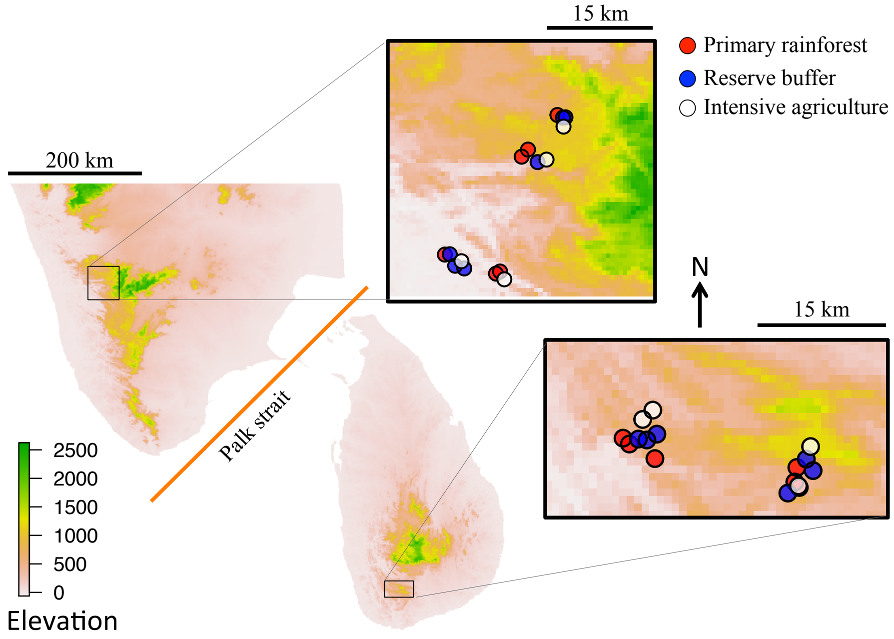

FIGURE 4.1 Map showing the 32 transects that were used to sample birds in South Asia, 16 transects on either side of the Palk strait, and 8 in each elevation type on either side: low (<500 m) and mid (<1300 m). Elevation above sea-level data was downloaded from http://www.worldclim.org/.

A team of two walked along transects at 1 km/hr and identified all the individual birds seen and heard. Each transect was visited an average of 7.2 times per year in both breeding and non-breeding seasons. Transects were walked in the morning (08:00 – 10:00) and in the afternoon (15:00 – 17:00). Relative densities of each species were estimated by accounting for the detection probability of each species using DISTANCE (http://distancesampling.org). We used half normal models with 100 m truncation and cosine adjustments selected by Akaike Information Criterion (AIC) (Sreekar et al. 2015, 2017). We estimated detectability for species that have more than forty observations. If a species had less than 40 observations, we gave them the detectability of the average species.

We used haversine method to measure the shortest distance (in kms) between transects (*distm* function in 'geosphere' package; Sinnott 1984; Hijmans et al. 2011). We used mean annual precipitation and mean monthly temperature data extracted from WORLDCLIM database (30 arc-seconds resolution data; http://worldclim.org/version1; Hijmans et al. 2005) to measure environmental differences. We quantified variation in land-use by assigning ranks to land-use types: protected primary forests to '3', reserve buffers to '2' and intensive agriculture to '1'.

Data analysis

We measured the variation in species composition (beta diversity) between two transects using a comparatively robust abundance-based pairwise dissimilarity metric, Bray-Curtis dissimilarity (Beck et al. 2013). We partitioned Bray-Curtis dissimilarity into abundance gradient and balanced turnover components using the *bray.part* function in 'betapart' package in R (Baselga and Orme 2012). Abundance gradients are biological subsets where species remain constant, but individuals are lost from richer sites to poorer sites. Balanced turnover is defined as species replacement between sites with constant number of individuals (Baselga 2013). Here, abundance gradients and balanced turnover were used as response variables to estimate variation across multiple spatial scales, and to determine the drivers of variation. We used a non-parametric multivariate analysis of variances based on distance to centroid to compare the bird beta diversity in India and Sri Lanka (Anderson et al. 2006; 'betadisper' function in *vegan* package). Similarly, we also used 'betadisper' to compare beta diversity in lower and middle elevation within each country. This procedure compares the homogeneity of beta diversity within each group.

Previous studies suggested that variation in pooled species richness (gamma diversity) can explain gradients in observed beta diversity due to random sampling effects (Kraft et al. 2011; Ashton et al. 2016). Therefore, we used a Mantel test to determine the correlation between beta diversity and pooled species richness (gamma diversity). Mantel test produces a matrix correlation value between two distance matrices. A regular correlation test (e.g. Pearson test) cannot be used because distance matrices have inherent non-independence.

We used distance-based redundancy analysis ('dbrda' function in *vegan* package) to determine the influence of land-use, environment and space variables on bird abundance gradients and balanced turnover. The distance-based redundancy analysis performs automatic data standardization using non-metric dimensional scaling. Therefore, we used the metric multidimensional scaling (MDS) to visualize the effects of land-use, environment and space variables on bird beta-diversity. We used principal coordinates of neighbourhood matrices (PCNM) to transform spatial distances into matrices (eigenvectors), which are suitable for ordination analysis (Legendre et al. 2009). We considered latitude, longitude and eigenvectors as our spatial variables. Latitude and longitude were highly correlated with each other at large all spatial scales (Pearson's $r > 0.75$; Table S4.1). Latitude was also highly correlated with the first eigenvector of PCNM ($r > 0.80$; Table S4.2) at all spatial scales. Our exploratory analysis suggested that the remaining eigenvectors did not explain significant variation in the response variable at any spatial scale ($P > 0.05$). Therefore, we included latitude as a spatial variable at all spatial scales. In practice, space means North and South of the Palk Strait at the large spatial scale.

Environmental variables included mean annual temperature and precipitation. Mean annual temperature and precipitation were highly correlated at all spatial scales ($r > 0.75$; Table S4.3). Therefore, only mean annual temperature was included as an environmental variable. Ranked land-use type was used a land-use variable at all spatial scales.

We used forward model selection to obtain significant explanatory variables (Blanchet et al. 2008) using 'ordistep' function in the *vegan* package, and partitioned the observed variance into proportions explained by each variable based on adjusted R^2 using the 'varpart' function in *vegan* package. We used non-parametric bootstrapping to determine the difference in the variation explained by land-use, environmental and spatial variables. We sampled communities with replacement, generated the response matrix with resampled data, and ran dbRDA to determine the variance explained by each variable. We repeated the process 1000 times to generate mean and 95% quantiles of the variance explained by each variable.

4.4 Results

We detected 37,370 individuals across 196 species (Sri Lanka - 107 species, India – 152 species) along temperature (19.6-27.8 ºC), precipitation (1868-3765 mm/yr), elevation (45–1295 m) and spatial (5-500 km) gradients in the Western Ghats–Sri Lanka biodiversity hotspot. There were no significant predictors of abundance gradients at any of the examined spatial scales. In contrast, balanced turnover was influenced by different variables at different spatial scales (Fig. 4.2, Fig. 4.3). Balanced turnover was highly correlated with Bray-Curtis dissimilarity (Mantel $r > 0.85$; Table S4.4), and gamma-diversity did not influence balanced turnover at any spatial scale—therefore suggesting no significant random sampling effects (Table S4.5).

At the largest spatial scale, balanced turnover was influenced by dissimilarity in all measured variables (land-use, environment and space; Fig. 4.2), which explained c. 65% of the total observed variation (Fig. 4.3). Space explained higher variation (c. 36%) than environment (c. 9%) and land-use (c. 14%), respectively, while land-use and environment explained similar amount of variation.

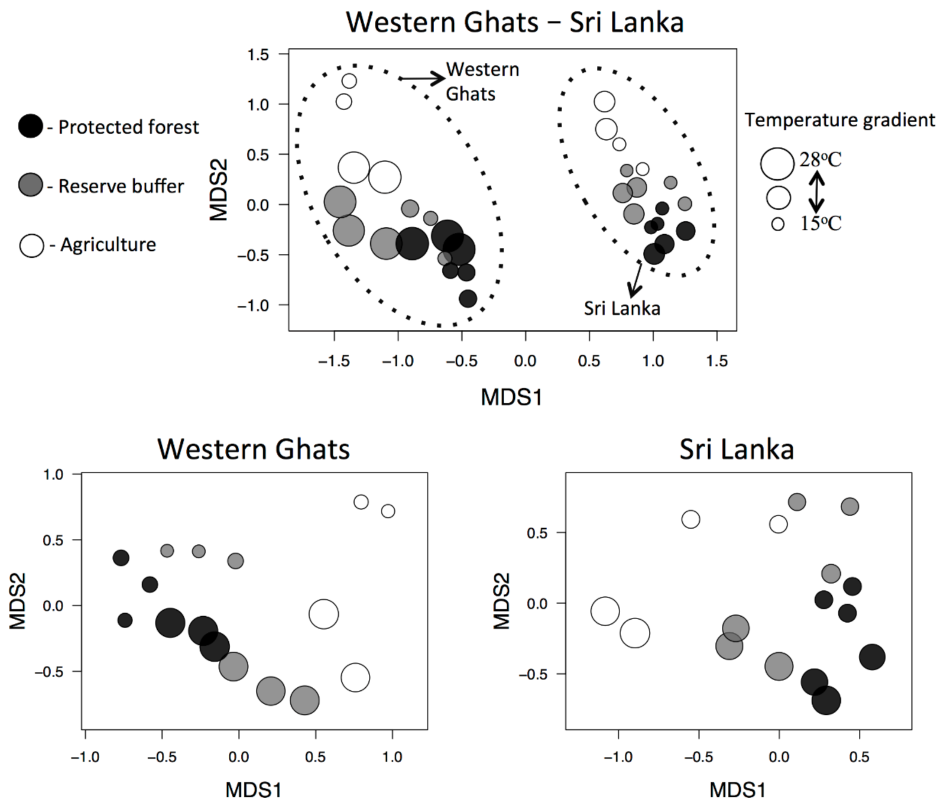

FIGURE 4.2 Drivers of bird beta-diversity (balanced turnover) at multiple spatial scales presented using multi-dimensional scaling (MDS). Balanced turnover was highly correlated with Bray-Curtis dissimilarity (Mantel $r > 0.85$; Table S4). The ordination plots are for visualization only. See figure 4.3 for statistical analysis.

At intermediate spatial scales, the net balanced turnover in Sri Lanka and India was similar ($F_{(1,30)} = 0.17$, $P = 0.69$; Fig. S4.1). Balanced turnover was influenced by environment and land-use, (Fig. 4.2) which together explained 74% and 60% of the total variation in Sri Lanka and India, respectively. Forward model selection suggested that space did not drive bird community assembly at the intermediate scale, in either of the countries. In Sri Lanka, environment (c. 32%) and land-use (c. 38%) were equally important in driving bird community assembly (Fig. 4.3). Similarly, environment (c. 27%) and land-use (c. 36%) were also equally important in driving bird assembly in India (Fig. 4.3).

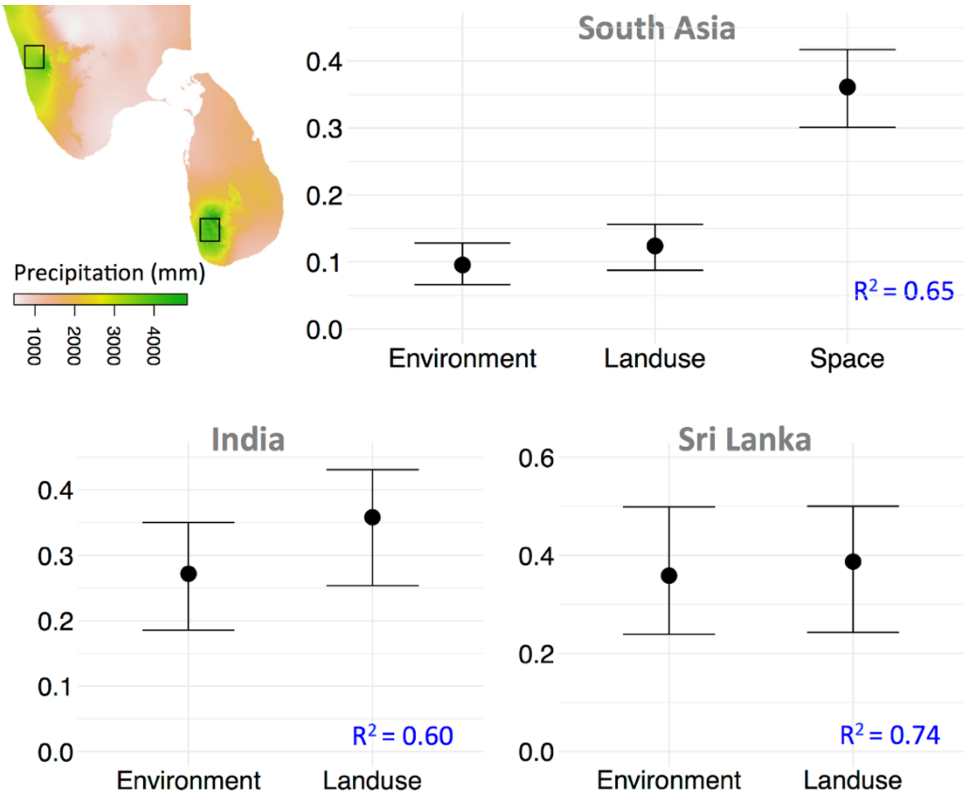

FIGURE 4.3 Variation explained (adjusted R^2) by space (dispersal limitation), environment (temperature and precipitation) and land-use type at large and intermediate spatial scales in Western Ghats – Sri Lanka biodiversity hotspot (south Asia). Dispersal limitation was the most important driver of bird community assembly in the hotspot. Environment and land-use were equally important for driving bird assembly in Western Ghats, India and Sri Lanka. Space did not drive bird community assembly at intermediate spatial scales in both countries. The error bars are the 95% quantiles generated by non-parametric bootstrapping.

4.5 Discussion

We show that the bird beta-diversity in the Western Ghats–Sri Lanka biodiversity hotspot was predominantly driven by balanced turnover (species replacement) and not abundance gradients (species loss). Our results suggest that spatial scale changes the relative importance of variables that drive the balanced turnover of birds in the Western Ghats–Sri Lanka biodiversity hotspot, South Asia (Fig. 4.3). At the large spatial scale, our results show that space is the most important variable that drives balanced turnover in the biodiversity hotspot, up to three times more important than land-use change due to forest loss (Fig. 4.3). Our result reflects high bird endemicity on either side of the physical barrier—the Palk Strait—caused by many birds' inability to cross the sea (dispersal limitation). At intermediate scales, on either side of the Palk Strait, our results show that both land-use and environment were equally important in driving balanced bird species turnover, indicating the role of niche-based processes. The environmental differences between sites at intermediate scales was c. 4°C (range: 2.8°C to 5.8°C) in temperature and/or c. 1350 mm (range: 1063 mm to 1580 mm) in precipitation. Therefore, our results suggest that balanced turnover caused by c. 4°C change in temperature and/or c. 1350 mm change in precipitation is numerically similar to balanced turnover caused by land-use change due to conversion of tropical rainforests into intensive agriculture in the Western Ghats–Sri Lanka biodiversity hotspot.

There are two main limitations in our study. First, we only sampled the low- (<500 m) and mid-elevation (800-1300 m) regions of the Western Ghats–Sri Lanka biodiversity hotspot. The high elevation (>1500 m) regions were not sampled in this study. The inclusion of high elevation regions into balanced turnover analysis may increase the importance of environment in comparison to land-use because multiple high elevation endemic bird species occur from 1500 m upwards (Robin et al. 2014, Sreekar et al. 2017). Second, the distance between our Western Ghats and Sri Lankan plots was c. 600 km (Fig. 4.1). Therefore, it could also be possible that the balanced bird species turnover at large spatial scales was simply caused by the decay of community composition with geographic distance (distance decay; Nekola and White 1999), and not by the physical biogeographic barrier – the Palk Strait. However, we are confident that the Palk Strait is causing balanced turnover in the region because our results were in concordance with previous studies that have used different methods (molecular and species distributions) to show that the Palk Strait is the major physical barrier in the region causing balanced turnover between Western Ghats and Sri Lanka (Bossuyt et al. 2004; Ramachandran et al. 2017).

Spatial scale changes the drivers of bird community assembly

Most previous studies assessing the importance of forest loss on balanced species turnover are restricted to small spatial scales with minimal differences in environment and space (see Newbold et al. 2016). To our knowledge, our study is the first to simultaneously sample birds across a land-use, elevation and latitude gradient to determine the relative importance of land-use, environment and space on bird species composition. We showed that, in the Western Ghats–Sri Lanka biodiversity hotspot, space (the Palk Strait) is the most important variable that causes species aggregations. It explained c. 36% of the total variation in balanced turnover. Therefore, our result reflects the importance of dispersal limitation (over sea) processes in the biodiversity hotspot. Land-use and environment explained c. 14% and c. 9% of the total variance, respectively. This implies smaller influence of land-use and environment on balanced bird species turnover at large spatial scales in the biodiversity hotspot. Although the endemicity of birds within Sri Lanka is low when compared to other threatened taxa like amphibians, freshwater fishes, molluscs and reptiles (Bossuyt et al. 2004; Gunawardene et al. 2007), our results show that the Palk Strait is the most important cause of balanced bird species turnover in the biodiversity hotspot, surpassing the effects of changes in land-use and environment. This only heightens the importance of dispersal limitation for balanced turnover in most other taxa with lower dispersal abilities. It is also important to note that the dry savannahs that surround the Palk Strait also act as a dispersal barrier for rainforest organisms. Although a land bridge connected India and Sri Lanka on several occasions in the last 10,000 years, the climate remained similar (Pan & Kumar 1997; Bossuyt et al. 2004). Therefore, the strait along with the dry savannah region act as a barrier for rainforest organisms to disperse between the rainforests of Western Ghats and Sri Lanka. If savannah habitats were sampled in southern India and Sri Lanka, their species composition would be more similar than species composition of rainforest habitats (Rasmussen & Anderton 2012). Our study along with previous studies suggests that the dissimilarity in ecological communities between Western Ghats and Sri Lanka should be taken into account during the global analysis of biodiversity hotspots (Bossuyt et al. 2004; Ramachandran et al. 2017; Wickramasinghe et al. 2017).

At intermediate spatial scales, our study showed that the variation explained by land-use change due to forest loss is similar to the variation explained by environment (Fig. 4.3). The changes in environment (temperature and precipitation) in our study were caused by differences in elevation. We obtained similar results in both Western Ghats, India and in Sri Lanka. Both regions also had similar beta-diversity (Fig. S4.1), which means that the net outcome of community assembly processes was also similar. Therefore, our study suggests that both land-use and environment are equally important for causing cause species aggregations, and together explained c. 60-74% of the total variation in balanced bird species turnover at intermediate scales. Unmeasured environmental variables (e.g. canopy cover, basal area, distance to edge, litter depth, undergrowth thickness) and stochastic processes could explain the remaining 26-40% variation in balanced turnover. In highly mobile taxa like birds, the influence of stochastic processes (e.g., chance colonization) should be small, especially at intermediate spatial scales (<50 km as a crow flies) in a well-sampled dataset (37,370 individuals).

Conclusions

Our results suggest that bird community assembly in the Western Ghats–Sri Lanka biodiversity hotspot is heavily influenced by dispersal limitation across a physical biogeographic barrier – the Palk Strait (space; Fig. 4.2, Fig. 4.3). Therefore, increasing the percentage of forested area only on one side of the Palk Strait does not prevent further loss of threatened species. This may also apply to other dispersal barriers within the Western Ghats–Sri Lanka biodiversity hotspot (Robin et al., 2015; Vijayakumar et al. 2016; Ramachandran et al. 2017). On either side of the Palk Strait, bird community assembly was equally influenced by differences in land-use change and elevation (Fig. 4.3). Therefore, to prevent threatened species loss, protected areas should be expanded across the full available elevation gradient. Expanding protected areas without considering important ecological processes (e.g. dispersal limitation and niche-based processes) that structure communities will only be useful for conservation at small spatial scales. It is well known that the current protected area estate is biased towards certain regions that are not important for biodiversity, or are homogenous (low species turnover) in nature (Venter et al. 2014). Considering community assembly at multiple spatial scales while selecting sites for biological conservation holds promise for preventing further loss of threatened species.

4.6 References

Anderson, M. J. (2006). Distance-based tests for homogeneity of multivariate dispersions. *Biometrics*, 62, 245–253.

Ashton, L. A., Nakamura, A., Basset, Y., Burwell, C. J., Cao, M., Eastwood, R. … Kitching, R. L. (2016). Vertical stratification of moths across elevation and latitude. *Journal of Biogeography,* 43, 59–69.

Audino, L. D., Murphy, S. J., Zambaldi, L., Louzada, J., & Comita, L. S. (2017). Drivers of community assembly in tropical forest restoration sites: role of local environment, landscape and space. *Ecological Applications,* 20, 1469–1478.

Baselga, A., & Orme, C. D. L. (2012). betapart: an r package for the study of beta diversity. *Methods in Ecology and Evolution*, 3, 808–812.

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

Becca, G., Vancine, M. H., Carvalho, C. S., Pedrosa, F., Alves, R. S. C., Buscariol, D., … Galetti, M. (2017). High mammal turnover in forest patches immersed in biofuel plantations. *Biological Conservation*, 210, 352–359.

Bennett, J. R., & Gilbert, B. (2016). Contrasting beta-diversity among regions: how do classical and multivariate approaches compare? *Global Ecology and Biogeography*, 25, 368–377.

Blanchet, F. G., Legendre, P., & Borcard, D. (2008). Forward selection of explanatory variables. *Ecology*, 89, 2623–2632.

Bossuyt, F., Meegaskumbura, M., Beenaerts, N., Gower, D. J., Pethiyagoda, R., Roelants, K., … Milinkovitch, M. C. (2004). Local endemism within the Western Ghats – Sri Lanka biodiversity hotspot. *Science,* 306, 479–481.

Chase, J. M., & Myers, J. A. (2011). Disentangling the importance of ecological niches from stochastic processes across scales. *Philosophical Transactions of the Royal Society London B,* 366, 2351–2363.

Chen, Y., Yuan, Z., Li, P., Cao, R., Jia, H., & Ye, Y. (2016). Effects of environment and space on species turnover of woody plants across multiple forest dynamic plots in east Asia. *Frontiers in Plant Sciences*, DOI: 10.3389/fpls.2016.01533.

Davey, C. M., Devictor, V., Jonzen, N., Lindstrom, A., & Smith, H. G. (2013). Impact of climate change on communities: revealing species' contribution. *Journal of Animal Ecology*, 82, 551–561.

Elsen, P. R., Kalyanaraman, R., Ramesh, K., & Wilcove, D. S. (2017). The importance of agricultural lands for himalayan birds in winter. Conservation biology, 31, 416–426.

Goodale, E., Kotagama, S. W., Raman, T. R. S., Sidhu, S., Goodale, U., Parker, S., & Chen, J. (2014). The response of birds and mixed-species bird flocks to human-modified landscapes in Sri Lanka and southern India. *Forest Ecology and Management,* 329, 384–392.

Gunawardene, N. R., Daniels, A. E. D., Gunatilleke, I. A. U. N., Gunatilleke, C. V. S., Karunakaran, P. V., Nayak, K. G., ... Vasanthy, G. (2007) A brief overview of the Western Ghats – Sri Lanka biodiversity hotspot. *Current Science,* 93, 1567–1572.

Hansen, M. C., Potapov, P. V., Moore, R., Hancher, M., Turubanova, S. A., Tyukavina, A., … Townshend, J. R. G. (2013). High resolution global maps of the 21st century forest cover change. *Science*, 342, 850–853.

Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G., & Jarvis, A. (2005). Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology,* 25, 1965–1978.

Hijmans RJ, Williams E, Vennes C. 2011 Package 'geosphere'. Available: https://cran.r-project.org/web/packages/geosphere.

Hubbell, S.P. (2001). *The unified neutral theory of biodiversity and biogeography.* Princeton University Press, Princeton, NJ.

Karp, D. S., Rominger, A. J., Zook, J., Ranganathan, J., Ehrlich, P. R. & Daily, G. C. (2012). Intensive agriculture erodes b-diversity at large scales. *Ecology Letters,* 15, 963–970.

Karp, D. S., Frishkoff, L. O., Echeverri, A., Zook, J., Juarez, P., & Chan, K. M. A (2018). Agriculture erases climate-driven β-diversity in neotropical bird communities. *Global Change Biology*, 24, 338–349.

Kraft, N. J. B., Comita, L. S., Chase, J. M., Sanders, N. J., Swenson, N. G., Crist, T. O., … Myers, J. A. (2011). Disentangling the drivers of β-diversity along latitudinal and elevational gradients. *Science*, 333:1755–1758.

Legendre, P., Mi, X., Ren, H., Ma, K., Yu, M., Sun, I., & He, F. (2009). Partitioning beta diversity in a subtropical broad-leaved forest of China. *Ecology*, 90, 663–674.

Mammides, C., Chen, J., Goodale, U. M., Kotagama, S. W., Sidhu, S., & Goodale, E. (2015). Data from: Does mixed-species flocking influence how birds respond to a gradient of land-use intensity? Dryad Digital Repository. (doi:10.5061/dryad. vk070).

Myers, J. A., Chase, J. M., Jimenez, I., Jorgensen, P. M., Araujo-Murakami, A., Paniagua-Zambrana, N., & Seidel, R. (2013). Beta-diversity in temperate and tropical forests reflects dissimilar mechanisms of community assembly.

Ecology Letters, 16, 151–157.

Myers, J. A., Chase, J. M., Crandall, R. M., & Jimenez, I. (2015). Disturbance alters beta-diversity but not relative importance of community assembly mechanisms. *Journal of Ecology*, 103, 1291–1299.

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

Newbold, T., Hudson, L. N., Hill, S. L. L., Contu, S., Gray, C. L., Scharlemann, J. P. W., …Purvis, A. (2016) Global patterns of terrestrial assemblage turnover within and among land uses. *Ecography*, 1151–1163.

Ramachandran V, Robin VV, Tamma K, Ramakrishnan U (2017) Climatic and geographic barriers drive distributional patterns of bird phenotypes within peninsular India. *J. Avian Biol.* 48:620–630.

Ricklefs, R. E. (1987). Community diversity – relative roles of local and regional processes. *Science*, 235, 167–171.

Robin, V. V., Vishnudas, C. K., & Ramakrishnan, U. (2014) Reassessment of the distribution and threat status of the Western Ghats endemic bird, Nilgiri Pipit *Anthus nilghiriensis. Current Science*, 107, 622–630.

Sreekar, R., Srinivasan, U., Mammides, C., Chen, J., Goodale, U. M., Kotagama, S. W., … Goodale, E. (2015) The effect of land-use on the diversity and mass-abundance relationships of understorey avian insectivores in Sri Lanka and southern India. *Scientific Reports,* 5, 11569.

Sreekar, R., Corlett, R. T., Dayananda, S., Goodale, U. M., Kilpatrick, A., Kotagama, S. W., … Goodale, E. (2017). Horizontal and vertical species turnover in tropical birds in habitats with differing land use. *Biology Letters*, 13, DOI: 10.1098/rsbl.2017.0186.

Venter, O., Fuller, R. A., Segan, D. B., Carwardine, J., Brooks, T., Butchart, S. H. M., … Watson, J. E. M. (2014). Targeting Global Protected Area Expansion for Imperiled Biodiversity. *PLOS Biology,* 12, e1001891.

Wickramasinghe, N., Robin, V. V., Ramakrishnan, U., Reddy, S., Seneviratne, S. S. (2017). Non-sister Sri Lankan white-eyes (genus *Zosterops*) are a result of independent colonizations. *PLOS ONE,* 12, e0181441.

4.7 Supporting information

TABLE S4.1 Correlation between latitude and longitude at all spatial scales.

Spatial scale	**Pearson's r**	**P**
Large	-0.994	<0.0001
Intermediate (Sri Lanka)	0.763	0.0005
Intermediate (India)	0.88	<0.0001

TABLE S4.2 Correlation between latitude and 'PCNM 1' at all spatial scales.

Spatial scale	**Pearson's r**	**P**
Large	-0.998	<0.0001
Intermediate (Sri Lanka)	0.806	<0.0001
Intermediate (India)	0.974	<0.0001

TABLE S4.3 Correlation between mean annual temperature and precipitation at all spatial scales.

Spatial scale	**Pearson's r**	**P**
Large	0.752	<0.0001
Intermediate (Sri Lanka)	0.958	<0.0001
Intermediate (India)	0.981	<0.0001

TABLE S4.4 Beta-diversity (Bray-Curtis pairwise dissimilarity) was highly correlated with balanced turnover (pairwise dissimilarity of balanced variation in abundance) at all spatial scales.

Spatial scale	**Mantel r**	**P**
Large	0.957	0.001
Intermediate (Sri Lanka)	0.927	0.001
Intermediate (India)	0.881	0.001

TABLE S4.5 Pooled species richness (gamma-diversity) did not influence balanced turnover at all spatial scales. In our study, balanced turnover was highly correlated with beta diversity (mantel r > 0.85; Table S4).

Spatial scale	**Mantel r**	**P**
Large	-0.049	0.394
Intermediate (Sri Lanka)	0.047	0.688
Intermediate (India)	-0.114	0.398

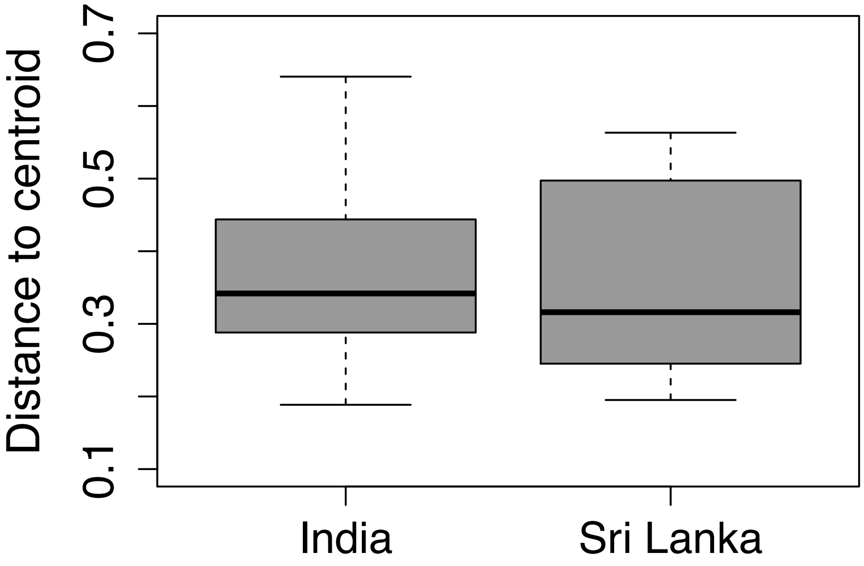

FIGURE S4.1 Distance to centroid values for plots within each country shows no difference between them ($F_{(1,30)} = 0.17$, $P = 0.69$).

Chapter 5

General Conclusions

In this thesis I have shown that spatial scale has a profound impact on biotic beta-diversity and the processes that shape them. My thesis can help resolve a long-standing discrepancy in community ecology, and has important implications for both ecology and conservation. I conclude that the lack of consensus regarding the basic patterns in beta-diversity and processes that shape them is due to the differences in spatial scale among studies.

Contrasting results among studies that examine the relationship between beta-diversity and latitude are well known (Kraft *et al.* 2011; Qian *et al.* 2013; Ashton *et al.* 2016). In Chapter Two, I have shown that spatial scale changes the relationship between tree beta-diversity and latitude. As studies often sample at different spatial scales, contrasting results can therefore be expected. Similarly, contrasting results among studies comparing beta-diversity between natural and human-modified habitats are also well known (Berry et al. 2008, Karp et al. 2012, Kitching et al. 2013, Newbold et al. 2016). In Chapter Three, I have shown that the bird beta diversity along a geographic gradient in natural forest is similar to that in intensive agriculture, but beta diversity along an environment gradient in natural forest is higher than intensive agriculture. As field-studies are often conducted at relatively small spatial scales with no or little variation in environment, beta-diversity between habitats can remain similar or can be higher in the habitat that shows higher variation in environment. In Chapter Four, I have shown that the relative importance of the drivers of bird community assembly also change with spatial scale. Niche-based mechanisms are important at small spatial scales, but the relative importance of dispersal limitation increases with increasing spatial scale. In this final chapter, I will compare the results in existing literature with the results presented in this thesis to discuss the importance of considering spatial scale in community ecology.

Latitude does not affect tree beta-diversity

Although the relationship between beta-diversity and latitude were widely studied, spatial scale effects are often ignored (Tuomisto and Ruokolainen, 2012). In Chapter Two, I have shown that all measured beta-diversity metrics are dependent on spatial scale. Beta-diversity was especially sensitive to scale-dependent effects at small grain sizes, however it was comparatively robust at large grain sizes. I show that the strength of correlation between gamma- and beta-diversity weakens with increasing grain size and becomes insignificant at around 50 m x 50 m (0.25 ha). Their correlation is problematic because the observed variation may be entirely caused by gamma-diversity, not beta-diversity. The use of large samples is therefore the best-known method for measuring beta-diversity (Beck et al. 2013, Sreekar et al. 2018). At relatively large grain sizes (>0.24 ha), I showed that beta-diversity remained similar across the examined latitudinal gradient (3°-30°) in the Asia-Pacific region.

Inadequate sampling of local communities (α-diversity) could explain the correlation between beta- and gamma-diversity. A 50 ha plot in a tropical rainforest can contain more than a thousand species and requires a large number of individuals to be representative of local communities (Chao et al. 2009, Tuomisto and Ruokolainen 2012). A 10 m x 10 m grain or a 20 m x 20 m grain has only around 50 and 200 individuals, respectively, which is sometimes smaller than the species richness of the entire community. Therefore, lower α-diversity can simply be an artefact of inadequate sampling, which then erroneously inflates β-diversity values ($\beta = \gamma/\alpha$). Inadequate sampling is especially high in habitats with higher species diversity (e.g. lower latitudes), in comparison with habitats with lower species diversity (e.g. higher latitudes). For example, Pitman et al. (1999) sampled trees using large grain sizes (0.9 – 2.5 ha) and showed that Amazonian tree communities have low β-diversity. This contrasted with many earlier studies that suggested high tree β-diversity, as they were not large enough to eliminate artifactual β-diversity caused by insufficient sampling (Pitman et al. 1999). Site-to-site variation in species composition (β-diversity) between two small grains in species-rich habitat could therefore just be caused by sampling effects, and not be due to ecological processes such as environmental filtering, competitive interactions or dispersal limitation. In summary, our results suggest that just standardizing grain size is not enough (Chase and Knight 2013); grains should be large enough for adequate sampling (>50 m x 50 m for trees in forests with DBH ≥1 cm).

The deviation of observed β-diversity from stochastic expectations generated by a null model (β-deviation) remained similar across the latitudinal gradient, suggesting no differences in the strength of intraspecific aggregation in all forests across the examined latitude gradient. The β-deviation values remained close to zero when sampling at small spatial scales indicating that sampling effects produce the measured β-diversity. Recently, a few studies have challenged the use of β-deviation for comparing between habitat types (Bennett and Gilbert 2016, Ulrich et al. 2017), as studies that used β-deviation have resulted in contrasting conclusions across studies (Kraft et al. 2011, Qian et al. 2013, Ashton et al. 2016). We suggest that unstandardized sampling could cause such contrasting results. Standardizing grain size does not necessarily standardize the number of individuals sampled, as 30 m x 30 m plot in Pasoh, Malaysia and Fushan, Taiwan had 493 and 495 individuals, respectively, whereas 30 m x 30 m plots in Sinharaja, Sri Lanka, and Lienhuachih, Taiwan, had 728 and 756 individuals respectively. The number of individuals does not necessarily correlate with latitude or γ-diversity. Consequently, as β-deviation is sensitive to the number of individuals sampled, it cannot maintain directionality (negative and positive correlation) with habitat change (see Qian et al. 2013, Ashton et al. 2016).

I showed that the use of large grain sizes is the most simple and straight-forward method to avoid correlation between species richness and beta-diversity. Furthermore, I show that the beta-diversity in species rich tropical forests is similar to comparatively species poor subtropical forest. It should not come as a surprise because beta-diversity in species-rich natural forests is similar to species-poor intensive agriculture (Newbold et al. 2016). I will discuss the possibility of higher beta-diversity in species rich areas below.

Human-modified landscapes erode bird beta-diversity

In a seminal paper, Newbold et al. (2016) synthesized that the beta-diversity in natural habitats is similar to beta-diversity in highly modified habitats like pasture. In Chapter Three, I have also shown that the beta-diversity in protected rainforests and intensive agriculture are similar because beta-diversity is generally small along a relatively short distance gradient and in the absence of significant environmental variation (Sreekar et al. 2017). In, this study, I showed that beta-diversity along an elevation gradient with significant variation in environment can be around 100 times higher. Therefore, environmental variation drives beta-diversity at small spatial scales and beta-diversity in protected rainforests is higher than intensive agriculture when there is environmental variation. In Chapter Two, although we showed that there is no difference in tree beta-diversity between tropical and subtropical forests, it could just be because of the lack of environmental variability. Comparing tree beta-diversity along a standardised environmental gradient in tropical and sub-tropical forests might lead to different conclusions.

High rates of turnover with changing temperature can actually be a problem in the context of climate change. As temperature and habitat becomes more suitable for birds in lower elevations, they might compete with birds at higher elevations, which have nowhere to go. This might be especially problematic to island fauna where dispersal is limited due to the sea-barrier. In Sri Lanka, there are 14 threatened endemic diurnal forest bird species, which are all (except one, spot-winged thrush) effected by change in temperature. Among these 14 species, five of them are restricted to high elevation forests (>1500 m) and should be of conservation priority as 2ºC rise in temperature can reduce their already small distribution size by 75% and extirpate populations (Figure S3.3).

High turnover rates in mountain areas also emphasizes the importance of protecting the entire elevation gradient. Currently, Asia has the lowest elevational protection among all continents and should be improved (Elsen et al. 2018). Another major reason for improving elevational protection in Asian tropics is islands – a significant land area of tropical Asia is on islands. Mountain tops and islands limit dispersal, therefore, most small-ranged threatened endemic species are found here (Pimm et al. 2018). Even though elevational protection in Sri Lanka is comparatively high (Elsen et al. 2018), more conservation actions are required because endemicity in certain groups with lower dispersal abilities like amphibians and molluscs is over 75%.

In conclusion, I presented the importance of conserving forest along entire elevational gradients, especially in island nations like Sri Lanka with high endemism. Furthermore, I showed that the difference in beta-diversity between natural and human-modified landscapes are dependent on environmental variation (Sreekar et al. 2017). Measuring the relative importance of ecological mechanisms that shape bird beta-diversity can also be important for ecological management and conservation (Audino et al. 2017). In the next paragraph, I will discuss the ecological mechanisms that drive bird community assembly in the Western Ghats-Sri Lanka biodiversity hotspot.

Ecological mechanisms that create and maintain bird communities

The inability of species to persist in all environments shapes ecological community assembly in a landscape (Keddy 1992, Baldeck et al. 2013). In Chapter Four, I show that spatial scale changes the relative importance of the drivers that shape bird community assembly in Western Ghats–Sri Lanka biodiversity hotspot. Currently, most currently research is conducted at landscape scales and they have already shown that human-driven habitat change is the most important driver of biotic community assembly. For example, Becca et al. (2017) showed that difference in forest cover is the only variable that explained mammal turnover among forest patches in biofuel plantations. Similarly, Audino et al. (2017) showed that difference in canopy cover nearly explained all the variance in dung beetle species composition among tropical forest restoration sites. However, habitat change is not just human-driven, but also occurs naturally. For example, change in soil type and/or elevation can also result in habitat and biodiversity change (Katabuchi et al. 2012, Liu et al. 2014, Salindra et al. 2017). Few studies have examined the relative importance of natural habitat change in comparison to human-driven habitat change. In Chapter Four, I show that elevational variation in habitat change can be as important as human-driven habitat change for species community assembly. Therefore, conservation efforts should look beyond the proportion of natural habitat cover. At larger scales, dispersal limitation due to biogeographic barriers like large rivers and seas can shape biotic community assembly (Ramachandran et al. 2017). When I determined the drivers of bird community assembly at large spatial scales, space was the most important variable to explain bird species composition in the Western Ghats–Sri Lanka biodiversity hotspot. This suggests that dispersal limitation over the Palk Strait is the most important driver of bird community assembly in the biodiversity hotspot. My results indicate that there needs to be matched conservation effort on both sides of the biogeographic sea barrier, and protected areas on either side of the barrier need to include a range of elevations.

Recommendations for future work

The results of this research improves our understanding of the mechanisms that structure biodiversity. Specifics such as changing latitudinal beta-diversity patterns with changing spatial scale, changing differences in bird beta-diversity between habitats with changing spatial scale, changing community assembly mechanisms with changing spatial scale, and importance of using beta-diversity for monitoring and managing biodiversity. Throughout the research, future recommendation have been identified to advance our understanding of patterns and processes that shape biodiversity. Some of these recommendations include:

1. The research in Chapter Two focuses on the relationship between beta-diversity and latitude. But, it does not include sites from temperate regions (greater than 30 degrees). Recently, Castro-Insua et al. (2016) suggested the existence of thresholds in the latitudinal beta-diversity

patterns It is possible that the relationship between beta-diversity and latitude on either side of the 30° latitude may be different (Castro-Insua et al. 2016). However, we do not know if such thresholds exist at all spatial scales. Moreover, most tropical Asian sites are on large islands, a feature in this part of the world that is difficult to omit while studying latitudinal patterns. Therefore, future studies should replicate our Chapter Two by determining beta-diversity at multiple spatial scales along latitudinal gradients in America or Africa and Europe by including tropical, sub-tropical and also temperate sites.

Random sampling effects will cause beta-diversity values to be highly dependent on species pool size (gamma-diversity) – a major issue in beta-diversity research (Kraft et al. 2011, Ashton et al. 2016, Bennett & Gilbert 2016). In all my research chapters, I show that beta-diversity is not correlated with gamma-diversity as our sampling grains were adequately sampled. Therefore, adequate grain sampling still remains to be the best method to avoid gamma-dependence of beta-diversity. Previous researchers suggested the use of null models, and in Chapter Two we showed that the results of our null models were similar to the results of well-sampled grains. However, Ulrich et al. (2017) argues that the use of null models may result in type-II errors as some of the variation explained by non-random processes can be lost while calculating null-model based beta-deviation. More studies should be conducted to determine the best method to account for random sampling effects when studying biodiversity at small grains, where sampling effects are unavoidable.

2. The research in Chapter Three showed that beta-diversity in species rich tropical rainforests are similar to intensive agriculture when sampling along a geographic gradient with no environmental variation. We showed that beta-diversity in species rich tropical rainforest is higher than intensive agriculture when sampling along an elevation gradient with environmental variation. Although, in Chapter Two, we showed

that beta-diversity in tropics is similar to beta-diversity in sub-tropics, this pattern may change when measuring beta-diversity along elevation gradients. Future studies should examine beta-diversity along a fixed elevation gradient and at different latitudes, to determine if beta-diversity in species rich tropics is similar to higher latitudes.

The research in Chapter Three also showed that the turnover along elevation gradients is so steep that high-elevation threatened endemic bird species of Sri Lanka may lose 75% of their available range, if climate change increases the temperature by 2^{o}C (also see Freeman et al. 2018). Therefore, future studies should conduct experimental warming experiments in the high-elevation regions of Sri Lanka to determine the species that may be vulnerable to climate change and start ex-situ conservation programs wherever required.

3. In Chapter four, I showed that spatial scale changes the relative importance of ecological mechanisms that drive bird community assembly. At the largest scale, dispersal limitation due to the spatial differences between plots was the most important driver of bird community assembly. In our study, the maximum distance between two points was around 600 km. However, space was also influenced by a biogeographically important sea-barrier, the Palk Strait (Bossuyt et al. 2004, Ramachandran et al. 2017). We consider Palk Strait as the main driver of bird community assembly in the biodiversity hotspot. Future studies should determine the importance of large distances between points without biogeographical barriers on bird species composition. Novotny et al. (2007) sampled herbivorous insects across 75,000 km^2 of lowland rainforests in Papua New Guinea to show that space has little effect on species composition. A study dedicated to partitioning the effects of biogeographical barriers from spatial distance on biotic beta-diversity is required.

At intermediate scale, elevation and land-use change had similar effects on bird species composition in the Western Ghats–Sri Lanka biodiversity hotspot. However, it should be noted that we did not investigate the entire elevation range. Our study was restricted to elevations below 1300 m, but mountains can reach heights over 2000 m in both Western Ghats and Sri Lanka. Therefore, elevation may be more important than land-use change if the whole elevation range was sampled. As the results suggests, spatial scale can change the relative importance of the drivers that shape bird species composition. Future studies that examine community assembly in biodiversity hotspots should sample complete elevation range to better inform conservation practitioners.

References

Ashton LA, *et. al.* (2016) Vertical stratification of moths across elevation and latitude. *J. Biogeogr.* 43:59-69.

Audino LD, Murphy SJ, Zambaldi L, Louzada J, Comita LS (2017) Drivers of community assembly in tropical forest restoration sites: role of local environment, landscape and space. *Ecol. Appl.* 20:1469–1478.

Baldeck CA, *et al.* (2013) Habitat filtering across tree life stages in tropical forest communities. *Proc. R. Soc. B* 280:20130548.

Becca G, *et. al.* (2017) High mammal turnover in forest patches immersed in biofuel plantations. *Biol. Conserv* 210:352–359.

Beck J, Holloway JD, Schwanghart W (2013) Undersampling and the measurement of beta diversity. *Methods Ecol. Evol.* 4: 370–382.

Bennett JR, Gilbert B (2016) Contrasting beta diversity among regions: how do classical and multivariate approaches compare? *Glob. Ecol. Biogeogr.* 25:368–377.

Berry NJ, Phillips OL, Ong RC, Hamer KC (2008) Impacts of selective logging on tree diversity across a rainforest landscape: the importance of spatial scale. *Landsc. Ecol.* 23: 915-929.

Bossuyt F, *et al.* (2004) Local endemism within the Western Ghats – Sri Lanka biodiversity hotspot. *Science* 306:479-481.

Castro-Insua A, Gomez-Rodriguez C, Baselga A (2016) Break the pattern: breakpoints in beta diversity of vertebrates are general across clades and suggest common historical causes. *Glob. Ecol. Biogeogr.* 25:1279–1283.

Chao A, Colwell RK, Lin C-W, Gotelli NJ (2009) Sufficient sampling for asymptotic minimum species richness estimators. *Ecology* 90:1125-1133.

Chase JM, Knight TM (2013) Scale-dependent effect sizes of ecological drivers on biodiversity: why standardization in not enough. *Ecol. Lett.* 16:17-26.

Dayananda SK, *et al.* (2017) Topography and soil type are critical to understanding how bird and herpetofaunal communities persist in forest fragments of tropical China. *Biol. Conserv.* 215:107-115.

Elsen PR, Monahan WB, Merenlender AM (2018) Global patterns of protection of elevational gradients in mountain ranges. *Proc. Nat. Acad. Sci. USA* DOI:10.1073/pnas.1720141115.

Freeman B, Lee-Yaw JA, Sunday JM, Hargreaves AL (2018) Expanding, shifting and shrinking: The impact of global warming on species' elevational distributions. *Glob. Ecol. Biogeogr.* DOI:10.11111/geb.12774.

Karp DS, Rominger AJ, Zook J, Ranganathan J, Ehrlich PR, Daily GC (2012) Intensive agriculture erodes beta-diversity at large scales. *Ecol. Lett.* 15:963-970.

Katabuchi M, Kurokawa H, Davies SJ, Tan S, Nakashizuka T (2012) Soil resource availability shapes community trait structure in a species-rich dipterocarp forest. *J. Ecol.* 100:643–651.

Keddy PA (1992) Assembly and response rules: two goals for predictive community ecology. *J. Veg. Sci.* 3:157-164.

Kitching RL, Ashton LA, Nakamura A, Whitaker T, Khen CV (2013) Distance-driven species turnover in Bornean rainforests: homogeneity and heterogeneity in primary and post-logging forests. *Ecography* 36:675-682.

Kraft NJB, *et al.* (2011) Disentangling the drivers of β diversity along latitudinal and elevational gradients. *Science* 333:1755-1758.

Liu JJ & Slik JWF (2014) Forest fragment spatial distribution matters for tropical tree conservation. *Biol. Conserv.* 171, 99-106.

Mori AS, Isbell F, Seidl R (2018) Beta-diversity, community assembly, and ecosystem functioning. *Trends Ecol. Evol.* DOI:10.1016/j.tree.2018.04.012.

Newbold T, *et.al.* (2016) Global patterns of terrestrial assemblage turnover within and among land uses. *Ecography* 39:1151-1163.

Novotny V, *et al.* (2007) Low beta diversity of herbivorous insects in tropical forests. *Nature* 448:692-697.

Pimm SL, Jenkins CN, Li BV (2018) How to protect half of Earth and ensure it protects sufficient biodiversity. *Science Advances* DOI: 10.1126/ sciadv.aat2616.

Pitman NCA, Terborgh J, Silman MR, Nunez P (1999) Tree species distributions in an upper Amazonian forest. *Ecology* 80:2651-2661.

Qian H, Chen S, Mao L, Ouyang Z (2013) Drivers of β-diversity along latitudinal gradients revisited. *Glob. Ecol. Biogeogr.* 22:659-670.

Ramachandran V, Robin VV, Tamma K, Ramakrishnan U (2017) Climatic and geographic barriers drive distributional patterns of bird phenotypes within peninsular India. *J. Avian Biol.* 48:620–630.

Socolar JB, Gilroy JJ, Kunin WE, Edwards DP (2016) How should beta-diversity inform biodiversity conservation. *Trends Ecol. Evol.* 31:67-80.

Sreekar R, *et al.* (2017) Horizontal and vertical species turnover in tropical birds in habitats with differing land use. *Biol. Lett.* 13: DOI: 10.1098/rsbl.2017.0186.

Terborgh JW (2015) Toward a trophic theory of species diversity. *Proc. Natl. Acad. Sci. USA* 37:11415-11422.

Tuomisto H, Ruokolainen K (2012) Comment on "Disentangling the drivers of β diversity along latitudinal and elevational gradients". *Science* 335:1573.

Ulrich W, Baselga A, Kusumoto B, Shiono T, Tuomisto H, Kubota Y (2017) The tangled link between β- and γ-diversity: a Narcissus effect weakens statistical influences in null model analyses of diversity patterns. *Glob. Ecol. Biogeogr.* 26:1–5.

Ulrich W, Kubota Y, Kusumoto B, Baselga A, Tuomisto H, Gotelli NJ (2018) Species richness correlates of raw and standardized co-occurrence metrics. *Glob. Ecol. Biogeogr.* 27:395-399.

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SHORT COURSES

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2013	***PLANTS OF TROPICAL ASIA***. Program for Field Studies, China.
2011	***HERPETOLOGY***. SACON, India.
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TEACHING EXPERIENCE (biological statistics)

2014	***INSTRUCTOR***, *basic biological statistics,* Kunming Institute of Botany, Chinese Academy of Sciences, Kunming, China.

2013-17 ***TEACHING ASSISTANT,*** *advanced biological statistics,* Association of Tropical Ecology and Conservation (In: Australia, China, Indonesia).

2011-14 ***TEACHING ASSISTANT,*** *advanced field ecology course,* Program for Field Studies (PFS), China.

AWARDS

2017	***OUTSTANDING REVIEWER AWARD,*** Biological Conservation
2015	***SHIVARAMA-KARANTH CONSERVATION AWARD****,* Best student talk at Students Conference for Conservation Science, India.
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SCHOLARSHIPS & GRANTS

2015 – 2018	The University of Adelaide Postgraduate Award
2011 – 2014	Xishuangbanna Botanical Garden Postgraduate Award
2011	Madras Crocodile Bank Research Grant (1000 USD)
2010	The Gerry Martin Project Research Grant (250 USD)
2009	Harvard Summer School Scholarship (2000 USD)

PROFESSIONAL EXPERIENCE

2015 ***CONSULTANT,*** Kunming Institute of Botany, China.
Project: Mushroom diversity across a latitudinal gradient.

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2011 ***IUCN RED LIST ASSESSOR,*** Indian lizards.

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Projects: 1) Agamid ecology, 2) King cobra radio telemetry.

2009 ***INTERN,*** National Centre for Biological Sciences, India
Project: Risk discrimination in Indian rock lizards.

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Project: Tiger survey using faecal DNA analysis.

CITIZEN SCIENCE

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JOURNAL REFEREE

Global Change Biology, Diversity and Distributions, Journal of Biogeography, Biological Conservation, Animal Behaviour, Frontiers in Plant Sciences, Biodiversity and Conservation, Global Ecology and Conservation, Biotropica, Ecological Research, Tropical Conservation Science, Herpetological Journal, Herpetological Review, Indian Birds

JOURNAL ARTICLES

Sreekar R, Koh LP, Mammides C, Corlett RT, Dayananda SK, Goodale UM, Kotagama SW, Goodale E (*in review*). Bird community assembly at multiple spatial scales in the Western Ghats – Sri Lanka biodiversity hotspot: roles of land-use, environment, and space. *Landscape Ecology.*

Sreekar R, Katabuchi M, Nakamura A, Corlett RT, Slik F, *et al.* (2018). Spatial scale changes the relationship between beta diversity, species richness and latitude. *Royal Society Open Science,* 5: 181168.

Li H, Guo J, Goldberg SD, ***Sreekar R,*** Ye L, Luo X, *et al.* (2018). Fruiting patterns of macrofungi in tropical and temperate land use types in Yunnan Province, China. *Acta Oecologica,* 91: 7-15.

Sreekar R, Corlett RT, Dayananda SK, Goodale UM, Kilpatrick A, Kotagama SW, Koh LP, Goodale E (2017). Horizontal and vertical species turnover in tropical birds in habitats with differing land-use. *Biology Letters,* 13: 20170186.

Dayananda SK, Mammides C, Lee M, Liu J-J, Pasion BO, **Sreekar R**, et al. (2017). Topography and soil type are critical to understanding how bird and herpetofaunal communities persist in forest fragments of tropical China. *Biological Conservation,* 215: 107-115.

Gnanaolivu C. ***Sreekar R**,* Veerapan D (2017). An ontogenetically stable sexual character in a montane lizard *Salea horsfieldii* Gray, 1845 (Reptilia: Agamidae) from Nilgiris, India. *Journal of Natural History,* 51: 39-40.

Harrison RD, ***Sreekar R**,* Brodie JF, Brook S, Luskin M, *et al.* (2016). Impacts of hunting and wildlife trade on Asian tropical forests. *Conservation Biology*, 30: 972-981.

***Sreekar R**,* Huang G, Yasuda M, Quan R, Goodale E, et al. (2016). Effects of forests, roads and mistletoes on bird diversity in monoculture rubber plantations. *Scientific Reports* 6: 21822.

Dayananda SK, Goodale E, Liu J, Mammides C, ***Sreekar R**,* et al. (2016). Effects of fragmentation on nocturnal Asian birds: A case study from Xishuangbanna, China. *Zoological research* 37: 151-158.

Kamath A, ***Sreekar R*** (2016). Morphology, ecology and behaviour of *Hylarana intermedius,* a Western Ghats frog. *Acta herpetologica* 11: 15-20.

Velho N, ***Sreekar R**,* Laurance WF (2016). Terrestrial species assemblage in protected areas and community managed lands of Arunachal Pradesh, India. *Land,* 5: 35.

Kong Y, Wang R, Yang D, ***Sreekar R**,* Peng Y, Compton SG (2016). Non-pollinator fig wasp impact on the reproductive success of an invasive fig tree: why so little? *Biocontrol Science and Technology* 26: 1432-1443.

***Sreekar R**,* Huang G, Zhao J, Pasion BO, Yasuda M, *et al.* (2015). The use of species-area relationships to partition the effects of deforestation and hunting in a fragmented landscape. *Diversity and Distributions* 21: 441-450.

***Sreekar R**,* Zhang K, Xu J, Harrison RD (2015). Yet another empty forest: Considering the conservation value of a recently established nature reserve in Xishuangbanna, China. *PLOS ONE* 10: e0117920.

***Sreekar R**,* Goodale E, Harrison RD (2015). Flight initiation distance as a behavioural indicator of hunting pressure: a case study of the Sooty-headed Bulbul (*Pycnonotus aurigaster*) in Xishuangbanna, China. *Tropical Conservation Science* 8: 505-512.

***Sreekar R**,* Srinivasan U, Mammides C, Chen J, Goodale UM, *et al.* (2015). The effects of land-use on the diversity and mass-abundance relationships of understory avian insectivores in Sri Lanka and India. *Scientific Reports* 5: 11569.

Balaji D*, ***Sreekar R***,* Rao S (2014). Drivers of reptile and amphibian assemblages outside the protected-area network of Western Ghats, India. *Journal for Nature Conservation* 22: 337-341. [*Both authors contributed equally to the work]

***Sreekar R**,* Purushotham CB, Saini K, Rao SN, Pelltier S, Chaplod S (2013). Photographic capture-recapture sampling for assessing populations of the Indian Gliding Lizard *Draco dussumieri*. *PLoS ONE* 8: e55935.

***Sreekar R**,* Quader S (2013). Influence of gaze and directness of approach on the escape responses of the Indian rock lizard, *Psammophilus dorsalis. Journal of Biosciences* 38: 829-833.

***Sreekar R**,* Mohan A, Das S, Agarwal P, Vivek R (2013). Natural windbreaks sustain bird diversity in a tea-dominated landscape. *PLoS ONE* 8: e70379.

***Sreekar R**,* Saini K, Rao SN, Purushotham CB (2011). Predicting lizard gender: sexual dimorphism in *Calotes rouxii*. *Herpetological Conservation and Biology* 6: 75-80.

Ganesh SR*, ***Sreekar R***,* Pal SP, Ramachandran G, Srinivasulu B, Srinivasulu C (2011). Discovery and first description of male *Cnemaspis heteropholis* Bauer, 2002 (Reptilia: Gekkonidae) from Agumbe, central Western Ghats, India. *Journal of Threatened Taxa* 3: 2023-2027. [*Both authors contributed equally to the work].

***Sreekar R**,* Nghiem TPL, Harrison RD (2010). Vertebrate assemblage at a fruiting fig (*Ficus caulocarpa*) in Maliau Basin, Malaysia. *Tropical Conservation Science* 3: 218-227.

Seetharamaraju M*, ***Sreekar R***,* Srinivasulu C, Srinivasulu B, Kaur H, Venkateshwarulu P (2009). Rediscovery of Vosmer's writhing skink *Lygosoma vosmaerii* (Gray, 1839) with a note on its taxonomy. *Journal of Threatened Taxa* 1: 624-626. [*Both authors contributed equally to the work].

CONFERENCE SYMPOSIA

Sreekar R, Harrison RD (2014). **Hunting in Asia: an invisible threat**. *Society for Conservation Biology Asia, Malaysia.*

CONFERENCE PRESENTATIONS

2018. Spatial scale changes the relationship between beta-diversity and latitude. Annual meeting of the Association for Tropical Biology and Conservation (ATBC), Malaysia.

2017. Drivers of bird community composition in Sri Lanka. Annual meeting of the Association for Tropical Biology and Conservation (ATBC), China.

2015. Occupancy dynamics of birds and mammals in a rubber-forest mosaic affected by hunting. Students Conference for Conservation Science (SCCS), India.

2014. Hunting escalates bird extirpations in fragmented landscapes. *Society for Conservation Biology – Asia, Malaysia.*

2014. Flight initiation distance as a proxy measure for hunting pressure. Annual meeting of the Association for Tropical Biology and Conservation (ATBC), Australia.

2013. Hunting impacts on birds in Bulong Nature Reserve, Yunnan, China. Annual meeting of the Association for Tropical Biology and Conservation (ATBC), Indonesia.

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REFERENCES

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