



Determinants of the beta diversity of tree species in tropical forests: Implications for biodiversity conservation



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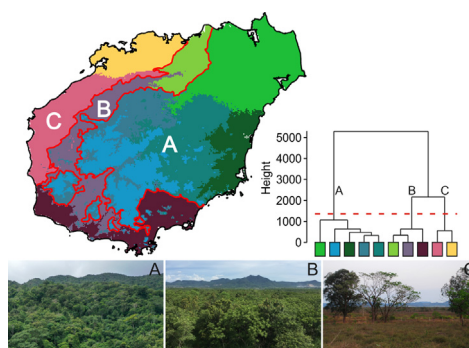
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HIGHLIGHTS

- Community data was used to model beta diversity of trees and delineated bioregions of Hainan Island.
- Beta diversity of tree in Hainan is controlled by water-related climatic factors.
- Beta diversity provides a promising tool to identify conservation gaps at a regional scale.

GRAPHICAL ABSTRACT



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ABSTRACT

The mapping of earth's biodiversity has advanced our theoretical and empirical understanding of biodiversity and has thus guided conservation efforts. Yet, early biodiversity maps often relied on alpha diversity indices, while beta diversity has rarely been used for practical conservation actions. We used generalized dissimilarity modelling (GDM) and variance partitioning to map beta diversity patterns of Hainan Island, China, and explore its underlying factors based on a large dataset of 248,538 individual trees belonging to 1,016 species in 902 forest plots. We used principal component analysis and hierarchical clustering to visualize community similarity, and spatial overlap analysis to assess the ability of the current protected areas (PAs) to encompass beta diversity. The GDMs explained 27.65% and 26.58% of the variation in beta diversity at the genus and species levels, respectively. The community composition of tree species in Hainan presented a general east-to-west gradient, and three floristic regions were delineated. This biogeographical pattern is predominantly structured by mean annual precipitation. Environmental variables, rather than geographical distance, were the most important factors determining present beta diversity patterns. Currently, PAs of Hainan Island are concentrated on mountain forest areas, while the lowland forest has largely been ignored. Thus, we suggest that biodiversity mapping based only on alpha diversity is not enough to identify conservation gaps, and the inclusion of beta diversity in such maps constitutes a promising tool to maximize the biodiversity coverage of PAs. Our study provides empirical evidence that a spatially explicit analysis of beta diversity in a specific region can be used for conservation planning.

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1. Introduction

Mapping the biodiversity patterns of the earth is crucial to define conservation priorities and determine management strategies (Ferrier, 2002; Brooks et al., 2006; Brum et al., 2017). Early species distributions maps can be traced as far back as expeditions of the 19th century, when naturalists began to describe spatial gradients in species richness and their relationships with climatic variables (Hawkins, 2001). Over the last decades and in the face of the current biodiversity crisis, conservation biologists have increasingly used biodiversity maps to highlight regions rich in threatened species (Myers et al., 2000; Brooks et al., 2006). However, most of these studies have used alpha diversity indices such as species richness, rarity, or endemism (Orme et al., 2005; Pimm et al., 2014), and beta diversity has only recently attracted interest from conservation scientists (Ferrier et al., 2007; Overton et al., 2009; Socolar et al., 2016).

Beta diversity assesses species composition difference between communities (Whittaker, 1960); it not only indicates the spatial structure of local species assemblages (Anderson et al. 2011) but also sheds light on the mechanisms underpinning these patterns (Socolar et al. 2016). For example, beta diversity can be partitioned into turnover and nestedness components to assess the biogeographical processes underlying local biodiversity (Baselga, 2010). Disentangling the relative effects of environmental gradients and geographical space on beta diversity can test ecological hypotheses, e.g. the niche-based hypothesis, or dispersal limitation hypothesis (Fitzpatrick et al., 2013; König et al., 2017). Further, documenting beta diversity over time can illustrate the role of historical processes (Xing et al., 2015) or more recent anthropogenic impacts (Capinha et al., 2015) in structuring present-day diversity patterns.

Increasingly, beta diversity is being incorporated into conservation science, for example in the study of biological invasions (Capinha et al., 2015); evaluation of biodiversity loss (Olden and Rooney, 2006); or identification of gaps in protected area (PA) networks (Overton et al., 2009). The mapping of beta diversity can highlight regions that are environmentally and biologically distinct (Saiter et al., 2016; Jiménez-Alfaro et al., 2018; Slik et al., 2018), and thus provide a spatial framework to identify high-priority conservation areas (Wiersma and Urban, 2005; Overton et al., 2009). To date, community-level models (e.g., generalized dissimilarity models or gradient forest models) have been developed to model beta diversity along environmental and geographical gradients to identify relative effects of important factors (Ferrier et al., 2007; Fitzpatrick et al., 2013). However, the strength of spatial and environmental factors of beta diversity may vary among different scales (Keil et al., 2012; Ibanez et al., 2018) and across regions (Fitzpatrick et al., 2013; Myers et al., 2013), which may be due to scaling effects and differences between biogeographical regions (König et al., 2017). For example, the vast majority of studies that have been performed in tropical forests have suggested that spatial beta diversity patterns are primarily driven by climate-related variables (e.g., Tuomisto et al., 2003; Swenson et al., 2011; Franklin et al., 2018). In contrast, the effects of geographical distance have been found to be more prominent in temperate zones (Qian et al., 2005; Keil et al., 2012; Jiménez-Alfaro et al., 2018). Therefore, understanding the spatial patterns and underlying determinants of beta diversity in specific regions can provide essential information, not only for answering conceptual macroecology and biogeography questions, but that also for the practical conservation of regional biodiversity (Ferrier et al., 2007; Saiter et al., 2016; Heino et al., 2018). Nonetheless, empirical studies of beta diversity in tropical Asia are rare, and owing to specific biogeographical contexts, the patterns and underlying determinants of biodiversity in tropical Asia maybe distinct (Ibanez et al., 2018).

Hainan Island (hereafter Hainan) is found within the Indo-Burma Biodiversity Hotspot (Myers et al., 2000), and is home to the most extensive tropical forest in China (Francisco-Ortega et al., 2010; Wan et al., 2018). In the last 30 years, the number of Hainan's PAs has rapidly increased and currently cover more than 8.4% of the total land surface (Wu et al., 2011a) and as of 2010, these PAs cover ~40% of the natural forests present (Lin et al., 2017). However, the effectiveness of these PAs in protecting the biodiversity of Hainan has been questioned (Wu et al., 2011a; Wang et al., 2013) given that few studies have evaluated the patterns and drivers of the biodiversity present there (Zhu, 2016; Ali et al., 2019). Moreover, the distribution of PAs in Hainan is designed primarily to protect terrestrial habitats and species richness (Wu et al., 2011a; Zhang et al., 2011) and little is known regarding the ability of these PAs to encompass the species composition present within communities.

The knowledge gaps present with regard to the Hainan PA system hamper practical conservation activities in this tropical island. It is therefore important to incorporate the spatial patterns of beta diversity into conservation efforts. In this study, we explore the patterns and determinants of beta diversity in tropical forests of Hainan to identify conservation gaps in the PA network. Specifically, our objectives were to (1) quantify the spatial patterns of beta diversity of the tree species present, (2) assess the degree to which species composition variation may be explained by geographical distance or environmental gradients, and (3) identify the conservation gaps in the present-day PA network with regard to beta diversity.

2. Material and methods

2.1. Study region

Hainan (~33,900 km²; 18°10'–20°10' N, 108°37'–111°03' E) is a tropical island located approximately 24 km from southern China (Fig. 1). Hainan has an elevation of up to 1867 m above sea level, and total annual precipitation decreases from the northeast (2000 mm) to the northwest (400 mm; Fig. A.1). Mean annual temperature shows a slight south-to-north gradient (from 24 to 26 °C) that decreases with increasing elevation (from 16 to 26 °C; Fig. A.1). The island setting, tropical climate, and environmental heterogeneity contribute to Hainan being a biodiversity hotspot with high levels of species richness and endemism (Francisco-Ortega et al. 2010). It has been estimated that Hainan has 4579 species of native vascular plants, including 483 endemic species (Chen et al., 2016).

2.2. Forest inventory data

Tree communities were sampled within inventory plots in the natural forests across Hainan during 2003–2018 (Fig. 1). Plots were square in shape and of two main sizes: 0.25 ha (50 m × 50 m) or 0.0625 ha (25 m × 25 m), which were randomly distributed across Hainan (Fig. A.2). Plot coordinates were recorded with a handheld GPS. In each plot, all individual trees larger than 3 cm in diameter at breast height were recorded and identified to the species level. We standardized taxonomy according to *Flora of China* (<http://foc.iplant.cn>) and excluded taxa that could not be identified to the species level. Plots with <10 native plant species were also excluded as they could potentially increase statistical uncertainty. The final database included 902 forest plots that contained a total of 248,538 individual trees, representing 1016 identified species and 391 genera.

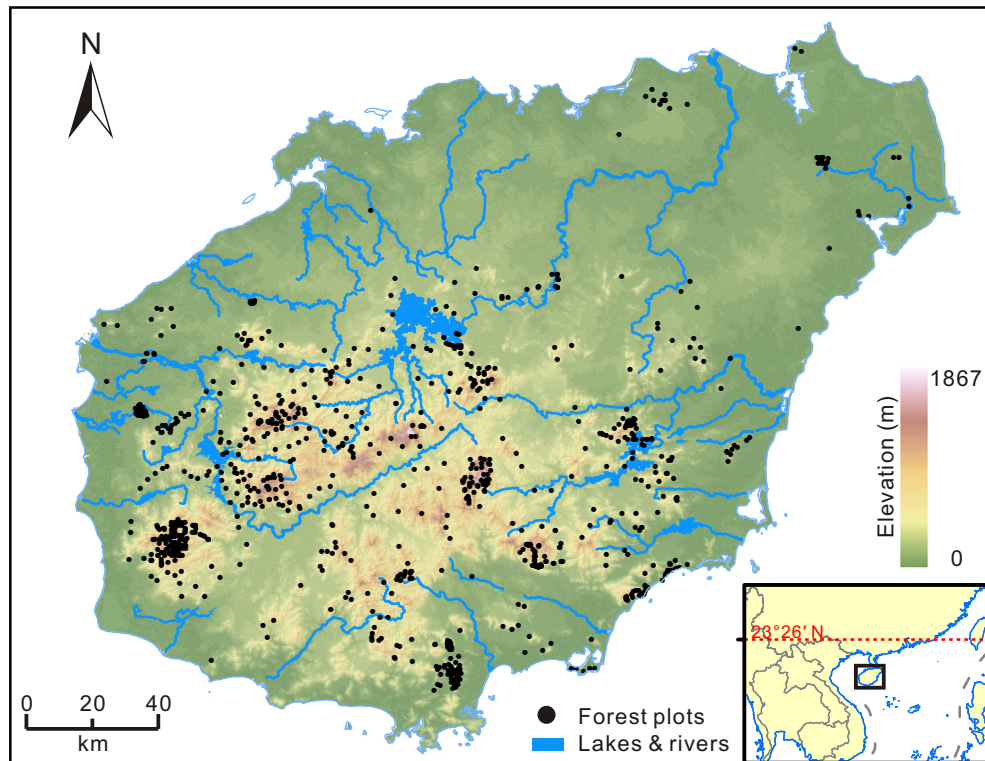


Fig. 1. Map showing the topography of Hainan Island, China, with forest inventory plots indicated by black markers.

2.3. Abiotic factors

We evaluated the environmental and spatial factors that may influence tree beta diversity in Hainan. Environmental factors included climatic and topographic variables, while the spatial factor comprised geographical distance. Climatic variables were averaged for the period from 1950 to 2000, and were derived from the WorldClim dataset with a resolution of 30 arc-seconds ($\sim 1 \text{ km} \times 1 \text{ km}$; Hijmans et al., 2005; <http://www.worldclim.org>). Potential evapotranspiration (PET) and elevation were downloaded from the Consortium for Spatial Information (Jarvis et al., 2008; Trabucco and Zomer, 2019; <http://www.cgiar-csi.org>). Given that most candidate predictors were highly correlated ($r \geq 0.7$; Table A.1), we only included in our models those variables that represent the ecologically relevant major axes of environmental space (Franklin et al. 2013; König et al. 2017; Jiménez-Alfaro et al. 2018). The selected variables were mean annual temperature (MAT; Bio 1), temperature seasonality (TS; Bio4), mean annual precipitation (MAP; Bio 12), precipitation seasonality (PS; Bio 15), and PET. All spatial predictor raster layers were converted to the same grid size ($\sim 1 \text{ km} \times 1 \text{ km}$) and coordinate system as the climatic predictors.

2.4. Biological and environmental dissimilarity

Composition dissimilarity was based on presence-absence comparisons between all pairs of sample plots and was calculated by the Sørensen dissimilarity index (Eq. (1)) as follows:

$$\beta = \frac{(b + c)}{(2a + b + c)} \quad (1)$$

where, a is the number of shared species between two communities, and b and c are the number of species exclusive to each community, respectively. The geographical distance and environmental difference of continuous predictors were measured using

the Euclidean distance between all site pairs. Mantel tests were used to examine species composition along environmental and spatial gradients by calculating Pearson's correlation coefficients (r_m) between biological dissimilarity matrices and environmental or geographical distance matrices. Statistical significance was calculated using a Mantel Carlo permutation test with 999 permutations, and the conventional 0.05 level of significance was used.

2.5. Generalized dissimilarity modelling

Generalized dissimilarity modelling (GDM) is a statistical method that evaluates the spatial turnover in species composition along environmental gradients and in geographical space (Fitzpatrick et al., 2013). Compared with classical linear matrix regression, this type of modelling accounts for two types of nonlinearity: (1) the variation in the rate of compositional turnover along individual environmental gradients, and (2) the curvilinear relationship between compositional dissimilarity and geographical or environmental distance gradients (Ferrier et al. 2007). Here, we performed GDM with the 'gdm' package (Manion et al., 2018) in R version 3.6.0 (R Core Team, 2019) and included environmental dissimilarity and geographical distance as predictor variables and community composition as the response variable. The compositional dissimilarity between any two unsampled grid cells was then predicted based on its environmental and geographical properties. The fit of each GDM was measured by the percentage of explained variance (Ferrier et al., 2007), and the importance of each predictor in the determination of community composition was obtained from the maximum height of the l-spline produced by the GDM (Fitzpatrick et al., 2013). To determine the independent and joint effects of climate and geography, we calculated the variance explained by different GDMs by either including all predictors, only geographical distance, or only the environmental variables (König et al., 2017). Finally, to visualize the predicted compositional dissimilarity in space, we used a principal component analysis (PCA) to reduce

dimensionality and assigned the first three ordination axes in the PCA to a red–greenblue colour palette.

2.6. Hierarchical clustering

To better visualize the spatial pattern in beta diversity and to identify priority areas for conservation, we used 'ward' hierarchical clustering with the Euclidean distance matrix to separate the continuous GDM into several major regions. The 'ward' cluster method calculated the total within-cluster error sum of squares and produced balanced clusters that fit the objectives of this study. We used the major frequency of 22 indices of validity and determine the optimal number of clusters using the 'NbClust' package (Charrad et al., 2014). Because of memory limitations and processing time, we randomly sampled 10,000 site pairs across Hainan to perform this analysis. To identify the characteristic species that defined different floristic regions, an indicator value was measured for each species using the 'multipatt' function from the 'indispesies' package (Cáceres and Legendre, 2009). The statistical significance of each indicator value was assessed using a randomization test with 999 permutations. Species that had significant indicator value ($p < 0.001$) were considered indicator species of their respective floristic regions.

2.7. Representativeness of the PA system

To identify priority conservation areas, we estimated the proportion of species protected by the current PA system using the framework provided by Ferrier et al. (2004) and Allnutt et al. (2008). We calculated compositional dissimilarity between any pair of cells and converted it to a similarity value as follows:

$$s_{ij} = 1 - d_{ij} \quad (2)$$

where, d_{ij} is the compositional dissimilarity between any pair of cells, while S_{ij} is the compositional similarity. All grid-cells which were wholly or partially covered by PAs were assigned a value (h_j) of 1 (i.e., protected), and the remaining non-PA cells were assigned a value of 0 (i.e., unprotected). We then estimated the proportion (p_i) of species in each cell which are currently protected by PAs:

$$p_i = \frac{\sum_{j=1}^n s_{ij} h_j / \sum_{j=1}^n s_{ij}^z}{\sum_{j=1}^n s_{ij}^z} \quad (3)$$

where, z is the exponent of the species-area relationship. We used a z -value of 0.25, which is commonly used value for these kind assessments (Ferrier et al. 2004; Allnutt et al. 2008). We also down-scaled the resolution of the raster layer to save computation memory and processing time. Finally, we used spatial overlap analysis to evaluate the representativeness of the PAs in terms of the protection of biodiversity of the remaining natural forest areas among the different floristic regions. Given that genus-level results were broadly similar to species-level results (Fig. 2), we distribute only species-level results when evaluating the representativeness of the PAs. All spatial analyses were conducted using a geographical information system (ArcGIS version 10.2., ESRI, 2013).

3. Results

The total variance in species composition explained by the GDMs was 27.65% and 26.58% for the genus and species levels, respectively (Table 1). MAP emerged as the most important variable in the GDMs (with an I-spline maximum height of 0.92 and 1.22 for genus and species, respectively) followed by MAT (the I-spline maximum height was 0.58 and 0.90 for the genus and species levels, respectively). The relative importance of predictor

variables at the genus level was highly similar to that of the species level (Table 1) and was demonstrated by shapes of the transformation functions of the fitted GDMs (Figs. A.3-A.4). The variance partitioning analysis showed that environmental factors independently explained most of the variance (22.35% and 21.32% for the genus and species levels, respectively; Table A.2). By contrast, geographical distance independently explained a negligible amount of the variance (<1%), but this increased to approximately 5% of variance when combined with environmental variables (Table A.2). The compositional dissimilarity of tree species showed the highest Mantel correlation with the difference in MAP ($r_m = 0.41$ and 0.38 for the genus and species levels, respectively, $p < 0.001$), followed by MAT ($r_m = 0.30$ and 0.38 for the genus and species levels, respectively, $p < 0.001$), and PET ($r_m = 0.21$ and 0.27 for the genus and species levels, respectively, $p < 0.001$). Mantel tests indicated that geographical distance showed a relatively weak but significant correlation with compositional dissimilarity ($r_m = 0.18$ for both the genus and species levels, $p < 0.001$).

The GDM model predicted that tree species would exhibit a spatial gradient of community similarity from east to west (Fig. 2a, b). The hierarchical clustering analysis indicated that the continuous GDM framework could be used to delineate several floristic regions that also presented a general east-to-west gradient (Fig. 2). Of the 22 indices used by the 'NbClust' function to determine the optimal number of clusters, the majority of indices demonstrated that three clusters provided the best partition pattern at both the genus and species levels (Fig. A.5). Consequently, three major floristic regions in Hainan were identified and delimited (Fig. 2c and d). When the major floristic regions were split into several subregions, the spatial structure of the subregions at the genus level was highly consistent with that at the species level (Fig. 2c and d). Indicator species analysis revealed that floristic region A was characterized by *Schefflera*, *Adinandra*, *Xanthophyllum*, and *Lindera* species, while region B was characterized by *Amesiodendron*, *Sindora*, and *Hunteria* species, and region C was characterized by *Grewia*, *Lepisanthes*, and *Lagerstroemia* species (Table A.3).

Our analyses predicted that the proportion of tree species in each grid cell that were protected in the existing PA system ranged from approximately 53% to 65% (Fig. 3a). The grid cells located in the northeast of Hainan (region A) were comprised by a higher proportion of PA-protected tree species compared to those in the northwest of Hainan (region C), which were less representative (Mann-Whitney U test, $p < 0.01$; Table A.6). Additionally, grid cells at higher elevation generally conserved a higher proportion of tree species (Fig. 1 and Fig. 3). Similarly, grid cells located in regions A and B had higher proportions of PA-protected tree species within the remaining natural forest of Hainan (Fig. 3b, c), with region C containing several fragmented grid cells which protected the lowest proportions of species.

4. Discussion

4.1. Beta diversity of Hainan trees

Our study used GDMs to provide a quantitative and ecologically coherent scheme for floristic regions in Hainan based on the spatial variation in species composition. Although there have been few attempts to explore the biogeographical regions of Hainan (Chen, 2008), some previous national and global regionalization schemes have subdivided Hainan into several distinct bioregion (Zhang, 1999; Olson et al. 2001; Zhang et al. 2007; Fig. A.7). For example, the global delineation of the ecoregions of Hainan has characterized monsoon rainforest in the mountains and subtropical evergreen forest in the coastal zones (Olson et al. 2001). From a

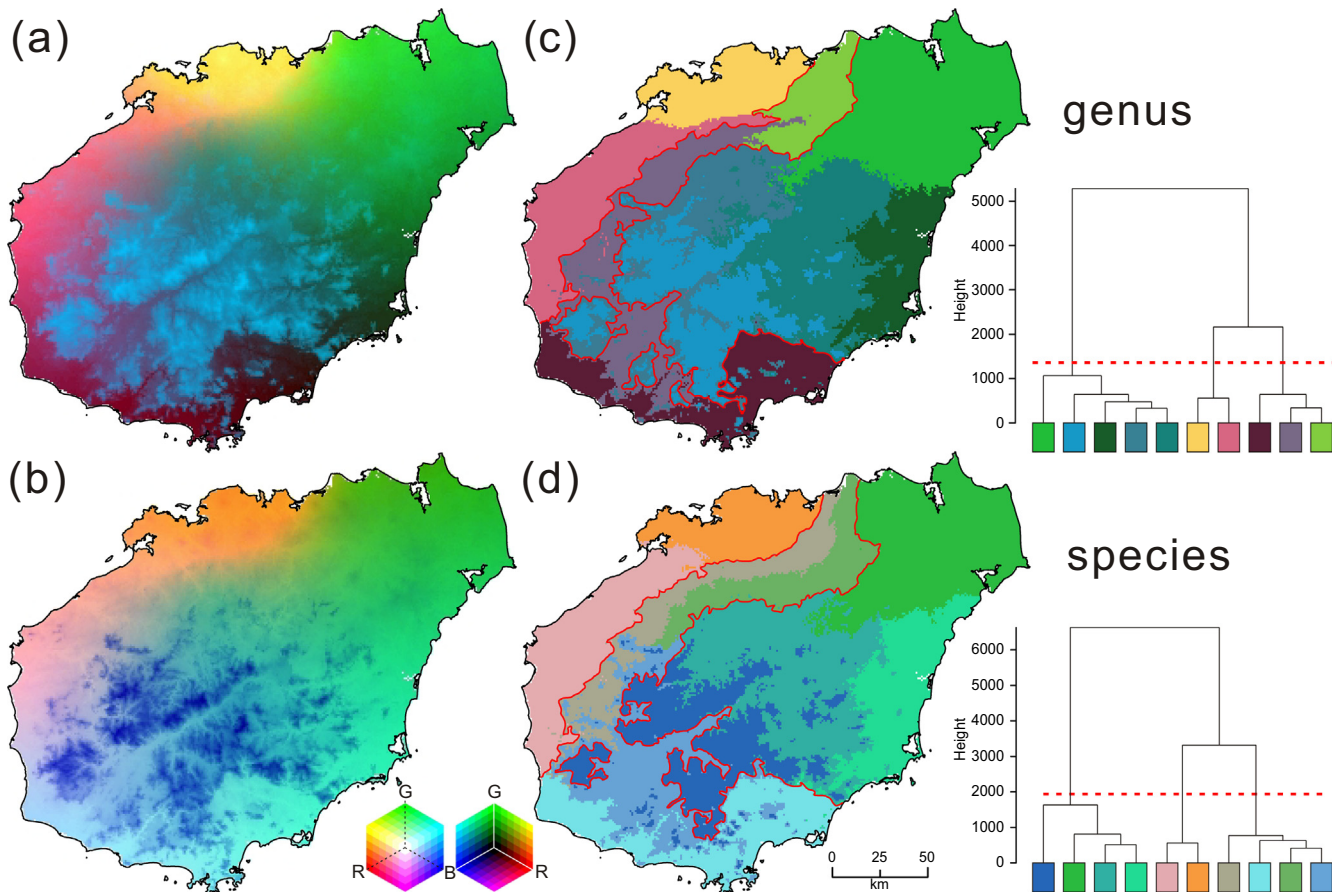


Fig. 2. Beta diversity predictions for tree species in Hainan, with major floristic regions classified from generalized dissimilarity modelling (GDM). The continuous GDM framework displays the first three PCA axes in a red–greenblue colour palette, with similar colour tones indicating similar biological compositions. Ten major floristic regions were classified by hierarchical clustering based on the GDMs. The red dashed lines in the dendrogram indicate the best clustering scheme. These results show in (a) and (c) for the genus level and in (b) and (d) for the species level. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1
Models evaluating relationships between environmental and biological dissimilarities.

Predictors	Mantel r_m^a		Relative Importance ^b	
	Genus	Species	Genus	Species
Geographical distance	0.18	0.18	0.17	0.39
Mean annual temperature	0.30	0.38	0.58	0.90
Mean annual precipitation	0.41	0.38	0.92	1.22
Temperature seasonality	0.16	0.14	0.26	0.35
Precipitation seasonality	0.12	0.09	0.26	0.19
Potential evapotranspiration	0.21	0.27	0.46	0.99
$R^2_{model}^c$	–	–	27.65%	26.58%

^a Mantel correlation coefficients (r_m) were measured based on biological and environmental dissimilarity matrices. All tests were highly significant ($p < 0.001$).

^b Relative importance of space and environment in shaping beta diversity of tree species on Hainan Island using generalized dissimilarity models (GDMs).

^c R^2_{model} presents the proportion of variance explained by GDMs.

national perspective, two bioregions with a north–south division have been broadly recognized, based on the distribution of animal communities (Zhang, 1999; Chen, 2008) and vegetation zones (Zhang et al., 2007). However, our results demonstrated that, based on tree community similarity, biodiversity in Hainan has an east-to-west gradient. The discrepancy between our results and those of previous studies is presumably due to differences in key variables controlling species composition turnover. For example, the

characterizations of Zhang (1999) and Zhang (2007) largely agree with regard to temperature gradients, while the classification proposed by Olson et al. (2001) was based on vegetation maps and is broadly congruent with regard to elevation gradients (Fig. A.7). We propose that Hainan should be split in to three floristic regions along an east-to-west gradient (Fig. 2) given the longitudinal gradient of climatic water availability in Hainan.

4.2. Environmental determinants

In recent decades, dozens of studies have investigated the factors that are responsible for composition dissimilarity between communities (e.g., Tuomisto et al., 2003; Fitzpatrick et al., 2013; König et al., 2017). However, debate continues with regard to the roles of both contemporary and historical processes that control the observed patterns (Jones et al., 2013; Ibanez et al., 2018; Jiménez-Alfaro et al., 2018). In this study, the results of the GDMs and variance partitioning based on the tree species in Hainan demonstrate that the effects of environmental factors are far more significant than geographical distance (Table 1; Table A.4), indicating that compositional dissimilarity here is largely determined by niche-based processes rather than dispersal limitations. One possible explanation may be that Hainan does not have any appreciable biogeographical barriers that may limit the dispersal of tree species. Alternatively, given that Hainan is found within the tropical zone, it may have been minimally influenced by past extinction and recolonization events (Sandel et al., 2011), unlike regions at

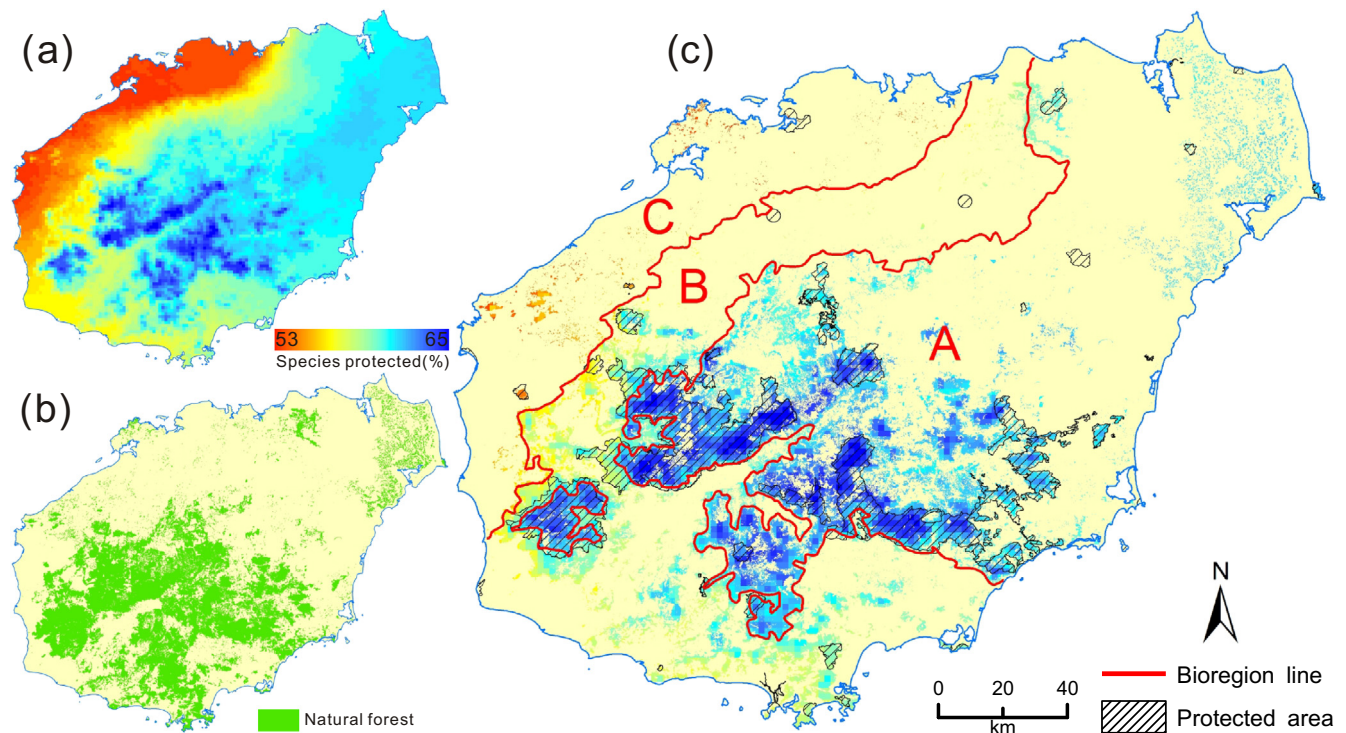


Fig. 3. Efficiency of the protected-area network in protecting species-level biodiversity on Hainan Island, China. (a) Proportion of local tree species protected by the existing protected area network, derived from the generalized dissimilarity modelling. (b) Distribution of the remaining natural forest. (c) Spatial overlap of protected areas, natural forest, the proportion of protected species, and the identified floristic regions (A, B, C) of Hainan Island.

high latitudes that have been dramatically shaped by historical processes (e.g., Pleistocene glacial events; Keil et al., 2012). As such, the structure of tree communities in Hainan is primarily the result of environmental filtering, and significantly deviates from the predictions of dispersal-based stochastic models, which agrees with earlier studies that have been performed in other tropical forests (Swenson et al., 2011; Jones et al., 2013).

The results of this study confirmed that MAP is the most important factor structuring the tree communities in Hainan (Table 1). This is presumably because MAP in Hainan ranges from 400 to 2000 mm, and therefore presents notable longitudinal gradients and structures tree community dissimilarities, as reflected by the shape of the I-spline lines in the GDMs (Fig. A.3-A.4). This finding is not only supported by a recent study that highlights the strong influence of humidity on the species diversity and aboveground biomass in Hainan forest areas (Ali et al., 2019), but also agrees with previous work in tropical forests that shows the importance of precipitation on plant species composition (Jones et al., 2013, 2016; Franklin et al., 2018). In fact, even at larger scales or in other biogeographical contexts, precipitation is often the key factor determining regional biodiversity patterns (e.g., Swenson, 2011 in India; Lu et al., 2018 in China). Although energy has long been considered to be a dominant environmental factor controlling floristic dissimilarity (e.g., Tang et al., 2012; Kubota et al., 2014), our results indicated that temperature played a secondary role in determining the floristic bioregions of Hainan (Table 1). Consequently, our results, which are based on beta diversity patterns, expand upon the conclusions of earlier studies that found water-related variables are limiting factors that govern species distributions in high-energy regions, such as the tropics (Hawkins et al. 2003; Krefl and Jetz, 2007).

4.3. Conservation applications

Although more than 2700 PAs have been established in China over the past 60 years (Ma et al., 2019), alpha diversity (Huang

et al., 2016; Xu et al., 2019) and ecosystem services (Wu et al., 2011b; Xu et al., 2017; Liang et al., 2018) have been most commonly used as a framework from which to organize conservation efforts, while the importance of compositional patterns has largely been overlooked (Socolar et al., 2016). In this study, we used community-level modelling and hierarchical clustering to map the spatial gradients of beta diversity to identify floristic regions, and to assess the ability of the PAs to encompass the biodiversity present (Overton et al., 2009). We found that the proportion of tree species in existing PAs varied substantially among different floristic regions (Fig. 3a). The northeast of Hainan (region A) had the most effective conservation coverage, while conservation in the northwest of Hainan (region C) was highly biased (Fig. A.6). This pattern is probably because the protection present in region A encompasses the most extensive natural forest area and thus captured most of the species richness present (Zhang et al., 2011; Table A.4). Consequently, maximizing the PA coverage in region A might be the easiest way in which to achieve the proposed conservation targets of the Central Government of China considering a minimum amount of area (Ren et al., 2015). By contrast, region C appears to be a low-priority area for conservation. Nevertheless, we argue that as many different floristic regions that represent unique sets of tree species should be preserved as possible. Thus, in order to maximize the protection of gamma diversity (i.e., the total species diversity of Hainan), the northwest of Hainan (region C) also deserves to be high-priority area for future conservation efforts.

Our study took the tree species of Hainan as an example to provide a quantitative framework for mapping the spatial variations in species composition and the identification of conservation gaps. This methodology may be applied to other regions of the world and in a range of biogeographical contexts. Importantly, plot-based community data may be used to map beta diversity patterns even when the geographical range of individual species is lacking (Ferrier et al., 2007). However, given that beta diversity factors

may vary at different scales and across regions (see section 4.2), it is necessary to first understand the underlying factors of a specific region before mapping biodiversity patterns (König et al., 2017). We suggest that future studies that incorporate phylogenetic and functional composition in their mapping criteria rather than only the presence or absence of species may reveal more about community assembly processes (Graham and Fine, 2008; Siefert et al., 2013) and thus provide a more promising tool that may be used to guide future conservation efforts.

4.4. Limitations

Our study inevitably suffers from several limitations. First, the proportions of compositional variation explained by our GDMs were not high (27.65% and 26.58% at the genus and species levels, respectively; Table 1). However, this result is consistent with other similar studies in which, for example, only 33.5% (Jones et al., 2016), 34–40% (Franklin et al., 2018), or 15–19% (Jiménez-Alfaro et al., 2018) of the total variance was explained by GDMs. Statistical noise and stochastic variation in species occurrence data derived from forest inventory plots are thought to explain these consistently low values (Jones et al., 2016). Another possible explanation is that some key explanatory factors (e.g., soil characteristics, or biotic interactions) that accounted for community composition variation were missing from our models (Saiter et al., 2016). In particular, it is difficult to estimate the effects of anthropogenic impacts (e.g., the history and strength of human disturbance) on the community composition of each plot (Franklin et al., 2018; Ibanez et al., 2018). Although some approaches have recently been developed to interpret unexplained compositional variation (Jones et al., 2016), disentangling the relative effects of environmental gradients and historical processes remains a challenge. Second, any attempt at biodiversity mapping is inevitably faced with uneven spatial sampling; our forest plot sampling was no exception. Although we included extensive samples across the full range of natural forests in Hainan (Fig. A.8), the plots were unavoidably concentrated in mountainous areas because any remaining natural forest on the plains is extremely fragmented due to human activity. Hence, if additional plots located in the plains could have been included, it is possible that different results may have emerged. Despite these shortcomings, our study was highly quantitative, and we believe this study provides important, scientifically reliable insights into conservation biogeography at a regional scale.

5. Conclusion

Although mapping the biodiversity of the Earth has provided a spatial framework for conservation, previous biodiversity maps have been heavily biased towards alpha diversity indices. We suggested that mapping spatial gradients in beta diversity would identify bioregions that were environmentally and biologically distinct from other areas, and that this approach could facilitate the selection of complementary regions to optimize PA coverage. This study, which is based on a large dataset of tree plots, demonstrated that: (1) The beta diversity of the tree species in Hainan shows an east-to-west gradient, and can be used to divide Hainan into three floristic regions. (2) Environmental factors play a greater role than geographical distance in determining the distribution of tree species, with mean annual precipitation playing a key role in structuring communities. (3) Future efforts should target the remaining lowland forest in northwestern Hainan to maximally preserve floristic dissimilarity. Overall, our study highlights the importance of beta diversity in understanding the determinants of biodiversity and in prioritizing conservation efforts.

Data Accessibility

The dataset used for this study is available upon reasonable request to the authors.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2019.135301>.

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