



Temperature and historical land connectivity jointly shape the floristic relationship between Hainan Island and the neighbouring landmasses

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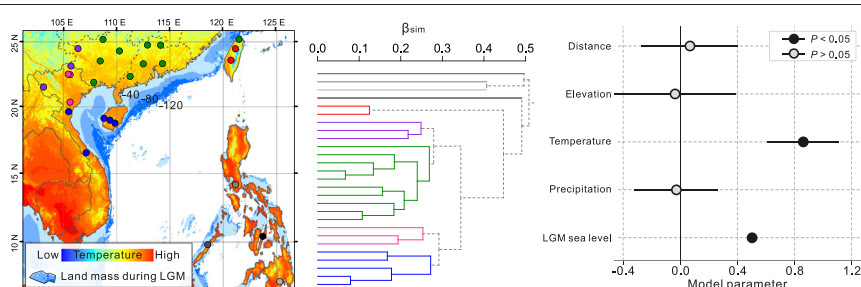
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HIGHLIGHTS

- Floristically, Hainan is more similar to Vietnam than nearby mainland China.
- Nestedness and turnover components of the total beta diversity vary across space.
- Temperature and historical land connectivity have shaped the current beta diversity.

GRAPHICAL ABSTRACT



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ABSTRACT

Present-day biodiversity in insular biota results from the interplay among geographical barriers, environmental filtering, and historical biogeography, but how these factors interact on insular biodiversity patterns is poorly understood. Here, we analysed the geographical patterns of beta diversity of seed plants between Hainan Island and the neighbouring landmasses in relation to space and the environmental factors to assess the relative effects of historical processes and ecological gradients on community assembly. We assessed beta diversity patterns by quantifying the turnover and nestedness components and used clustering and ordination to investigate the relationships between local floras from Hainan and the neighbouring landmasses. Utilising simple linear regression and linear mixed effect models, we evaluated the importance of historical processes and environmental gradients in shaping these beta diversity patterns. Our results show that the contributions of nestedness and turnover components to the total beta diversity vary across space. The flora of Hainan predominantly nests with the flora of Vietnam but shows larger species turnover with Guangdong, Guangxi, and Taiwan. Clustering and ordination analyses indicate that Hainan is first merged with Vietnam, after which it is grouped with mainland China and finally with Taiwan and the Philippines. The results of the linear mixed effect models consistently reveal that temperature, followed by the historical land connectivity, has the most important role in shaping the floristic dissimilarity. We conclude that the flora of Hainan is of continental origin and has the highest floristic affinity with Vietnam. The periodic emergence of a land bridge during Quaternary glacial cycles determines the origin of Hainan's flora, and temperature shapes the floristic dissimilarities via environmental filtering. Our study highlights the critical roles of historical sea level change and current environmental limitation in structuring the plant communities on Southeast Asian islands.

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1. Introduction

Understanding biodiversity patterns and their underlying mechanisms is a fundamental goal in the fields of macroecology and biogeography (Anderson et al., 2011; Socolar et al., 2016). Present-day biodiversity patterns in insular biota are influenced by several factors

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including geographical barriers, climatic factors, and historical biogeography (MacArthur and Wilson, 1967; Kreft et al., 2008; Weigelt et al., 2016). However, the relative effects of these factors on insular biodiversity patterns remain poorly understood because they vary across taxonomic groups and spatial scales (Fattorini, 2010; König et al., 2017; Ibanez et al., 2018) owing to substantial differences in island systems (Gillespie and Roderick, 2003), historical structure (Ali, 2017a), and bioclimatic environments (Weigelt et al., 2013).

Beta diversity quantifies the difference in species composition between communities across space and time (Whittaker, 1960), and provides a quantitative means of linking species composition and their environment (König et al., 2017). For example, assessing multiple facets of beta diversity across spatial gradients can disentangle the relative importance of environmental filtering vs. dispersal limitation (Hardy et al., 2012; Gómez-Rodríguez and Baselga, 2018), and historical legacies vs. contemporary processes (González-Trujillo et al., 2020) in structuring the assembly of biological communities. Moreover, on the temporal scale, quantification of the changes in beta diversity are used not only to illustrate the historical processes underlying biodiversity patterns (Cowman et al., 2017; Mazel et al., 2017) but also to document the anthropogenic impacts on biotic homogenisation (Winter et al., 2009; Capinha et al., 2015).

Several hypotheses have been proposed to explain the spatial patterns of beta diversity (Legendre et al., 2005). Among them, geographical distance has long been regarded as the most important driver of compositional similarity owing to dispersal limitation (distance decay of similarity; Nekola and White, 1999). Moreover, community composition patterns are likely controlled by ecological factors via the effects of environmental filtering (Svenning et al., 2011). This hypothesis suggests that whether a species exists in a community depends on the match between species environmental tolerance and the local climatic conditions (Qian et al., 2020). Accordingly, communities with greater distance/difference in space and environment are expected to host more different species assemblages (Keil et al., 2012). On a larger spatial scale, the historical factor is considered as another crucial determinant of community similarity between sites as it strengthens or weakens the species' dispersal limitation. For example, tectonic movements (Xing et al., 2015; Mazel et al., 2017), orogenic uplifts (He et al., 2020a), and palaeoclimatic changes (Svenning et al., 2011; Dobrovolski et al., 2012) have been reported to alter geographical barriers and facilitate species extinction and recolonisation, resulting in the present-day beta diversity gradients on the continent scale. In short, geographical distance, ecological factors, and historical events might not be mutually exclusive, but interact to influence the beta diversity patterns (Svenning et al., 2011; Keil et al., 2012). Although many studies have disentangled the relative roles of historical and ecological factors in driving the present-day beta diversity on global and continental scales (Svenning et al., 2011; König et al., 2017; Qian et al., 2020), few studies have focused on island systems (but see Kubota et al., 2014; Weigelt et al., 2016; Franklin et al., 2018; Ibanez et al., 2018), particularly in Southeast Asia.

Hainan Island (hereafter Hainan) is located on the northern edge of tropical Asia (Zhu, 2017; Fig. 1), and it lies within the Indo-Burma Biodiversity Hotspot (Myers et al., 2000). During Quaternary glacial cycles, the emergence of a land bridge as a result of sea level lowstands is known to have facilitated biotic interchanges between Hainan and the neighbouring landmasses (Ali, 2017b; Jiang et al., 2019; Fig. 1). While still being debated, plate tectonic movements that occurred much deeper in the past might have even had an impact on present-day community composition in this region (Zhu, 2016; Luo and Li, 2017). Considering that Hainan is geographically located at the interface between tropical and subtropical zones and historically underwent extensive biotic interchanges with mainland Asia, its floristic origin and its relationship with the neighbouring landmasses remain debatable. From a traditional point of view, the flora of Hainan was considered as a part of Chinese mainland flora (Wu et al., 1996). However, a recent study

proposed that its flora has the most similarities with the flora of Vietnam and China's Guangxi province as a consequence of the plate tectonic history of the area, which assumes that Hainan was connected to Guangxi and northern Vietnam during the early Cenozoic (Zhu, 2016). Moreover, a global-scale study on tropical forests (Slik et al., 2018) suggested that the flora of Hainan might merge with the Indo-Pacific group (e.g. Hainan, Vietnam, the Philippines) and have a species composition distinct from that of the Subtropical group (e.g. mainland China, Taiwan, the Ryukyu Archipelago). The authors attributed this division to temperature differences, as the Subtropical group has cooler climates and higher elevations than those of the Indo-Pacific group (Slik et al., 2018). These contrasting hypotheses and their proposed mechanisms ultimately come back to one of the fundamental questions in biogeography: to what extent the historical and ecological factors shape the present-day patterns of beta diversity.

In the present study, we used a regional floristic database comprising 9719 seed plant species of Hainan and the neighbouring landmasses to assess the spatial patterns of taxonomic and phylogenetic beta diversity and to unravel the relative contributions of historical and ecological drivers in shaping this pattern. Owing to the ability of comparisons of beta diversity patterns between taxonomic and phylogenetic indices to identify evolutionary histories of present-day diversity patterns (Graham and Fine, 2008), we used both types of indices to quantify the beta diversity between the communities. Specifically, our objectives were to (1) disentangle the relative contributions of turnover and nestedness components to the beta diversity patterns between Hainan and the neighbouring landmasses and (2) assess the degree to which community composition variation may be explained by historical and environmental factors.

2. Materials and methods

2.1. Species data

We focused on Hainan and other neighbouring landmasses, including Guangdong, Guangxi, Taiwan, Vietnam, and the Philippines, as our study area (Fig. 1). To increase comparability among these floras, we used relatively small regions (e.g. nature reserves and national parks) as operational geographical units (OGUs), and assembled species lists of seed plants from published floras and regional checklists. For the Philippines, we obtained all records of seed plants available from Global Biodiversity Information Facility (GBIF; <http://www.gbif.org>, accessed October 2020). The detailed processes regarding the data filtering and taxonomic cleaning are provided in Appendix A in supplementary material. The resulted OGUs consisted of 19 nature reserves, 7 national parks and 2 islands; with size ranging from 10 to 1000 km² (see detailed information of each OGU in Table A.1). We combined all subspecies and varieties into single species and standardised the species names according to the *Flora of China* (<http://foc.iplant.cn>) and The Plant List (www.theplantlist.org). Non-native species were excluded from the list. Then, we combined the species checklist with a newly updated time-calibrated angiosperm phylogenetic tree from Janssens et al. (2020). This phylogenetic tree was reconstructed based on two plastid markers (matK and rbcL) of 36,234 plant species, and the divergence time was estimated using 52 fossil calibration points (Janssens et al., 2020). Owing to a much better resolution at the genus than at the species level of the phylogeny, we conducted this study only at the genus level to optimise the comparison between taxonomic and phylogenetic beta diversity patterns. As a result, our dataset included 27 OGUs which comprised a total of 9719 seed plant species belonging to 1873 genera and 235 families (see Appendix B in supplementary material).

2.2. Abiotic factors

Elevation data with a spatial resolution of one arc-minute were downloaded from the National Centers for Environmental Information

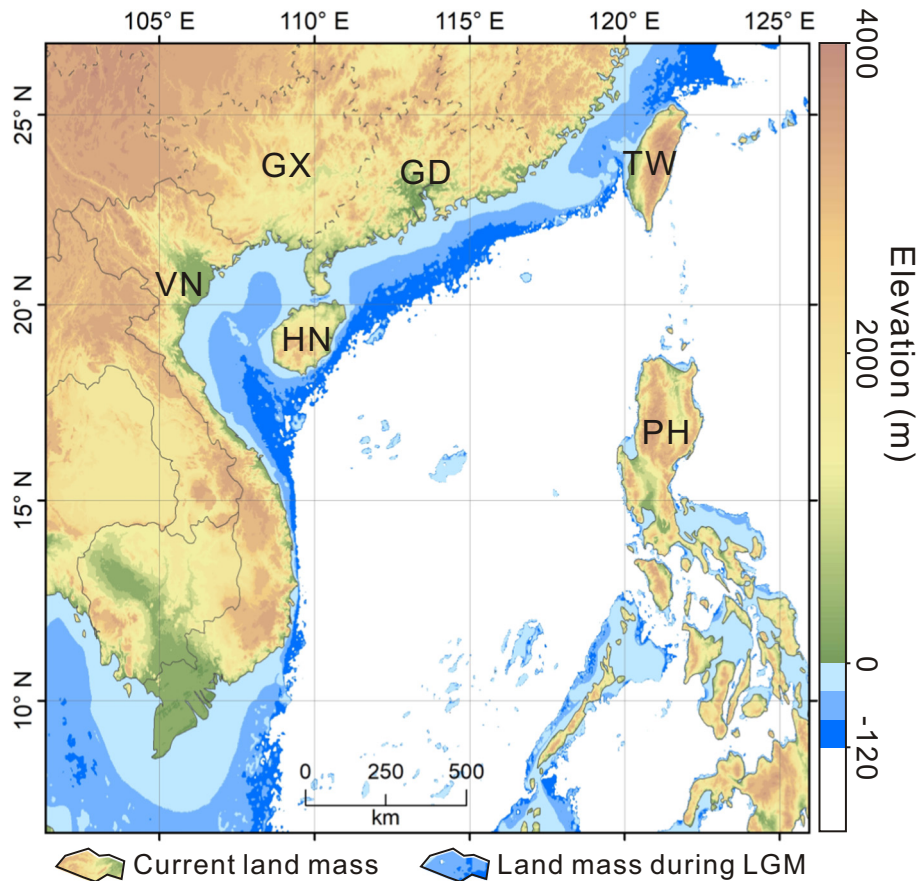


Fig. 1. The topography of Hainan Island and the neighbouring landmasses. The map was reconstructed from ETOPO1 one arc-minute global relief models, with land topography indicating current landmass and sea topography indicating the land bridge emerged during Quaternary glacial cycling. Abbreviation: GD, Guangdong; GX, Guangxi; HN, Hainan; PH, the Philippines; TW, Taiwan; VN, Vietnam.

(www.ngdc.noaa.gov/mgg/global/relief/ETOPO1/data/). Climate data were obtained from the WorldClim database with a resolution of 30 arc-seconds (Hijmans et al., 2005; www.worldclim.org). We calculated the elevation and climate variables for each OGU as the mean values of all pixels within the OGU. We calculated temperature and precipitation dissimilarity using the Euclidean distance based on the temperature-related variables (BIO 1–BIO 11) and precipitation-related variables (BIO 12–BIO 19), respectively (see detailed description of predictor variables in Tables A.2; A.3). In these analyses, we considered Hainan as the focal region and calculated the geographical distance, elevation difference, and climatic dissimilarity between Hainan and all other OGUs using Euclidean distance. We estimated the historical land connectivity between Hainan and the neighbouring landmasses based on the historical coastline. Each landmass was coded as one of three categories: (a) mainland Asia (connected to Hainan when the sea level was lower than -40 m), (b) Taiwan Island (connected to Hainan when the sea level was lower than -80 m), and (c) the Philippines (never connected to Hainan assuming a sea level drop of -120 m during the last glacial maximum).

2.3. Beta diversity indices

In order to understand the geographical patterns of beta diversity between Hainan and the neighbouring landmasses, we calculated the pairwise dissimilarity based on presence-absence comparisons between each pair of floras using Sørensen dissimilarity index (β_{sor}). Then, we partitioned β_{sor} into turnover (β_{sim}) and nestedness (β_{nes}) components, and we assessed the relative importance of turnover and

nestedness components for total beta diversity (Baselga, 2010; Leprieur et al., 2012). As a consequence of species replacement, the turnover component is primarily caused by dispersal limitations and niche constraints of the species in sites; the nestedness component represents the degree to which the species in the site with fewer species are a subset of the species in the site with more species (Baselga, 2010). These three indices were used to calculate the pairwise dissimilarity between two communities as follows:

$$\beta_{sor} = \frac{b + c}{2a + b + c}$$

$$\beta_{sim} = \frac{\min(b, c)}{a + \min(b, c)}$$

$$\beta_{nes} = \beta_{sor} - \beta_{sim}$$

where a is the number of shared taxa, and b and c are the numbers of taxa unique to each community (Baselga, 2010).

As taxonomic beta diversity considers taxa to be equally distinct from one another and disregards the difference in their evolutionary histories (Cardoso et al., 2014), we further incorporated phylogenetic information between taxa in our quantification of beta diversity (Graham and Fine, 2008). These indices are used to calculate the pairwise phylogenetic dissimilarity between two communities by replacing shared and unique species with shared and unique branch lengths, respectively (Leprieur et al., 2012), as follows:

$$p\beta_{\text{sor}} = \frac{2PD_{\text{Total}} - PD_k - PD_j}{PD_{\text{Total}}}$$

$$p\beta_{\text{sim}} = \frac{\min(PD_{\text{Total}} - PD_k, PD_{\text{Total}} - PD_j)}{PD_k + PD_j - PD_{\text{Total}} + \min(PD_{\text{Total}} - PD_k, PD_{\text{Total}} - PD_j)}$$

$$p\beta_{\text{nes}} = p\beta_{\text{sor}} - p\beta_{\text{sim}}$$

where PD_j and PD_k are total branch lengths of communities j and k , respectively. PD_{Total} is total branch length of a phylogenetic tree containing all species present in both j and k communities.

2.4. Beta diversity mapping

In order to map the beta diversity in space, we treated Hainan as the focal region and calculated the pairwise floristic similarity between Hainan and the neighbouring landmasses. In this analysis, we merged the species lists of three OGU within Hainan as a whole flora. We calculated the total beta diversity (β_{sor}) and the ratio of β_{nes} to β_{sor} (i.e. $\beta_{\text{ratio}} = \beta_{\text{nes}}/\beta_{\text{sor}}$; Dobrovolski et al., 2012) for both taxonomic and phylogenetic dissimilarities. While β_{sor} reflects compositional differences as the proportion of the sum of species richness in both sites, β_{ratio} indicates the relative importance of two aspects of the component (i.e. turnover and nestedness), which allowed us to test the mechanisms underlying the spatial patterns in beta diversity (Dobrovolski et al., 2012; Sojininen et al., 2017). We differentiated the ratio of β_{nes} to β_{sor} for taxonomic and phylogenetic beta diversity as β_{ratio} and $p\beta_{\text{ratio}}$, respectively. A value of β_{ratio} or $p\beta_{\text{ratio}}$ greater than 0.5 indicates that total beta diversity is determined mainly by the nestedness component. In contrast, if the value is lower than 0.5, it indicates that turnover plays a greater role than nestedness in determining total beta diversity (Dobrovolski et al., 2012). We generated the spatial patterns of floristic similarity between Hainan and the neighbouring landmasses using β_{sor} vs $p\beta_{\text{sor}}$ and β_{ratio} vs $p\beta_{\text{ratio}}$, respectively.

2.5. Statistic models

We conducted simple linear regression analyses based on ordinary least squares (OLS) models to examine the relationships between the turnover components (β_{sim} and $p\beta_{\text{sim}}$) of community dissimilarities and geographical or environmental distances. In these analyses, we considered Hainan as the focal region, and we assessed its floristic relationships to other landmasses. Thus, the community dissimilarity between Hainan and the neighbouring landmasses was the response variable, and their geographical or environmental distances were the independent variables.

In order to quantify the geographical and environmental effects on the community dissimilarities, we used linear mixed effects models (LMMs) with the 'lmer' function in the R package 'lme4' (Bates et al., 2015). The fixed effects were geographical distance, elevation difference, temperature dissimilarity and precipitation dissimilarity, and the random effect was historical land connectivity. The geographical distance was natural log-transformed to improve linearity. All continuous predictors were standardised before analysis (average = 0; SD = 1) to allow direct comparison of the effect sizes. Among all pairwise Pearson's correlations of fixed factors (Fig. A.1), only that between elevation difference and temperature dissimilarity was above the commonly used threshold of $|r| = 0.7$ (Dormann et al., 2013). We created different subsets of LMMs representing all possible combinations of the predictor variables using the 'dredge' function in R package 'MuMIn' (Bartoń, 2019). We used corrected Akaike's information criterion (AICc) scores to determine the best model ($\Delta\text{AICc} < 2$), and unravelled the relative importance of each variable based on standardised regression coefficients. In addition, we calculated marginal R^2 (accounting for fixed effects) and conditional R^2 (accounting for fixed and random effects) to assess the relative importance of fixed and random effects.

2.6. Classifications of floras

In order to investigate the floristic relationships between Hainan and the neighbouring landmasses, we classified the floras using hierarchical clustering and ordinations following the framework proposed by Kreft and Jetz (2010). We only used β_{sim} and $p\beta_{\text{sim}}$ to quantify pairwise taxonomic and phylogenetic dissimilarities because these indices are not affected by differences in species richness (Koleff et al., 2003). We calculated β_{sim} and $p\beta_{\text{sim}}$ between all pairs of floras using the R package 'betapart' (Baselga and Freckleton, 2013). We compared eight hierarchical clustering methods on the dissimilarity matrices and assessed the performance of different algorithms in transferring the matrices into dendrograms using cophenetic correlation coefficients (Kreft and Jetz, 2010). As the clustering obtained using the unweighted pair group method with arithmetic mean (UPGMA) always achieved the best performance (Table A.4), we only used UPGMA clustering for downstream analyses. We determined the optimal number of clusters using the Kelley-Gardner-Sutcliffe (KGS) penalty function (Kelley et al., 1996) in the R package 'maptree' (White and Gramacy, 2012). This function maximises the homogeneity within groups while maximising the differences between the groups, and its minimum value corresponds to the optimal number of clusters (Kelley et al., 1996). We performed non-metric multidimensional scaling (NMDS) ordination to illustrate the community dissimilarity between floras in two-dimensional space, and we coloured the floras based on UPGMA cluster membership. This was conducted with the 'monoMDS' function in the R package 'vegan' (Oksanen et al., 2019). Stress values were used to assess the fit between the NMDS and the original dissimilarity matrix, which ranged from 0 to 1 with lower values indicating better NMDS results.

To compare the difference in classifications of floras based on taxonomic and phylogenetic beta dissimilarities, we calculated the variation of information (VI) metric (Meilă, 2007) using 'vi.dist' function in the R package 'mclust' (Fritsch, 2012). The VI metric measures the amount of information lost and gained in changing clustering classifications. The value of 0 indicates that two classifications are identical, and higher values indicate increasing differences in clustering assignments between the two classifications. Moreover, we quantified the strength of the linear relationship between the β_{sim} and $p\beta_{\text{sim}}$ matrices using a Mantel test (999 permutations).

3. Results

3.1. Geographical patterns of community dissimilarity

Geographical patterns of β_{sor} and the β_{ratio} for seed plant community between Hainan and the neighbouring landmasses were highly congruent between taxonomic and phylogenetic measures (Pearson's correlation: $r = 0.998$ for β_{sor} vs $p\beta_{\text{sor}}$, and 0.995 for β_{ratio} vs $p\beta_{\text{ratio}}$; Fig. 2). Overall, there was no significant difference between the contributions of nestedness (β_{nes} or $p\beta_{\text{nes}}$) and turnover (β_{sim} or $p\beta_{\text{sim}}$) components to the total beta diversity (Wilcoxon signed rank test, $P > 0.05$; Table A.5). Based on the total beta diversity (i.e. β_{sor} and $p\beta_{\text{sor}}$), the flora of Hainan showed the closest floristic similarity with that of China's Guangdong and Guangxi provinces, followed by Vietnam, Taiwan, and the Philippines (Fig. 2). However, when we only considered the turnover component (i.e. $1-\beta_{\text{ratio}}$ or $1-p\beta_{\text{ratio}}$), which accounts for the different numbers of species (or phylogenetic branch length), the flora of Hainan showed a closer relationship to that of Vietnam than to the flora of any other investigated landmass (Fig. 2).

3.2. Predictors of community dissimilarity

The OLS models revealed that all variables had significant effects on community similarity ($R^2 = 0.13-0.73$; $P < 0.05$; Fig. 3), except for precipitation dissimilarity ($R^2 = 0.10$ and 0.04 , respectively; $P > 0.05$;

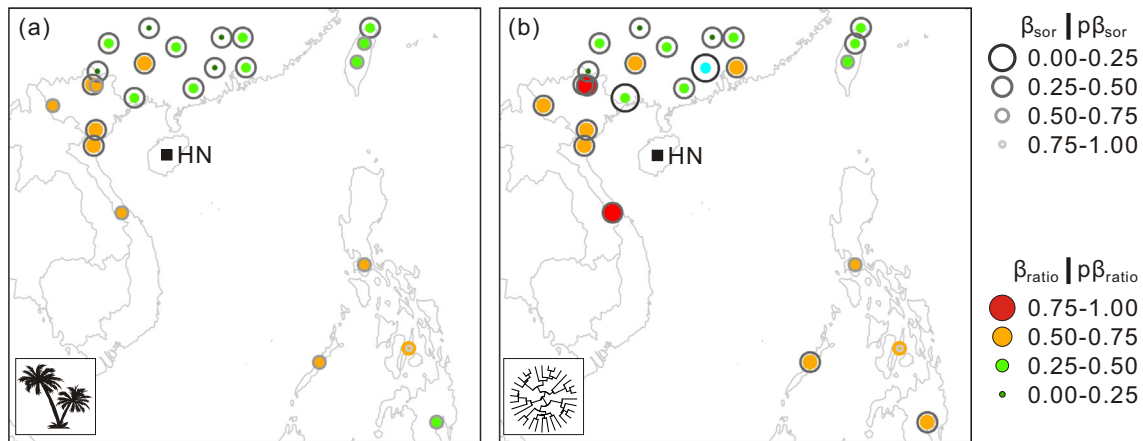


Fig. 2. Geographical patterns of beta diversity of seed plant communities between Hainan and the neighbouring landmasses. The beta diversity was calculated based on (a) taxonomic dissimilarity and (b) phylogenetic dissimilarity. The diameter of the circles is proportional to the Sørensen index (β_{sor} or $p\beta_{sor}$), and the ratio of nestedness components is proportional to total beta diversity ($\beta_{ratio} = \beta_{nes}/\beta_{sor}$ and $p\beta_{ratio} = p\beta_{nes}/p\beta_{sor}$). Larger rings and circles represent higher floristic similarity and higher ratio of nestedness components, respectively.

Table A.6). Temperature dissimilarity had the highest contribution to both taxonomic ($R^2 = 0.73$, $P < 0.001$) and phylogenetic similarity ($R^2 = 0.66$, $P < 0.001$), followed by elevation difference and geographical distance (Fig. 3). The fixed effects of the best LMMs explained 51% and 47% of the taxonomic and phylogenetic similarities, respectively, between Hainan and the neighbouring landmasses (R^2 marginal). Among the four fixed effects, temperature dissimilarity had the strongest effect on both taxonomic and phylogenetic dissimilarities (standardised coefficients were 0.86 and 0.83, respectively; Table 1). Furthermore, the standard deviations of random effects (i.e. historical land connectivity) were 0.50 and 0.54 for taxonomic and phylogenetic beta diversity (Table 1), which, combined with the fixed effects, explained 74% and 71% of the floristic dissimilarities (R^2 conditional), respectively (Table 1). This indicated that historical land connectivity also played an important role in shaping the geographical patterns of beta diversity.

3.3. Classification of floras

The hierarchical clustering analysis yielded nine clusters for taxonomic beta diversity and eight clusters for phylogenetic beta diversity based on KGS penalty function (Fig. A.3). Nonetheless, the classifications of floras showed a high level of agreement (Fig. 4), as supported by the relatively low variation of information metric between the classifications ($VI = 0.22$) based on β_{sim} and $p\beta_{sim}$ matrices. According to the UPGMA dendrograms based on both taxonomic and phylogenetic measures, Hainan was first merged with Vietnam, after which it was grouped with mainland China, Taiwan, and finally with the Philippines (Fig. 4). Although the results yielded by taxonomic and phylogenetic beta diversity showed highly similar patterns, some differences emerged. For instance, the floras at the boundary between China and Vietnam were first merged with China's Guangdong and Guangxi provinces based on taxonomic beta diversity. When we

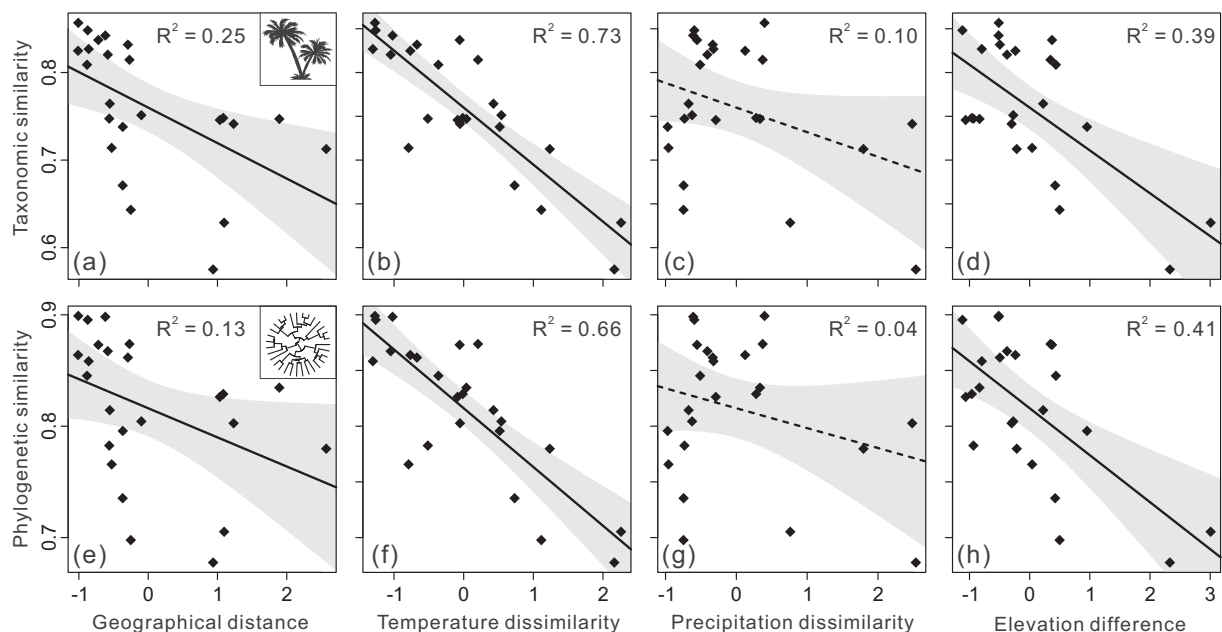


Fig. 3. Floristic similarity between Hainan and the neighbouring landmasses as a function of the geographical distance and environmental dissimilarity. The floristic similarity was calculated based on taxonomic (upper panels) and phylogenetic (lower panels) measures. Solid line indicates a relationship that is significantly different from zero (i.e. $P < 0.05$).

Table 1
Coefficient estimates from linear mixed models explaining the community dissimilarities between Hainan Island and the neighbouring landmasses.

	Taxonomic dissimilarity			Phylogenetic dissimilarity		
	β (SE)	95% CI	RI	β (SE)	95% CI	RI
Intercept	0.00 (0.11)	(−0.23, 0.23)		0.00 (0.12)	(−0.25, 0.25)	
Fixed effects						
Geographical distance	0.07 (0.16)	(−0.27, 0.41)	0.08	−0.09 (0.18)	(−0.47, 0.29)	0.09
Elevation difference	−0.04 (0.21)	(−0.46, 0.39)	0.07	0.06 (0.23)	(−0.42, 0.54)	0.09
Temperature dissimilarity	0.86 (0.12)	(0.61, 1.11)	1.00	0.83 (0.14)	(0.54, 1.11)	1.00
Precipitation dissimilarity	−0.03 (0.07)	(−0.32, 0.26)	0.06	−0.11 (0.14)	(−0.41, 0.19)	0.08
Random effects						
Historical land connectivity	0.50			0.54		
Goodness of fit statistics						
Marginal R^2	0.51			0.47		
Conditional R^2	0.74			0.71		

Fixed effects are indicated by standardised coefficients. Random effects are shown as one standard deviation. Marginal R^2 indicates variation explained by fixed effects, and conditional R^2 indicates variation explained by fixed and random effects. Abbreviations: SE, standard error; CI, confidence interval; RI, relative importance.

included the phylogenetic relationships between species (i.e. considering the branch lengths in the phylogenetic tree), these floras were first grouped with Hainan and Vietnam (Fig. 4).

The stress values of NMDS were 0.21 and 0.22 for β_{sim} and $p\beta_{sim}$, respectively, indicating that the NMDS ordination had an imperfect projection of the dissimilarity matrix into the two-dimensional ordination space. Nevertheless, both ordinations based on the β_{sim} and $p\beta_{sim}$ showed broadly similar patterns of floristic dissimilarity. This result was supported by the Mantel correlation test on these two dissimilarity matrices ($r_m = 0.993$, $P < 0.001$). Specifically, the floras of Taiwan and the Philippines were clearly separated from those of mainland Asia in the NMDS ordinations (Fig. 4).

4. Discussion

4.1. Geographical gradients of community dissimilarity

In the present study, we used taxonomic and phylogenetic measures to quantify the floristic relationships between Hainan and the neighbouring landmasses. Both taxonomic and phylogenetic beta diversities revealed that the flora of Hainan had the closest similarity with that of China's Guangdong and Guangxi provinces based on total beta diversity. This is consistent with the traditional view that the flora of Hainan was a part of Chinese mainland flora (Wu et al., 1996). However, when we deconstructed beta diversity patterns, the turnover

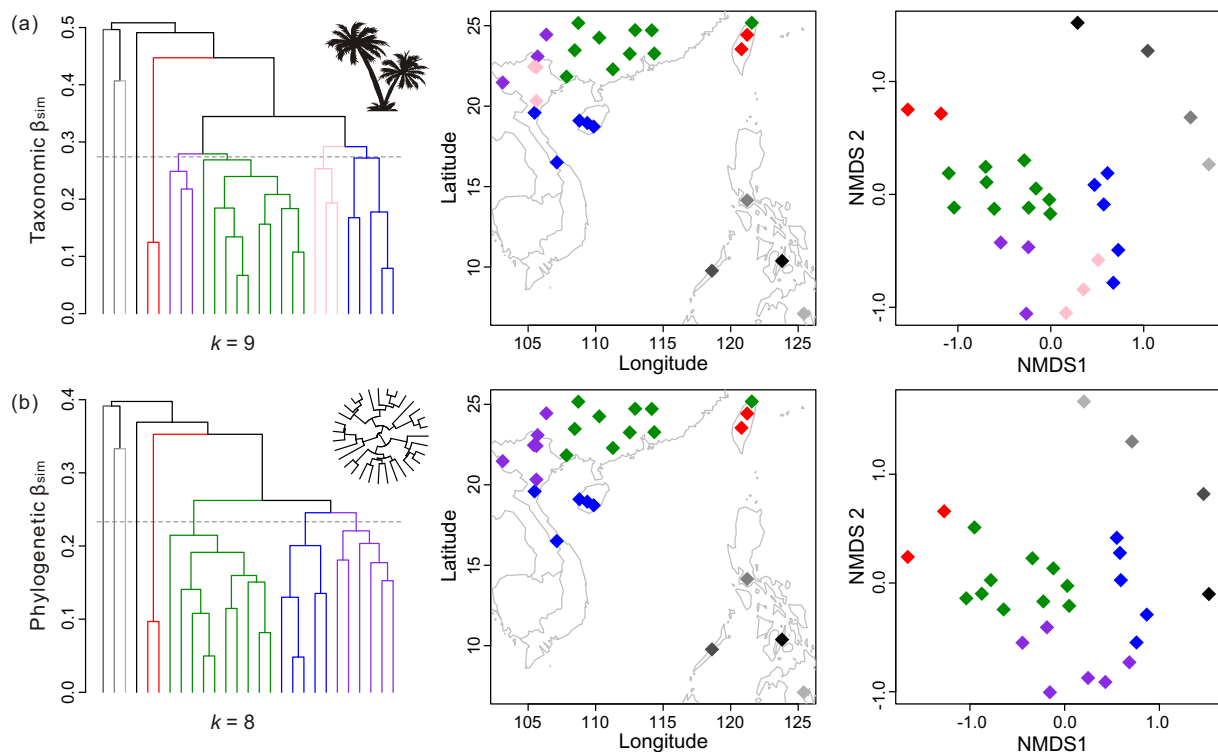


Fig. 4. Classification maps of seed plant communities of Hainan Island and the neighbouring landmasses. Dendrograms are yielded from hierarchical clustering obtained using the unweighted pair group method with arithmetic mean (UPGMA) based on (a) Simpson's dissimilarity index and (b) phylogenetic Simpson's dissimilarity index. The phenon line indicates the optimal cut-off location determined by the Kelley-Gardner-Sutcliffe penalty function. The colours of UPGMA clusters are identical to those on maps and in non-metric multidimensional scaling (NMDS) ordinations. The stress values of NMDS are 0.21 and 0.22, respectively.

component (i.e. $1-\beta_{\text{ratio}}$ or $1-p\beta_{\text{ratio}}$) evidences that the flora of Hainan is closer to that of Vietnam (Fig. 2). This supports a previous quantitative study claiming that the flora of Hainan is of continental origin and predominantly from Vietnam (Zhu and Roos, 2004). This inconsistency in the results might be due to differences in the method used in these analyses, their different spatial extents, or both.

Further, the relative contributions of nestedness and turnover components to the total beta diversity (partitioned using Baselga's (2010) method) varied across space (Fig. 2). For example, the flora of Hainan is predominantly nested with that of Vietnam (i.e. it is a subset of the species-richer flora) but showed larger species turnover with Guangdong, Guangxi, and Taiwan (i.e. with a higher importance of species replacement). This indicated that factors controlling their floristic relationships might be different (Fig. 1). The larger nestedness components between Hainan and Vietnam might result from a legacy of historical processes rather than present-day environmental conditions (Dobrovolski et al., 2012). However, environmental filtering might be the crucial driver shaping floristic relationships between Hainan and Guangdong or Guangxi; given larger species turnover in the north-south direction that parallels the latitudinal climate gradient (Svenning et al., 2011).

The UPGMA clustering, NMDS ordinations, and their resulting maps indicated that the flora of Hainan had the closest affinity to that of Vietnam, followed by that of mainland China, Taiwan, and the Philippines (Fig. 4). This finding is in high accordance with the analysis carried out by Zhu (2016), but it differs from the global-scale study by Slik et al. (2018), who first divided these floras into two thermoclimatic groups, i.e. the Indo-Pacific (Hainan + Vietnam + the Philippines) and the Subtropical groups (mainland China + Taiwan). One possible reason for this discrepancy is that this study and Zhu (2016) used whole regional seed plant checklists in the analysis, whereas Slik et al. (2018) included only tree species in their global-scale study. Previous studies have found that the factors underlying the beta diversity patterns vary among plant growth forms (i.e. trees, shrubs, lianas, and herbs; López-Martínez et al., 2013; König et al., 2017). For example, beta diversity patterns of trees were found to be determined by environmental filtering, whereas in shrubs, they are controlled by dispersal limitation (López-Martínez et al., 2013). Consequently, the north-south orientation division by Slik et al. (2018) might reflect the major effect of environmental filtering on tree species, which differs from the beta diversity patterns of all seed plants proposed by Zhu (2016) and the present study.

Our clustering and ordinations based on taxonomic and phylogenetic beta dissimilarities yielded highly similar results (Fig. 4). The results implied that there was no major allopatric speciation event in this region that could generate any differential distribution in seed plants, as supported by the results of previous studies on other taxa and regions (Hattab et al., 2015; Ye et al., 2019; Fluck et al., 2020). Nevertheless, some differences emerged in the assignment of the floras at the boundary between China and Vietnam. Based solely on the distributional data, these floras were found to be closer to China's Guangdong and Guangxi provinces (Fig. 4a), whereas they showed higher similarity to Hainan and Vietnam when we included the phylogenetic relationships between species into the analysis (Fig. 4b). This indicates that these floras might share more taxa with China's Guangdong and Guangxi provinces, but phylogenetically, their taxa could be closer to those that were located within Hainan and Vietnam in deep time. Alternatively, these floras have a relatively equivalent similarity to each of these two groups (i.e. Guangdong + Guangxi, and Hainan + Vietnam) and can be considered as transition elements, as shown in the NMDS ordinations (Fig. 4). Accordingly, the assignments of these floras might easily change in the clustering dendrograms (Kreft and Jetz, 2013).

4.2. Drivers of community dissimilarity

The current community composition is a result of the interplay of historical processes, ecological drivers, and biotic interactions

(Svenning et al., 2011; Mazel et al., 2017), but the relative contributions of these factors vary across taxonomic groups, geographical regions, and spatial scales (Qian and Ricklefs, 2012; König et al., 2017). Although many studies have investigated the factors underlying the present-day composition dissimilarity between communities (e.g. Fitzpatrick et al., 2013; König et al., 2017), these analyses performed in insular systems are relatively scarce (but see Kubota et al., 2014; Franklin et al., 2018; Ibanez et al., 2018), particularly in islands of Southeast Asia. In the present study, we focused on the floras of Hainan and the neighbouring landmasses, and we found that temperature and historical land connectivity were the most important factors shaping their floristic dissimilarities.

Our study highlighted the importance of temperature in structuring plant beta diversity (Table 1; Fig. 3). This is consistent with the results of many studies carried out on broad spatial scales (Tang et al., 2012; Qian et al., 2020), as temperature directly impact the distribution of plants via limitations to their physiology, survival, and reproduction (Bykova et al., 2012). However, on a regional scale, some studies have found that plant community composition is predominantly influenced by precipitation (Franklin et al., 2018; He et al., 2020b). This discrepancy supports the notion that the extent to which the interaction of temperature and precipitation influence plant community composition varies among different regions and scales (Tang et al., 2012), and their relative contributions presumably depend on the determinant environmental gradients within specific regions (Ali et al., 2019; He et al., 2020b). Considering that our study area is located in the transition between tropical and subtropical zones and shows large spatial temperature gradients, it is not surprising that the effect of temperature-related variables on geographical variations in community composition exceeds that of precipitation-related variables.

Apart from the temperature-related variables, historical land connectivity emerged as the second most important factor shaping the community composition between Hainan and the neighbouring landmasses (Table 1). Historical land connectivity is considered as a crucial factor in shaping alpha diversity (i.e. species richness; Weigelt et al., 2016), but little is known about its effect on beta diversity (but see Nakamura et al., 2009; Kubota et al., 2011; Wepfer et al., 2016). To date, the continent origin of Hainan's biota has often been explained by the plate tectonic history (Zhu, 2016; Luo and Li, 2017). These studies suggested that Hainan Island was in contact with the China-Vietnam border at least during the Eocene (56–33.9 Ma), as supported by palaeobotanical (Jin, 2009; Jin et al., 2009; Zhao et al., 2009) and palaeomagnetic studies (Liu and Morinaga, 1999; Fu et al., 2010). Most recently, however, the origin of Hainan's biota has received some concerns (Ali, 2017b). This author implied that the biotic interchanges caused by the emergence of a land bridge during Quaternary glacial cycling should have resulted in similar floristic affinity between Hainan and Vietnam. Further evidence from phylogenetic studies supporting the land bridge hypothesis was previously reported for several lineages, such as plants (Jiang et al., 2019), birds (Wu et al., 2012; Chen et al., 2015) and reptiles (Huang et al., 2013). Our results based on the seed plant community composition are consistent with the land bridge hypothesis. Thus, we believe that the strong affinity between Hainan and Vietnam is not necessarily related to the plate tectonic movement but more likely resulted from the emergence of a land bridge during sea level lowstands (Ali, 2017b).

4.3. Study limitations and future works

Our study has several inevitable limitations. First, our phylogenetic analysis was based on a phylogeny resolved mostly at the genetic level, and the evolutionary relationships between species were not considered. Therefore, the contributions of evolutionary processes to speciation events could only be evaluated to a certain extent. Although some studies based on other taxa have incorporated the phylogenetic information at the species level into the investigated biogeographical patterns (e.g. Rosauer and Jetz, 2015; Barreto et al., 2019), resolving the evolutionary

relationships between species of seed plants remains an ongoing challenge (Janssens et al., 2020). Nevertheless, our study successfully assessed the relative importance of historical and ecological factors in shaping the community composition between Hainan and the neighbouring landmasses by partitioning the turnover and nestedness components and by using linear mixed effect models. Second, any attempt to disentangle the drivers of biodiversity patterns cannot fully cover all aspects of predictive factors; our study is not an exception. While still being debated, several previous studies have asserted that the tectonic movements southeastward of Hainan have deeply influenced its current species composition (Luo and Li, 2017; Zhu, 2017). However, our analysis failed to include the palaeo-position of Hainan as a covariable because the knowledge on the palaeogeographical context in this region is poor. Therefore, future studies incorporating species-level phylogenetic information and taking into account the impact of tectonic movements can help shed light on the eco-evolutionary processes that shaped the present-day biodiversity patterns in the investigated area.

5. Conclusion

Understanding the spatial patterns and their underlying factors in specific regions is essential for answering conceptual questions on regional biodiversity conservation. However, the study of beta diversity of tropical continental islands, especially that of Southeast Asia, has not received much attention. The present study partitioned the turnover and nestedness components and used linear mixed effect models to quantify the relative importance of historical and ecological factors in shaping the community composition between Hainan and the neighbouring landmasses. Our results revealed that the floristic affinity of Hainan was closer to that of Vietnam than that of nearby mainland China. We found that the geographical patterns of seed plant community composition between Hainan and the neighbouring landmasses were jointly structured by temperature and historical land connectivity. Future studies on this topic should incorporate species-level phylogenetic trees and palaeogeographical factors to disentangle the effects of historical and ecological processes on the present-day diversity patterns.

CRediT authorship contribution statement

S. L., J. H. and H. J. designed the research; L. C., W. P. and J. Y. collected the data; S. L. and J. H. performed analyses with the help of H. J.; S. L., J. H. and H. J. analysed the results and wrote the manuscript. All authors contributed to the final version of the manuscript.

Declaration of competing interest

The authors declare that they have no competing interests.

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Data accessibility

The floristic data used in this study are available from supplementary material.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2020.144629>.

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