Research paper

Canopy structural heterogeneity drives α and β species–genetic diversity correlations in a Chinese subtropical forest

Zhiliang Yao [a, b], Xia Pan [a, b], Xin Yang [a, c], Xiaona Shao [a, d], Bin Wang [e], Yun Deng [a], Zhiming Zhang [e], Qiaoming Li [a, **], Luxiang Lin [a, f, *]

[a] CAS Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Kunming 650223, Yunnan, China
[b] University of Chinese Academy of Sciences, Beijing 100049, China
[c] School of Ecology and Environment, Hainan University, Haikou 570228, Hainan, China
[d] State Forestry and Grassland Administration Key Laboratory of Silviculture in Downstream Areas of the Yellow River, Mountain Tai Forest Ecosystem Research Station of State Forestry and Grassland Administration, Forestry College of Shandong Agricultural University, Tai'an 271018, Shandong, China
[e] School of Ecology and Environmental Sciences & Yunnan Key Laboratory for Plateau Mountain Ecology and Restoration of Degraded Environments, Yunnan University, Kunming 650500, Yunnan, China
[f] National Forest Ecosystem Research Station at Xishuangbanna, Mengla 666303, Yunnan, China

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ABSTRACT

Patterns and drivers of species–genetic diversity correlations (SGDCs) have been broadly examined across taxa and ecosystems and greatly deepen our understanding of how biodiversity is maintained. However, few studies have examined the role of canopy structural heterogeneity, which is a defining feature of forests, in shaping SGDCs. Here, we determine what factors contribute to α- and β-species –genetic diversity correlations (i.e., α- and β-SGDCs) in a Chinese subtropical forest. For this purpose, we used neutral molecular markers to assess genetic variation in almost all adult individuals of the dominant tree species, *Lithocarpus xylocarpus*, across plots in the Ailaoshan National Natural Reserve. We also quantified microhabitat variation by quantifying canopy structure heterogeneity with airborne laser scanning on 20 1-ha subtropical forest plots. We found that species α-diversity was negatively correlated with genetic α-diversity. Canopy structural heterogeneity was positively correlated with species α-diversity but negatively correlated with genetic α-diversity. These contrasting effects contributed to the formation of a negative α-SGDC. Further, we found that canopy structural heterogeneity increases species α-diversity and decreases genetic α-diversity by reducing the population size of target species. Species β-diversity, in contrast, was positively correlated with genetic β-diversity. Differences in canopy structural heterogeneity between plots had non-linear parallel effects on the two levels of β-diversity, while geographic distance had a relatively weak effect on β-SGDC. Our study indicates that canopy structural heterogeneity simultaneously affects plot-level community species diversity and population genetic diversity, and species and genetic turnover across plots, thus driving α- and β-SGDCs.

1. Introduction

Community genetics is a synthesis between community ecology and population genetics. One key goal of community genetics is to identify how intraspecific genetic variation affects and/or responds to community ecological properties and the factors that drive associations between population genetic variation and community species variation (Antonovics et al., 2003; Johnson and Stinchcombe, 2007). Understanding these associations often requires distinguishing between neutral and non-neutral genetic variations. Neutral genetic diversity encompasses genetic variation resulting from neutral processes such as individual migration and genetic drift, which is not related to any particular niche. Neutral genetic variation is strongly correlated with population size, and thus the combined effect of neutral genetic variation and

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* Corresponding author. CAS Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Kunming 650223, China.
** Corresponding author.
E-mail addresses: lqm@xtbg.ac.cn (Q. Li), linluxa@xtbg.ac.cn (L. Lin).
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population size may have an impact on overall community structure (Vellend and Geber, 2005; Whitlock, 2014). Understanding the interconnections and drivers of community species diversity and intraspecific genetic diversity across spatio-temporal scales is crucial for understanding species coexistence, community assembly mechanisms, and devising effective conservation strategies (Hughes et al., 2008; Kahilainen et al., 2014; Ehlers et al., 2016; Lamy et al., 2017).

A general theoretical framework has been proposed to predict the correlation between species and genetic diversity (SGDC) (Vellend, 2003). The framework underlines the parallel effects of ecological processes (e.g., environmental heterogeneity, neutral processes) on both species and genetic diversity. These parallel effects typically cause covariation in species and genetic diversity and are expected to result in positive SGDCs (Vellend and Geber, 2005). Empirical studies in various taxa and ecosystems have supported theoretical predictions of SGDCs (e.g., He et al., 2008; Papadopoulou et al., 2011; Fourtune et al., 2016; Xie et al., 2023). However, a review of SGDCs noted that the number of cases with significantly positive SGDCs was comparable to that with significantly negative SGDCs (Lamy et al., 2017). Furthermore, theoretical and empirical studies have indicated that negative SGDCs or a lack of SGDCs may be the result of several factors. For example, no or negative correlations may be caused by contrasting effects of potential ecological processes on species and genetic diversity, divergence in response to fluctuating environments between the target species and other species, or the possibility that increased species diversity may reduce the genetic diversity of some species by increasing interspecific competition or decreasing the average niche breadth within a species (Puşcaş et al., 2008; Taberlet et al., 2012; Xu et al., 2016; Marchesini et al., 2018).

Numerous studies have also examined SGDCs between communities and populations (i.e., β-SGDC) to explore potential drivers that induce covariation of species and genetic composition across communities at spatio-temporal scales and to shed more complete insights into the ecological and evolutionary processes underpinning SGDC patterns (Struebig et al., 2011; Kahilainen et al., 2014; Fourtune et al., 2016). Compared to α-SGDCs, β-SGDCs appear to be mostly positive (Lamy et al., 2017). This is possibly because species turnover and genetic differentiation may respond in parallel to isolation-by-distance (IBD) caused by neutral processes (e.g., dispersal limitation, drift) and/or isolation-by-environment (IBE) caused by individuals remaining in specific environments due to local adaptation, leading to a positive association between them (Sexton et al., 2014; Hahn et al., 2017). However, if species turnover is mainly influenced by environmental differences, whereas genetic differentiation is mainly driven by IBD, then negative β-SGDCs may occur when environmental conditions possess strong negative spatial autocorrelation (Derry et al., 2009). Thus, environmental conditions, neutral processes, and their interactions may produce mixed β-SGDCs. Simultaneous evaluation of α- and β-SGDCs could improve our understanding of how specific environmental conditions and neutral processes affect species and genetic diversity in parallel or in opposition at two diversity levels.

Environmental heterogeneity is a pivotal ecological factor that shapes SGDCs (Avolio and Smith, 2013; Kahilainen et al., 2014). The heterogeneity-diversity hypothesis predicts that sites with high spatial heterogeneity of environmental conditions have greater niche dimensions, provide favorable conditions for species with different requirements and growth strategies, and generally have higher diversity (Allouche et al., 2012; Stein et al., 2014). Environmental heterogeneity may influence genetic variation by shaping species migration patterns during adaptation to varying environments. Furthermore, environmental heterogeneity may indirectly influence neutral genetic variation by altering target species

population sizes and thereby affecting the intensity of genetic drift. If environmental heterogeneity increases the number of rare habitats, thereby reducing available suitable habitats for species to occupy, the population size will be reduced (i.e., area-heterogeneity trade-off, Allouche et al., 2012). Conversely, if the species is highly likely to colonize the increased rare habitat, it will expand its population size (Vellend, 2005). As a result, the strength and sign in which environmental heterogeneity drives the correlation between species diversity and neutral genetic diversity depend on the habitat requirements of the target species (Vellend, 2005).

Environmental heterogeneity has also been shown to have varied effects on β-SGDC. Increased environmental heterogeneity differences can lead to changes in species turnover between sites. If the more environmentally heterogeneous site is likely to contain more species with specific habitat needs, there will be higher species turnover between sites. If both sites are dominated by generalist species, these generalists outcompete specialists, leading to similar species composition between sites, and thus lower species turnover. Likewise, because increased environmental heterogeneity can result in decreasing average population sizes, environmental heterogeneity increases genetic differentiation between sites by enhancing genetic drift, especially at neutral loci (Kahilainen et al., 2014). However, increased environmental heterogeneity can select for generalist genotypes, and as most individuals have similar generalist genotypes, genetic differentiation will decrease (Ehlers et al., 2016).

Canopy structural heterogeneity (hereafter, CSH), the primary aspect of vegetation structure of forests, significantly regulates microclimate distribution within the canopy, including temperature, humidity, and light (Jucker et al., 2018; Moudrý et al., 2023). CSH, as an important component of environmental heterogeneity in forest communities, may determine α- and β-SGDCs. A number of studies have highlighted that CSH can not only influence diversity and genetic variation within communities (Marquardt et al., 2007; Gough et al., 2020; Zhang et al., 2022), but also play a role in driving species turnover among communities (Zellweger et al., 2017; Yao et al., 2023). However, its potential to explain α- and β-SGDCs has rarely been assessed. The advent of near-ground LiDAR technology has enhanced our ability to efficiently acquire point cloud data that characterizes forest structure. This enables the derivation of fine-grained structural heterogeneity metrics, offering new opportunities to assess the role of structural heterogeneity in driving SGDC patterns.

In this study, we selected widely distributed canopy dominant species as focal species to evaluate neutral genetic diversity in a subtropical broad-leaved evergreen forest, and assessed α- and β-SGDC patterns. Furthermore, we utilized CSH metrics obtained from unmanned aerial vehicle near-ground light detection and ranging technology (UAV-LiDAR) as environmental features to examine their potential in explaining the SGDCs. We employed general linear modelling to assess whether plot-level species and genetic α-diversity depend on CSH, and further applied structural equation modelling to clarify the potential mechanisms linking CSH to α-SGDC. We also employed generalized dissimilarity modelling to elucidate the role of CSH in β-SGDC.

2. Materials and methods

2.1. Study site and focal species

Our study was conducted in the Ailaoshan National Natural Reserve located in Yunnan, southwestern China. In the northern part of the reserve, 20 separate 1-ha forest dynamics plots were established according to standard measurement protocols, forming an Ailaoshan 1-ha plot network (i.e., metacommunity, Fig. 1). Our
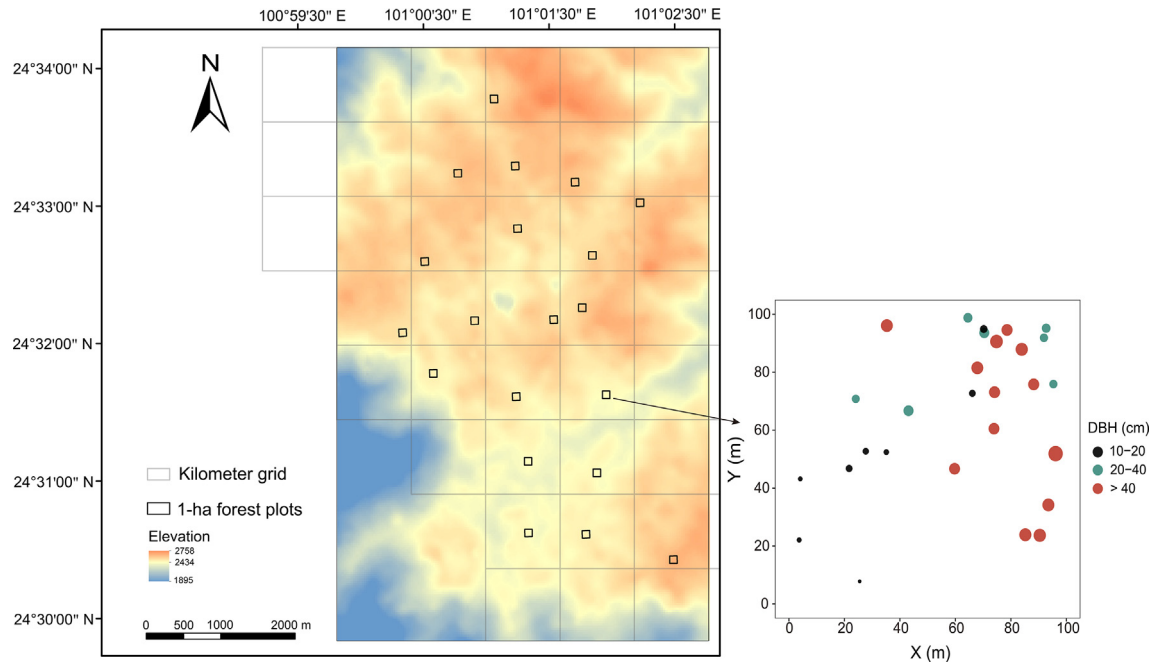
Fig. 1. The plot network (i.e., metacommunity) in the North Ailaoshan, consisting of 20 1-ha forest dynamics plots, and the distribution of the focal species *Lithocarpus xylocarpus* in a given plot.

focus was on free-standing woody stems with a DBH (diameter at breast height) $\geq$ 10 cm within the plot network. All focal individuals were labeled, measured, and identified to species; locations were also recorded. A total of 81 species and 14,281 individuals were documented. The vegetation type of the plot network is subtropical mid-mountain moist evergreen broad-leaved forest, and its composition and structure are mainly shaped by canopy dominant species belonging to Fagaceae, Theaceae, and Lauraceae.

We conducted genetic analysis of *Lithocarpus xylocarpus* (Fagaceae). *L. xylocarpus* is a keystone species and dominant species in Ailaoshan evergreen broad-leaved forests, often occupying and forming the canopy layer and playing a vital ecological role in the community (You, 1983). *L. xylocarpus* is wind-pollinated, with seeds spread by birds, small mammals, and gravity. In the plot network, *L. xylocarpus* is widely distributed, with a total of 880 individuals, ranging from 10 to 82 individuals across plots, and with obvious abundance gradients.

2.2. Community species α- and β-diversity

For each plot in the network, we computed species richness (S_richness), the exponential of Shannon entropy (S_shannon), and the inverse Gini-Simpson index (S_simpson) as community-level species α-diversity (Table S1). Species richness is the number of species in a plot, which counts species equally regardless of their abundance and thus is especially sensitive to rare species. The exponential of Shannon entropy counts individuals equally and weighs each species in proportion to its abundance, without favoring either rare or abundant species. The inverse Gini-Simpson index weighs each species by its squared abundance and thus disproportionately sensitive to dominant species. These three metrics represent Hill numbers (i.e., the effective number of species) of order $q = 0$, 1 and 2, respectively, which are commonly used to describe community diversity patterns (Hill 1973; Chao and Colwell, 2022). For a unified community species α-diversity, we conducted a principal component analysis (PCA) on these three mutually correlated diversity metrics. The first PCA axis was

extracted as integrated species α-diversity, which explained 64.9% of the total variance of the original diversity, largely contributed by S_shannon and S_simpson (Fig. S1).

Community-level species β-diversity, indicating compositional heterogeneity among communities, was measured using the abundance-based Sørensen dissimilarity index (i.e., Bray−Curtis index or percentage difference dissimilarity). It characterizes the proportion of the sum of absolute differences in abundance between two sites to the total abundance across both sites. Calculations of species α- and β-diversity at the community level were implemented using the '*vegan*' package (Oksanen et al., 2022) in R v.4.2.1 (R Core Team, 2022).

2.3. Population genetic α- and β-diversity

Molecular material was collected for all recorded individuals of *Lithocarpus xylocarpus* in 20 plots. Specifically, 2−3 fresh and tender leaves were chosen from each individual, packed in a tea bag and preserved with silica gel. Total DNA was extracted from leaves using a modified cetyltrimethylammonium bromide (CTAB) method, following Doyle (1991). Our study used microsatellite marker technology (i.e., simple sequence repeat, SSR) to detect and analyze the genetic diversity of *L. xylocarpus*. We selected six nuclear microsatellite loci with suitable levels of polymorphism (Table S2). PCR amplification and detection of each SSR locus was performed to obtain genetic data. Eventually, 840 individuals of *L. xylocarpus* had useable genetic data for genetic diversity calculations and analyses (see Table S1).

We considered each plot as a 'population' of *Lithocarpus xylocarpus* and used the abundance of *L. xylocarpus* with the available genetic information in each plot as its population size (Table S1). The allele frequency table for each locus was used to measure genetic α-diversity per locus. The average across all loci was obtained to represent population-level genetic α-diversity (see Table S1). We quantified three metrics of genetic diversity: the rarefied allele richness (G_richness), the exponential of genetic Shannon entropy (G_shannon), and the genetic inverse Gini-Simpson index

(equivalent to expected heterozygosity, G_simpson). These metrics correspond to community-level species α-diversity (Sherwin et al., 2017). The rarefaction analysis of allelic richness was implemented with the 'PopGenReport' R package (Adamack and Gruber, 2014), and the calculation of the other two genetic α-diversity metrics was performed using the 'adegenet' R package (Jombart, 2008). Analogous to the processing of species α-diversity, we performed a PCA on raw genetic α-diversity and applied the first PCA axis to represent integrated genetic α-diversity, which explains 92.8% of total variance in raw diversity (Fig. S2).

Conditional genetic distance (cGD) was used to measure population genetic β-diversity, representing genetic dissimilarity between populations. This metric was calculated using the 'graph4lg' R package (Savary et al., 2021). This metric is derived from population graph analysis, which takes into account information on genetic covariance in the entire population network created by direct pairwise and indirect connectivity among populations (Dyer and Nason, 2004). Dyer and Nason (2004) showed that cGD provided better-fit models of IBD. The cGD has been used as a primary measure of pairwise genetic distance in many studies (e.g., Noutsos et al., 2014; Quintela et al., 2014), and it provides a better fit than traditional pairwise statistics under many conditions due to its property of homoscedasticity (Dyer, 2015).

2.4. Canopy structural heterogeneity

Metrics of CSH were derived from UAV-LiDAR technology. We collected UAV-LiDAR point cloud data for each plot in the plot network from October 2018 to February 2019 using the Velodyne LiDAR PUCK-16 laser scanner. Point cloud data for each plot underwent pre-processing with a consistent protocol, encompassing denoising, filtering, and normalization. The details of point cloud data processing have been described in Yao et al. (2023). For each plot, we obtained two sets of products: canopy height model (CHM) with 1-m resolution and normalized point clouds data. Before point cloud processing, to eliminate the impact of point density variations across plots, we thinned plots with higher point density to achieve uniform point density across all plots.

CSH reflects the configuration and arrangement of aboveground vegetation elements in the forest canopy and is an important form of vegetation structure (Stein et al., 2014). From normalized point cloud data and CHM raster data, we calculated three metrics characterizing CSH in different dimensions for each 1-ha plot, and which described the structural variation of vegetation elements in the canopy vertically and horizontally: top rugosity (TR), calculated as the standard deviation (SD) of heights in 1 m² pixels within the plot, serves as a measure of outer canopy roughness (LaRue et al., 2020); canopy rumple index (CRI), which is the ratio of outer canopy surface area to ground surface area (Kane et al., 2010); the SD of vertical SD of height (StdStd), which is plot level SD of the SD of heights within 1 m³ voxels in plot and is a measure of internal and external canopy complexity (Hardiman et al., 2013). The calculated values of the CSH metrics across plots were shown in Table S1. These metrics were calculated in the 'lidR' package (Roussel et al., 2020).

2.5. Data analysis

To investigate whether the genetic α-diversity of *Lithocarpus xylocarpus* was related to community species α-diversity (i.e., α-SGDC) across the 20 1-ha plots in the plot network, Pearson product−moment correlation analysis of integrated species and genetic α-diversity was performed. The relationship between each original species and the genetic α-diversity indicators is illustrated in a correlation heatmap in Fig. S3. We used general linear models with ordinary least squares to assess whether species and genetic α-diversity are driven by CSH, where integrated species and genetic α-diversity were regressed separately on each of the CSH metrics. The bivariate relationships of integrated species and genetic α-diversity with the population size of *L. xylocarpus* and the correlations between population size and CSH were also analyzed (see Figs. S4 and S5). Further, structural equation models (SEM) were used to clarify the hypothesized causal relationships between species and genetic α-diversity, population size of *L. xylocarpus* and CSH (Lamy et al., 2017). The model assumes that CSH can directly affect species and genetic α-diversity, as well as indirectly affect α-SGDC by altering population size. We first formulated an *a priori* model (Fig. S6) based on the hypotheses, and simplified the model by removing non-significant paths. The goodness-of-fit of the SEM was determined by a maximum likelihood chi-square test, with the model judged as a good fit if $P > 0.05$. We also report the comparative fit index (CFI) and standardized root mean square residual (SRMR), which are least affected by sample size. CFI > 0.95 and SRMR < 0.08 suggest a good model fit (Rosseel, 2012). To reduce the number and collinearity of CSH metrics, the first PCA axis, which explained 74.6% of CSH metrics variability, rather than individual CSH metrics, was retained for SEM analysis. Prior to modelling, all variables were standardized to have a mean of zero and a standard deviation of 1. The SEM was implemented using the 'lavaan' R package (Rosseel, 2012).

To quantify the correlation between community species β-diversity and population genetic β-diversity of *L. xylocarpus* (i.e., β-SGDC), we calculated the correlation coefficient and its significance according to the Mantle test with 1000 permutations in the R package 'ecodist' (Goslee and Urban, 2007). To determine the importance of CSH in explaining species and genetic β-diversity, we used generalized dissimilarity modelling (GDM), which is a form of nonlinear matrix regression analysis widely used to detect the role of environmental factors in driving compositional turnover among sites (Ferrier et al., 2007; Mokany et al., 2022). In GDM, predictor variables are transformed using a series of I-spline basis functions and standardized to make the resulting coefficients comparable. GDM is generally insensitive to collinearity between predictor variables (Ferrier et al., 2007). Here, the four CSH metrics were used as the predictor variable set, and species β-diversity and genetic β-diversity served as response variables to construct the GDM, respectively. We applied Akaike's Information Criterion (AIC) for model selection and selected refined models with the lowest AICs as final models (Mokany et al., 2022). In the final model, we include geographic distance as one of the predictor variables to assess the influence of pairwise geographic distance on species and genetic β-diversity. From the final model, we plotted GDM spline curves for all remaining predictor variables for species and genetic β-diversity. The maximum height of each curve indicates the relative importance of that variable in explaining species β-diversity and genetic β-diversity, while keeping all other variables constant. The shape of each function indicates how the rate of species or genetic turnover varies along the gradient. The GDM model was implemented using the 'gdm' R package (Ferrier et al., 2007).

3. Results

3.1. Species-genetic α-diversity correlation (α-SGDC)

Pearson correlation showed that the community species α-diversity is negatively correlated with population genetic α-diversity of *Lithocarpus xylocarpus* ($R^2 = 0.34$, $P = 0.007$), a canopy-dominant species in Ailaoshan subtropical evergreen broad-leaved forests (Fig. 2). Bivariate correlation heatmap showed that genetic α-diversity was mainly related to S_simpson and S_shannon indices,
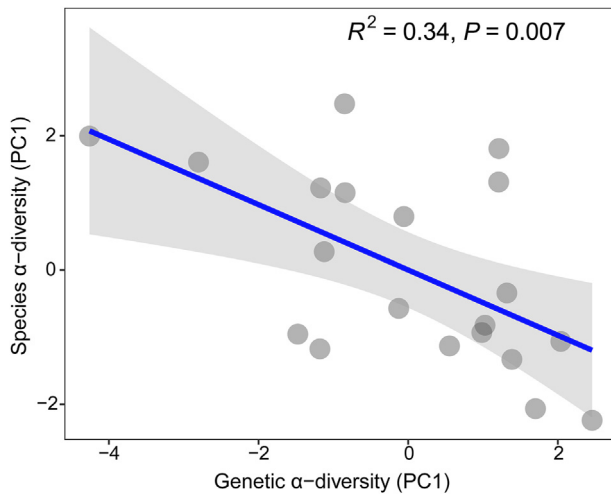
Fig. 2. Negative correlation between species α-diversity (the first principal component, PC1) and genetic α-diversity of *Lithocarpus xylocarpus* (the first principal component, PC1). The coefficients of determination (R^2) and *P* value for the linear model are shown. The error band is 95% confidence interval around the fitted regression line. Correlation heatmap for each of the original species and genetic α-diversity indicators is shown in Fig. S3.

but not to species richness (Fig. S3). General linear regression results revealed that CSH had contrasting effects on species and genetic α-diversity. Specifically, species α-diversity increased with TR, CRI and StdStd (Fig. 3). In contrast, genetic α-diversity decreased with increasing TR, CRI, and StdStd, where the effects of TR and CRI were significant (Fig. 3). Further analysis indicated that *L. xylocarpus* population size was positively correlated with genetic

α-diversity ($R^2 = 0.30$, $P = 0.013$) but negatively correlated with species α-diversity ($R^2 = 0.52$, $P < 0.001$, Fig. S4). Correlation analyses between population size of *L. xylocarpus* and CSH showed negative correlations between population size with TR, CRI and StdStd, where the effects of CRI and StdStd were significant or marginally significant (Fig. S5).

SEM visually depicted the potential pathways linking population size, CSH and α-SGDC (Fig. 4). The final model indicates that CSH affects α-SGDC indirectly by altering population size of *L. xylocarpus* (standardized path coefficient = -0.51, $P = 0.009$), while CSH positively affects species α-diversity directly (standardized path coefficient = 0.28, $P = 0.079$). In addition, population size negatively affects species α-diversity directly (standardized path coefficient = -0.58, $P < 0.001$) but positively affects genetic α-diversity (standardized path coefficient = 0.54, $P = 0.004$). After accounting for the effects of population size and CSH, the residual correlation between species and genetic α-diversity was much weaker and became non-significant (correlation coefficient = -0.13, $P = 0.280$). This suggests that population size and CSH largely explain the correlation between species and genetic α-diversity.

3.2. Species-genetic β-diversity correlation (β-SGDC)

Mantel tests showed that the population genetic β-diversity of *Lithocarpus xylocarpus* is positively correlated with the community species β-diversity (Mantel's $r = 0.36$, $P = 0.021$, Fig. 5), indicating a positive β-SGDC concerning the canopy-dominant species in the Ailaoshan subtropical evergreen broad-leaved forests.

We further explored the effects of geographic distance among plots and the gradient of CSH on β-SGDC using GDM analyses. We found that the best GDM models (i.e., with the lowest AIC) with
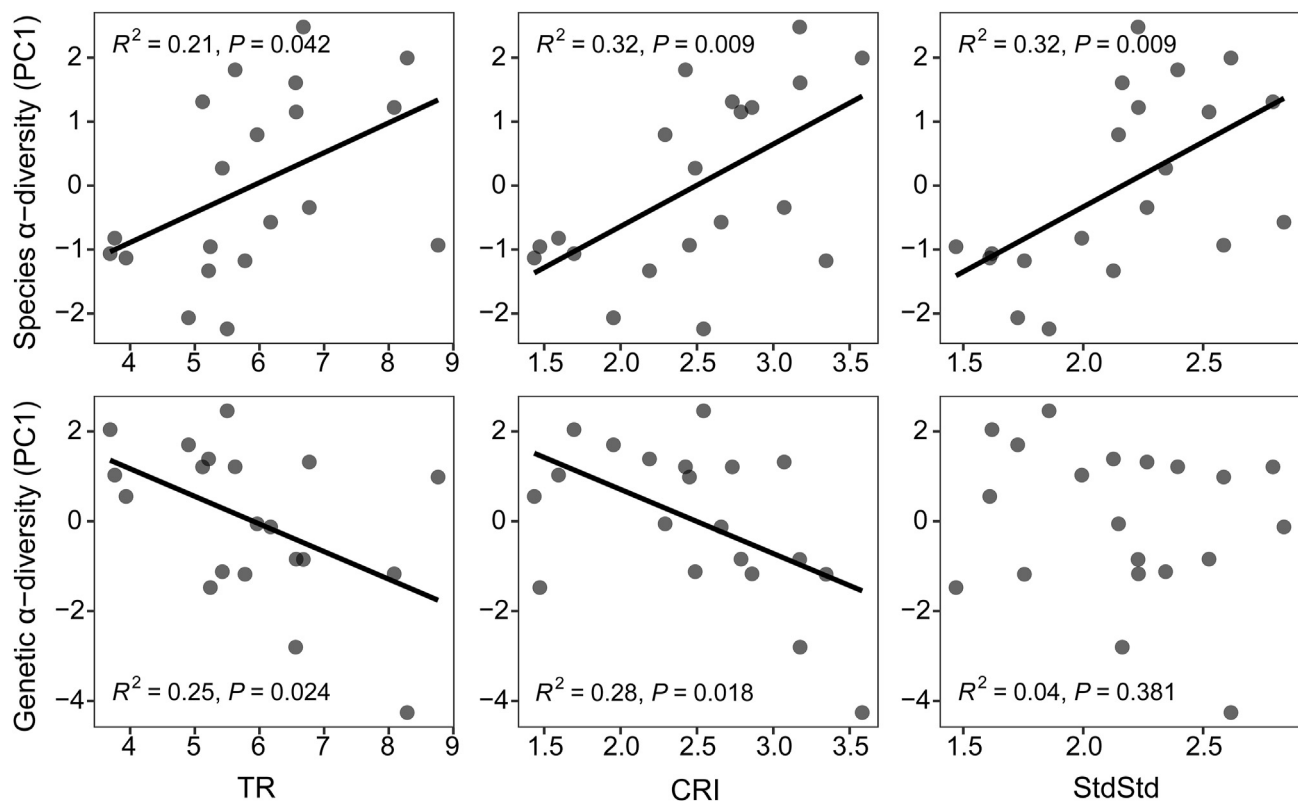

Fig. 3. Contrasting linear correlations of species α-diversity (PC1) and genetic α-diversity (PC1) on canopy structural heterogeneity. The coefficients of determination (R^2) and *P* values for the linear model are shown. Abbreviations: TR, top rugosity; CRI, canopy rumple index; StdStd, standard deviation (SD) of vertical SD of height.
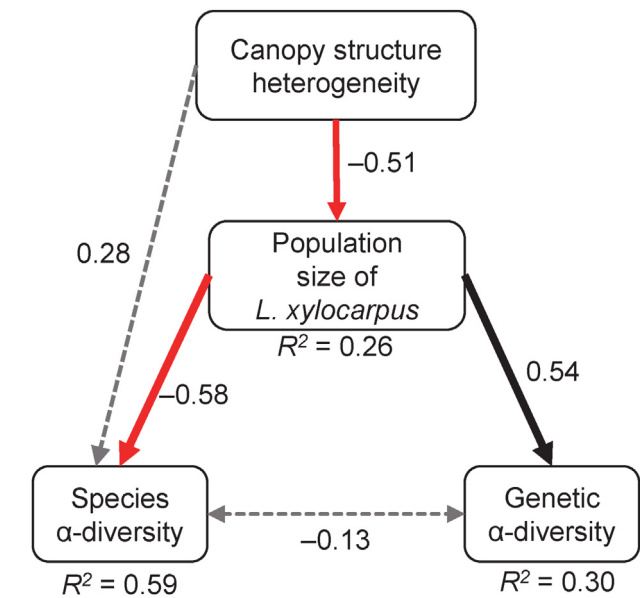
Fig. 4. The final best-fit structural equation model linking canopy structural heterogeneity, population size of *Lithocarpus xylocarpus*, genetic α-diversity and species α-diversity ($n = 20$, $\chi^2 = 1.701$, $df = 1$, $P = 0.192$, AIC = 150.801, CFI = 0.975, SRMR = 0.069). Solid black and red arrows represent statistically significant positive and negative paths ($P < 0.05$) respectively. Dotted grey arrows indicate non-significant paths ($P > 0.05$). R^2 values associated with response variables indicate the proportion of variation in a response variable explained by other predictor variables. The coefficients are standardized for each path.
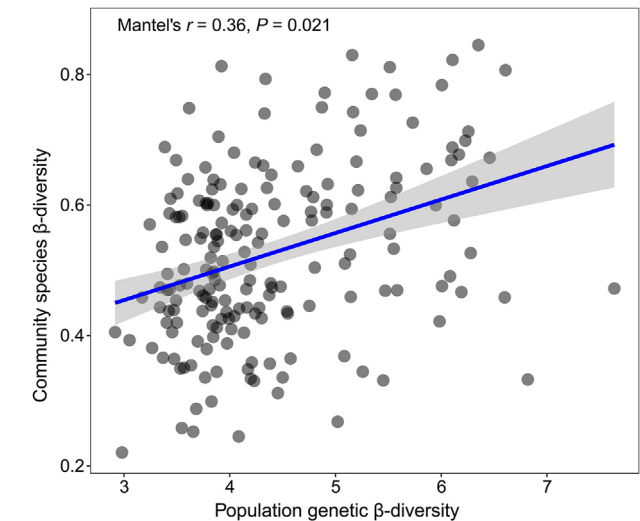

Fig. 5. Positive Mantel correlation between community species β-diversity and population genetic β-diversity of *Lithocarpus xylocarpus*. The Mantel's r and P values are shown. The error band is 95% confidence interval.

species β-diversity and genetic β-diversity as response variables both included only StdStd and CRI (Table 1). StdStd and CRI accounted for 34.6% and 48.3% of the GDM model deviance for species and genetic β-diversity, respectively (Table 1). StdStd had comparable relative importance in both GDMs, while CRI exhibited higher relative importance in the GDM of genetic β-diversity (Table 1; Fig. 6). However, geographic distance played a minimal role in explaining model deviance for the two GDMs (Fig. S7). StdStd and CRI exhibited positive and non-linear relationships with species and genetic compositional turnover (Fig. 6). Our results

Table 1
Model fit and relative importance of predictor variables (canopy structural heterogeneity, CSH) in the best generalized dissimilarity models (i.e., with the lowest AIC) with species and genetic β-diversity. *P* values for the relative importance of predictor variables are in parentheses. Abbreviations of CSH metrics follow Fig. 3.

	Species β-diversity	Genetic β-diversity
Model	StdStd + CRI	
Model deviance	9.16	6.32
Percentage explained (%)	34.6	48.3
P value	< 0.001	0.002
AIC	251.83	227.91
Relative importance		
StdStd	43.31 (0.039)	36.56 (0.091)
CRI	20.46 (0.136)	57.96 (0.06)

indicated that parallel changes in species β-diversity and genetic β-diversity across the gradient of CSH could partially account for the positive β-SGDC (Fig. 6).

4. Discussion

4.1. Contrasting effects of canopy structural heterogeneity on α-SGDC

We found that the genetic α-diversity of *Lithocarpus xylocarpus*, a canopy-dominant tree species, is negatively correlated with community species α-diversity in a subtropical broad-leaved evergreen forest (Fig. 2). Our results indicate that this negative α-SGDC pattern is related to the opposing effects of CSH on genetic α-diversity. CSH typically mirrors spatial variation in microhabitat resources (light, temperature, humidity) within sites (Ehbrecht et al., 2017; Matsuo et al., 2022). According to our final SEM, CSH increases species α-diversity and decreases genetic α-diversity by reducing the population size of target species (Fig. 4). This suggests that sites with more complex canopy structure have more diverse resources and can accommodate the co-existence of more species. In addition, this finding suggests that population size of target tree species tends to decrease in sites with higher resource heterogeneity owing to resource competition or area-heterogeneity trade-offs, leading to lower neutral genetic diversity (Wehenkel et al., 2006; Allouche et al., 2012). Previous studies that reported negative α-SGDCs have explored the opposing effects of various environmental variables (Silvertown et al., 2009; Xu et al., 2016; Marchesini et al., 2018). For example, previous research showed that long-term nutrient additions decreased species diversity but increased genetic diversity (Silvertown et al., 2009). Furthermore, certain soil properties (e.g., high soil pH and phosphorous availability) have been shown to promote the co-occurrence of more tree species in the community and decrease genetic diversity by shrinking the average niche breadth (Xu et al., 2016). Research also indicates that if the levels of these two diversity indices are affected by distinct resource heterogeneity, there is also the potential for non-significant species and genetic diversity correlations (Avolio and Smith, 2013).

The negative correlation between genetic and species α-diversity may also be explained by considering the intricate interplay between CSH, species and genetic diversity, and population size of *L. xylocarpus*. In the Ailaoshan region, *L. xylocarpus* dominates the canopy layer with large, broad crowns that significantly shape the canopy structure; hence, its population size contributes to CSH (You, 1983). Our findings indicate that communities with a high abundance of *L. xylocarpus* typically exhibit low canopy relief and roughness (Fig. S5). The presence of *L. xylocarpus* may also influence community-wide species diversity by altering community characteristics and ecosystem processes, thus affecting the population
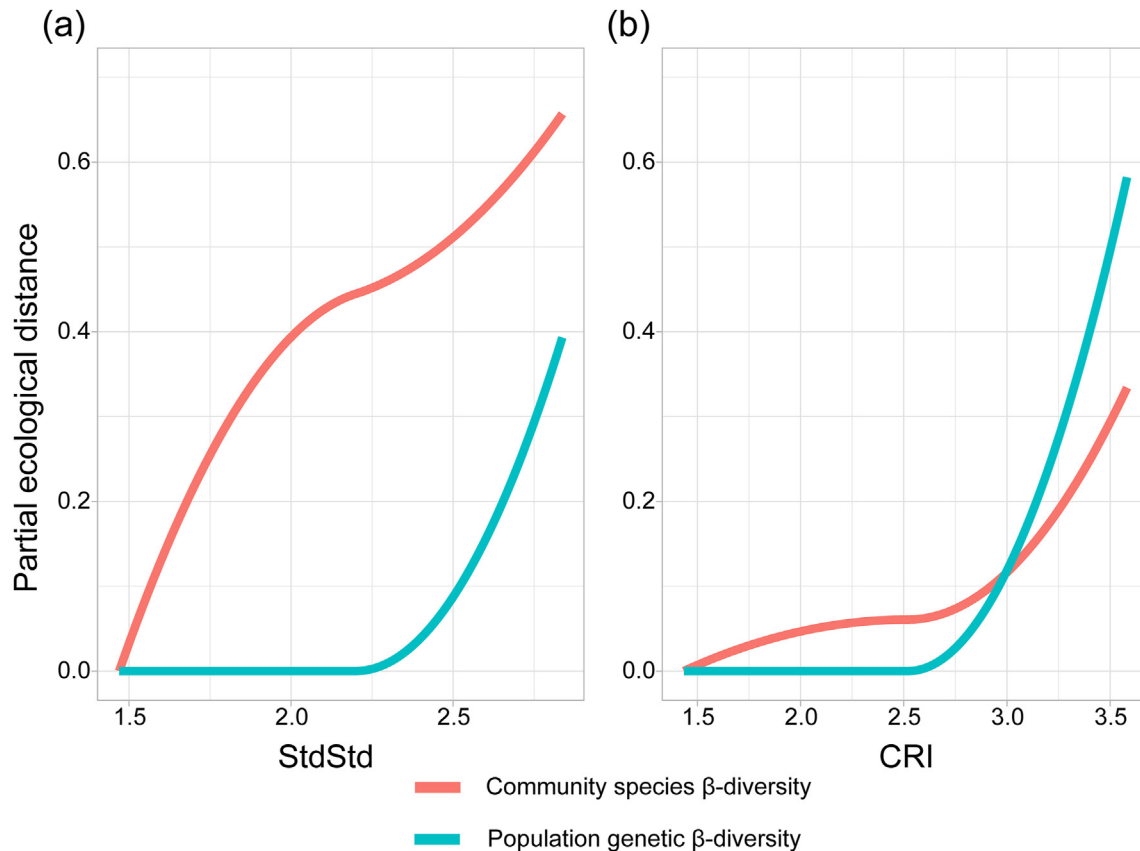
(a)

(b)

Fig. 6. GDM-fitted I-splines for canopy structural heterogeneity (StdStd and CRI) of community species β-diversity and population genetic β-diversity of *Lithocarpus xylocarpus*. The height of each I-spline indicates the relative contribution of each predictor to the species and genetic compositional turnover (i.e., the partial ecological distance). The abbreviations of CSH metrics follow Fig. 3.

growth and recruitment of associated species. Alternatively, it may limit the local diversity of co-occurring species by occupying the majority of the available space (Ellison et al., 2019; Qiao et al., 2021). We found that the abundance of *L. xylocarpus* directly, negatively affected species diversity (Fig. 4). This, in turn, led to high genetic diversity and low species diversity in communities with large *L. xylocarpus* populations, resulting in a negative α-SGDC.

Community species diversity can also contribute to canopy structure (Coverdale and Davies, 2023). We found that communities with higher species diversity tend to have greater complexity in canopy roughness, rugosity and internal spatial variability (Fig. 3). Nevertheless, further exploration of the intrinsic mechanisms governing the impact of dominant species abundance on community structure is required. This will help unravel the complex relationships between population size, CSH, and α-SGDC.

The census data of the plots of our study provide an adequate assessment of α-SGDCs by genetically estimating almost all individuals of the target tree species across the plots, reflecting more realistic levels of dominance and genetic potential. This study also emphasizes the importance of the identity of the target species and its position of optimal fitness along the ecological gradient of interest when exploring the patterns and drivers of α-SGDCs (Vellend, 2005).

4.2. Parallel effects of canopy structural heterogeneity on β-SGDC

We found a strong positive correlation between variation in species composition among communities and genetic differentiation among populations (Fig. 5). While consistent with previous studies (Yu et al., 2009; Robuchon et al., 2019; Ishii et al., 2022; Xie et al., 2023), the underlying causes of this result may vary. In multiple plant species, genetic β-diversity and species β-diversity have been shown to be positively correlated (Ishii et al., 2022). This positive correlation has been attributed to positive spatial auto-correlation effects of species and genetic β-diversity associated with a distance-decaying pattern of environmental similarity or high rates of migration of individuals among neighboring sites rather than to environmental drivers. Other studies have indicated that this positive correlation between population genetic differentiation and vegetation dissimilarity (referring to species compositional variation among communities) can be explained by vegetational heterogeneity that creates ecological barriers limiting gene flow, thus enhancing genetic differentiation among populations (Yu et al., 2009). Our findings suggest that increased differences in canopy structure between communities may contribute to both more dissimilar species composition and higher genetic differentiation of *Lithocarpus xylocarpus*. This parallel effect is a likely contributor to the observed positive β-SGDC. Nevertheless, it is noteworthy that geographic distance exhibited only a minor parallel effect on β-SGDC (Fig. S7). This study underscores the significance of recognizing non-linear parallel effects of ecological factors on β-SGDC, emphasizing that linear models may inadequately capture the underlying drivers. Therefore, we propose that the non-linear parallel effects of abiotic factors and spatial distances need to be thoroughly considered when investigating the underlying mechanisms of positive β-SGDC patterns to improve the understanding of what drives changes in species and genetic diversities over spatio-temporal scales. Currently, non-linear

extension of linear regression based on distance matrices (i.e., generalized dissimilarity model, GDM) is a potent statistical tool for analyzing non-linear parallel effects of β-SGDC (Fitzpatrick and Keller, 2015).

Previous insights drawn from this plot network suggested that canopy structure predominantly influences the nestedness components of species β-diversity, that is species abundance differences among plots (Yao et al., 2023). Here, we examined whether non-linear effects of canopy structure drive species β-diversity. Plots with distinct CSH may harbor varying microclimatic conditions that can (i) generate ecological barriers limiting gene flow between populations, (ii) influence the population immigration mode and rate, or (iii) alter population size, which in turn creates variation in allelic composition among plots and consequently contributes to inter-population genetic differentiation as quantified by neutral molecular markers (Yu et al., 2009; Sexton et al., 2014; Hahn et al., 2017). Thus, environmental filtering may occur simultaneously at the population and community levels to drive co-variation in the species and genetic compositions (Fourtune et al., 2016). This study did not detect a strong distance-decay effect of species composition similarity or an isolation by distance pattern of genetic differentiation. This might be attributed to the relatively short spatial distances between plots, which may not have been sufficient to impede species migration and dispersal, particularly concerning genetic compositional turnover (Fig. S7). Accordingly, our findings suggest that the positive β-SGDC observed in Ailaoshan broad-leaved evergreen forests is better explained by non-linear parallel effects of CSH than by positive spatial autocorrelation characterized by spatial distance.

Forest canopy structure can be influenced by biotic (e.g., density, tree size distribution) and abiotic (e.g., topography, soil) factors (Peck et al., 2014; Fotis et al., 2018; Muscarella et al., 2020; Gough et al., 2022). For example, variations in topography and soil properties create resource heterogeneity at the local scale, and this patchy distribution of environmental resources drives natural disturbance and tree performance, thereby affecting the complexity of canopy structure and composition (Ediriweera et al., 2016; Cushman et al., 2022; Gough et al., 2022). Clearly, further studies are required to reveal the biotic and abiotic factors that influence and shape forest canopy structure and composition, which may be potential drivers of α- and β-SGDCs. They may indirectly affect species composition and related-species genetic variation by impacting canopy structure and altering microenvironmental heterogeneity. Additionally, we recognize that insufficient field investigation may lead to biased estimates of species and genetic α- and β-diversity. Future studies on SGDC should aim to include all size classes of individuals to provide a more accurate and holistic understanding of diversity patterns.

5. Conclusions

Our study, centered on dominant tree species within forest dynamic plots, employed UAV-LiDAR to quantify canopy-related environmental heterogeneity and neutral molecular markers to assess genetic variation. Examining species-genetic diversity correlations within and between forest plots (α- and β-SGDCs), we found that species and genetic α-diversity are negatively correlated in a Chinese subtropical forest and that this correlation is driven by canopy structural heterogeneity and population size. Our results also indicate that species and genetic β-diversity are positively correlated in these forests and that this correlation is driven by non-linear parallel effects of canopy structural heterogeneity rather than spatial autocorrelation. This study underscores the pivotal role of canopy structural heterogeneity, a key aspect of environmental heterogeneity, in elucidating species—genetic diversity correlations

in forest ecosystems. Future investigations should comprehensively explore the impact of canopy structural heterogeneity on shaping community species distributions and population spatial genetic structures.

Data availability statement

Data are available in the GitHub Repository at https://github.com/zhiliang93/Data_of_SGDC_paper.

CRediT authorship contribution statement

Zhiliang Yao: Writing — review & editing, Writing — original draft, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Xia Pan:** Software, Resources, Data curation. **Xin Yang:** Software, Resources, Data curation. **Xiaona Shao:** Software, Resources, Data curation. **Bin Wang:** Software, Resources, Data curation. **Yun Deng:** Resources, Data curation. **Zhiming Zhang:** Resources, Data curation. **Qiaoming Li:** Resources, Conceptualization. **Luxiang Lin:** Writing — review & editing, Resources, Funding acquisition, Data curation, Conceptualization.

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.pld.2024.08.003.

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