Research paper

Adaptive genetic diversity of dominant species contributes to species co-existence and community assembly

Qiao-Ming Li [a, b, *], Chao-Nan Cai [c, d], Wu-Mei Xu [e], Min Cao [a], Li-Qing Sha [a], Lu-Xiang Lin [a], Tian-Hua He [f]

[a] CAS Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Mengla, 666303, Yunnan, China
[b] Center of Plant Ecology, Core Botanical Gardens, Chinese Academy of Sciences, Mengla, 666303, Yunnan, China
[c] School of Advanced Study, Taizhou University, Taizhou, 318000, Zhejiang, China
[d] Zhejiang Provincial Key Laboratory of Plant Evolutionary Ecology and Conservation, Taizhou University, Taizhou, 318000, Zhejiang, China
[e] School of Energy and Environment Science, Yunnan Normal University, Kunming, 650500, Yunnan, China
[f] School of Molecular and Life Sciences, Curtin University, PO Box U1987, Perth, WA, 6845, Australia

ARTICLE INFO

ABSTRACT

The synthesis of evolutionary biology and community ecology aims to understand how genetic variation within one species can shape community properties and how the ecological properties of a community can drive the evolution of a species. A rarely explored aspect is whether the interaction of genetic variation and community properties depends on the species' ecological role. Here we investigated the interactions among environmental factors, species diversity, and the within-species genetic diversity of species with different ecological roles. Using high-throughput DNA sequencing, we genotyped a canopy-dominant tree species, *Parashorea chinensis*, and an understory-abundant species, *Pittosporopsis kerrii*, from fifteen plots in Xishuangbanna tropical seasonal rainforest and estimated their adaptive, neutral and total genetic diversity; we also surveyed species diversity and assayed key soil nutrients. Structural equation modelling revealed that soil nitrogen availability created an opposing effect in species diversity and adaptive genetic diversity of the canopy-dominant *Pa. chinensis*. The increased adaptive genetic diversity of *Pa. chinensis* led to greater species diversity by promoting co-existence. Increased species diversity reduced the adaptive genetic diversity of the dominant understory species, *Pi. kerrii*, which was promoted by the adaptive genetic diversity of the canopy-dominant *Pa. chinensis*. However, such relationships were absent when neutral genetic diversity or total genetic diversity were used in the model. Our results demonstrated the important ecological interaction between adaptive genetic diversity and species diversity, but the pattern of the interaction depends on the identity of the species. Our results highlight the significant ecological role of dominant species in competitive interactions and regulation of community structure.

1. Introduction

The synthesis of evolutionary biology and community ecology aims to understand how genetic variation within one species can shape community properties, and how the ecological properties of a community can, in turn, drive the evolution of a species (Johnson and Stinchcombe, 2007). Genetic variation may determine the demographic performance of a species and its capacity for competition or facilitation; for a dominant species, it may also structure the biotic environment experienced by the rest of the community. Thus, species diversity (SD) may be causally influenced by the genetic diversity (GD) of a dominant species. The GD of a species may in turn be affected by the diversity and relative abundances of co-existing species as the SD in a community may govern the selection regime acting on component populations (Vellend and Geber, 2005). Quantifying the species-genetic

diversity correlations (SGDCs) has emerged as a new and powerful tool for understanding species co-existence and community assembly, and recent studies have moved the investigation of SGDCs from conventional pairwise correlation analysis to the multivariate analysis of hierarchical correlations (Lamy et al., 2017).

One of the major drivers of SGDCs has been hypothesized to be parallel responses to environmental characteristics at the same locality (Antonovics, 2003; Vellend and Geber, 2005; Cleary et al., 2006). Indeed, studies have shown that some key environmental variables shape observed SGDCs (e.g., He et al., 2008; Papadopoulou et al., 2011; Lamy et al., 2013; He and Lamont, 2014). Significant negative SGDCs have also been reported (Karlin et al., 1984; Silvertown et al., 2009). Xu et al. (2016) found that the increase in SD in the Xishuangbanna tropical seasonal rainforest reduced GD of *Beilschmiedia roxburghiana* Nees, a common tree species in the community. As tropical forests have very high SD, it is not clear whether the pattern of SGDCs depends on the ecological role of focal species.

It has long been believed that some species may have a greater influence on community properties (Paine, 1969). For example, dominant species may be more important to community structure by modulating physical habitats and regulating species interactions (Zacharias and Roff, 2001). Studies in community genetics have recently reported that the GD of a host plant significantly affects the composition of herbivore communities (Johnson and Agrawal, 2005; Barbour et al., 2015). However, outside the plant-herbivore system, few studies have attempted to identify the impacts of GD in dominant species on co-existing species in a community (Hughes et al., 2008).

Most studies of SGDCs have used GD derived from neutral genetic markers to infer patterns of SGDCs (reviewed in Kahilainen et al., 2014 and in Lamy et al., 2017), but answering questions related to the ecological influence of genetic variation on community assembly, the importance of species interactions, and the direct interaction of GD and SD involve genetic variation under natural selection (i.e., adaptive genetic diversity, GD_a; Lankau and Strauss, 2007; Hughes et al., 2008; Lamy et al., 2017). Watanabe and Monaghan (2017) suggested that both neutral and adaptive genetic variation may be involved in shaping patterns of SGDCs. High-throughput DNA sequencing technology is capable of screening thousands of polymorphic loci (e.g., SNPs) across the genome, creating the potential to derive a large number of putative loci under selection. Using high-throughput DNA sequencing to screen for adaptive genetic variation could represent a significant step towards understanding SGDCs.

Hierarchical relationships among GD, SD and environmental properties may exist within a community. For instance, limiting soil nutrients could influence the GD of dominant species, while the altered GD of dominant species may have important impacts on the species co-existence or GD of other species in a community (Vellend and Geber, 2005). However, few studies have explored such complex correlations among different levels of biodiversity and environmental properties. Structural equation modelling (SEM) has the special power to explain the complex hierarchical and causal effects in SGDC studies (Lamy et al., 2017). The models tested in SEM analysis are based on the mechanisms thought to operate in the system and multiple alternative hypotheses for how the observed pattern of SGDCs has been shaped can be tested (Mitchell, 1992; Grace et al., 2010). More importantly, SEM divides the combined effect of the interacting elements into direct and indirect effects, thereby enabling the specific mechanism underlying an SGDC to be deciphered.

Here, we used high-throughput DNA sequencing to derive the adaptive, neutral and total genetic diversity (GD_a, GD_n and GD_t) of two co-occurring tree species, a canopy dominant tree species, *Parashorea chinensis* Wang Hsie, and an understory-abundant tree

species, *Pittosporopsis kerrii* Craib, that may shape community characteristics in the speciose Xishuangbanna seasonal rainforest. We also quantified patterns of SGDCs of the GD_a, GD_n and GD_t of the two species and the SD of the communities in which they occur. We further employed SEM to decipher the hierarchical relationships among the GD and SD of the two species and environmental variables. Ultimately, we aimed to reveal the underlying mechanisms of species co-existence in species-rich communities. We specifically attempted to answer the following questions: 1) Is the tree diversity of a community correlated with the adaptive genetic diversity of both focal species, and if so, which key environmental property (e.g., soil nitrogen or phosphorus availability) drives SGDC patterns? 2) Do the SGDC patterns depend on the ecological role of focal species in the community?

2. Materials and methods

2.1. Study site and focal species

Fifteen 1-ha plots (100 m × 100 m) were established, with seven plots set in a 20-ha (400 m × 500 m) forest dynamics plot (FDP) and eight plots in the surrounding forest (centred at 21°36′00″–42′00″N and 101°30′00″–38′00″E), in the Xishuangbanna tropical seasonal rainforest in southwestern China (Fig. 1), which is within the Indo-
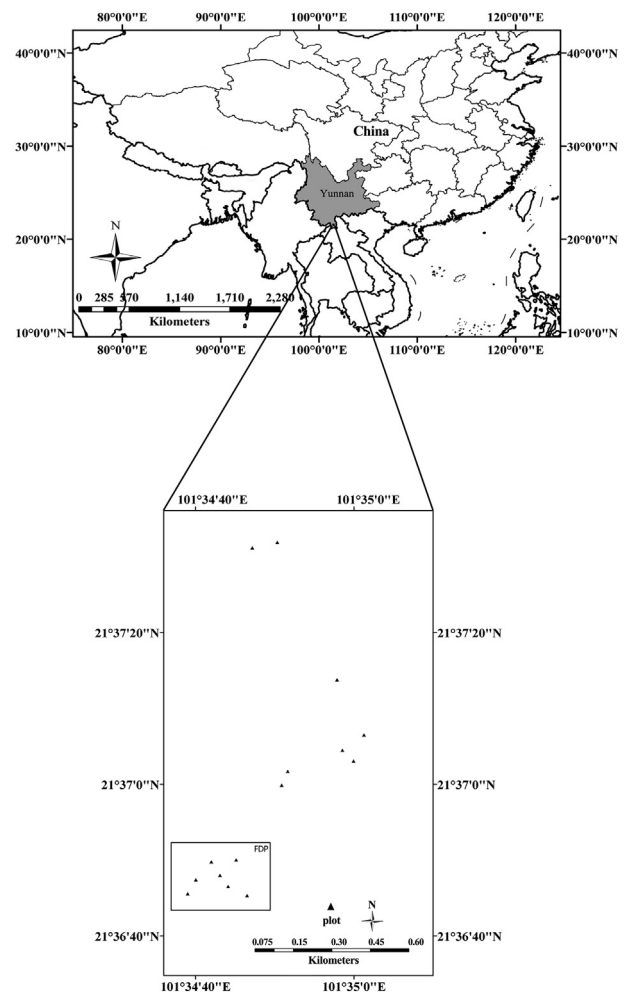

Fig. 1. The study area and relative locations of surveyed plots. "FDP" and the frame indicate the relative location of Forest Dynamics Plot in Xishuangbanna tropical seasonal rainforest.

Burma biodiversity hotspot. The average annual rainfall is approximately 1500 mm, with 80% occurring during the wet season (May−October) and 20% during dry months (November−April; Cao and Zhang, 1997); the average annual temperature is 22 °C. The plots generally have laterite soil developed from siliceous rocks. The elevation of the 15 plots ranged from 709 to 869 m. The location of the plots was chosen to enable a sufficient number of individuals of *Pa. chinensis* and *Pi. kerrii* (generally >400, approximately 10% of the total abundance), and the distance between plots ranged from 100 to 2000 m.

Two focal species were analyzed genetically. *Pa. chinensis* (Dipterocarpaceae) is a canopy dominant tree species in the Xishuangbanna tropical seasonal rainforest that generally occupies the canopy's top layer. In favourable sites, *Pa. chinensis* can reach a DBH of 1.5 m and a height of more than 80 m (Xu and Yu, 1982; Zhu, 1992). In the Xishuangbanna tropical seasonal rainforest, up to 200 tree species (with DBH > 1 cm) can co-exist within a 1-ha plot. The biomass of *Pa. chinensis* is by far the largest, averaging 27.7% (±8.0%) of the total aboveground biomass (Song et al., 2015); this species also has the highest coverage in the community (Xu, 1995). As the functional proportions of dominant species are usually close to their structural proportions (i.e., mass ratio hypothesis, Grime, 1998), *Pa. chinensis* has an important ecological role at all community levels. *Pa. chinensis* is insect-pollinated, its seeds are mainly dispersed by gravity, and seedlings require light for establishment (Ying and Shuai, 1990). *Pi. kerrii* (Icacinaceae) is a small tree that is usually one of the most abundant species in the forest (Lan et al., 2008). The fruit of *Pi. kerrii* is a drupe with a dry pericarp, suggesting that it is dispersed by frugivorous animals (Vander Wall, 2001; Li and Zhang, 2007). The pericarp quickly dehisces or rots after the fruit falls to the ground, and small rodents strip the pulp away and discard it while eating or hoarding the seeds.

2.2. Soil nutrients and species diversity

For each of the eight plots outside of the FDP, latitude, longitude and elevation were measured using a hand-held GPS unit. A 1-ha (100 × 100 m) plot was divided into 25 subplots (20 × 20 m) and soil samples were collected from depths of 1−10 cm at the four corners of each subplot. Nitrogen and phosphorus have been shown to be the most important limiting nutrients in the tropical forest ecosystem (Wright, 2019); therefore, total nitrogen (TN) and extractable phosphorus (EP) were determined for each subplot, with the values of all 25 subplots averaged to represent a plot. Plots within the FDP were also divided into 25 subplots, in which the content of TN and EP were obtained for each subplot using Kriging interpolation based on the data set from a 30 m × 30 m area across all the FDP and averaged. For all plots, the micro-Kjeldahl method was used to evaluate TN; extractable phosphorus (EP) was extracted with a solution containing 0.03 mol/L NH_4F and 0.025 mol/L HCl and estimated colourimetrically (Hu et al., 2012).

For the species diversity survey, five 20 m × 20 m subplots were randomly chosen within each 1-ha plot, and the species and total abundance of all trees with a diameter at breast height (DBH) > 1 cm were recorded to represent the species diversity of the 1-ha plot. The species diversity indices included species richness (SD), defined as the number of tree species in a plot, and Shannon's index = SI, which was calculated as $-\Sigma f_i \ln f_i$, where f_i is the proportion of stems in a plot belonging to the *i*th species. As the total tree abundance varies between plots, the SD of each plot was rarefied to the smallest sample size (i.e., 538) using the community ecology R package "vegan" (Oksanen et al., 2015; R Core Team, 2015). Data from the seven plots within the FDP were provided by the Xishuangbanna Field Station for Tropical Rain Forest Ecosystem Studies of the Chinese Academy of Sciences. We

collected data on both SD and soil nutrients for the other eight plots outside of the FDP following the same protocol.

2.3. Genotyping and genetic diversity analysis

In each plot, leaf samples were collected from six trees each of *Pa. chinensis* and *Pi. kerrii*. The trees selected for genotyping were random but we also considered trees with different DBH, and with distribution across the entire 1-ha plot to obtain representative genetic information in each plot. The total genomic DNA was extracted following a modified cetyltrimethylammonium bromide (CTAB) method and the samples were genotyped using SLAF-seq methods as described in Sun et al. (2013). Briefly, SLAF libraries were constructed after the genomic DNA was digested with *EcoR*I and *Mse*I, resulting in 500−550 bp library fragments. The libraries were then sequenced using the Illumina High-seq 2000 sequencing platform (Illumina, Inc; San Diego, CA, U.S.) at Biomarker Technologies Corporation in Beijing (http://Biomarker.com.cn/). In total, we generated an average of 289,036 clean pair-end reads for the *Pa. chinensis* samples and 4,264,505 pair-end reads for the *Pi. kerrii* samples. Thus, the genetic diversity of the six trees by SLAF-seq should sufficiently represent the population genetic diversity of each plot. As Nazareno et al. (2017) demonstrated empirically, a very small number of samples can accurately estimate population genetic diversity and structure with a large number of SNPs.

Clean SLAF reads were used for *de novo* SNP discovery. We employed a *de novo* approach to build a catalogue of loci and detect SNPs using STACKS (Catchen et al., 2013), as there are no reference genomes available for either species. We used the "denovo_map.pl" pipeline and the *population* program to assemble programs in STACKS, and the parameter settings followed the STACKS manual (Catchen et al., 2013). SNPs were detected by their maximum likelihood among all individuals genotyped at a locus (Catchen et al., 2013). We discovered 13,153 polymorphic SNP loci in *Pa. chinensis* and 1461 loci in *Pi. kerrii*.

To estimate population GD_a, we first used F_{ST}-outlier analysis to infer putative SNP loci under directional selection in both *Pa. chinensis* and *Pi. kerrii*. Loci under local directional selection should show large differentiation among populations and reveal an overall signal of adaptive variation related to the local environment, including soil nutrient availability, etc. The F_{ST}-outlier detection followed a hierarchy modelling and coalescent simulation approach and was implemented in Arlequin v.3.5 (Excoffier and Lischer, 2010). Briefly, the coalescent simulations generate a null distribution and confidence intervals, and the observed locus-specific F_{ST} values are then evaluated as potential F_{ST} outliers in the context of the globally observed F_{ST} value. With a stringency of $P < 0.01$, SNPs under directional selection were selected out. In total, 68 SNPs from *Pa. chinensis* and 72 SNPs from *Pi. kerrii* were selected out as putatively being under directional selection. We therefore categorized the total SNPs of each species into adaptive and neutral SNPs. GD_a, GD_n, and GD_t were then calculated as gene diversity (1- f_i^2 where f_i is the frequency of the *i*th allele for the population) for each population of both species using Genepop v.4.0 (Raymond and Rousset, 1995). As our study population was defined arbitrarily, we evaluated population genetic differentiation using Fisher's exact test in Genepop.

2.4. Data preparation and evaluation

The Shapiro−Wilk test was first implemented to evaluate the normal distribution of all variables (soil nutrients, species diversity and genetic diversity); the variables that did not meet normal distribution were log-transformed to promote normality. Analysis of variance (ANOVA) was carried to evaluate the difference of soil

variables among the plots. Pearson correlations were used to explore the relations among the variables investigated in this study. Since our study was carried out at a relatively small scale, spatial autocorrelation of the variables among the plots might be present. Thus, to evaluate spatial effects, we calculated Moran's I of each variable, with 9999 permutations to obtain the significance. We used Spatial Lag Model (SLM) to eliminate the spatial effects on variables with significant spatial autocorrelation. Shapiro–Wilk tests and ANOVA analysis were implemented using SPSS 16.0 (SPSS Inc., Chicago, IL). Spatial analysis was implemented using Geoda v.1.12 (Anselin et al., 2006).

2.5. Structural equation modelling

To explore the mechanisms underlying the correlation between GD and SD_r and how soil nutrient availability influences both levels of diversity and their interaction, we constructed four models to test four hypotheses (Fig. 2). As soil phosphorus availability was unrelated to GD in the correlation analysis (Table 2), only soil TN was included in the model. Model 1 (parallel effect) hypothesizes that soil nitrogen availability determines the level of species richness and the GD of canopy dominant species *Pa. chinensis* and understory-abundant species *Pi. kerrii*, there is no direct interaction between SD_r and the GD of both species (Vellend and Geber, 2005). Model 2 (species community effect) hypothesizes that soil nitrogen availability determines species richness while species richness determines the GD of both species (Xu et al., 2016). Model 3 (dominant species effect) hypothesizes that soil nitrogen availability determines the GD of *Pa. chinensis*, which further influences species richness (Hughes et al., 2008). Finally, model 4 (hierarchical effect) tests the hypothesis that soil nitrogen availability influences both SD_r and GD of dominant species, with both influencing the GD of other species in the community (Vellend and Geber, 2005). A best-fit model was selected for an insignificant Chi-square result of
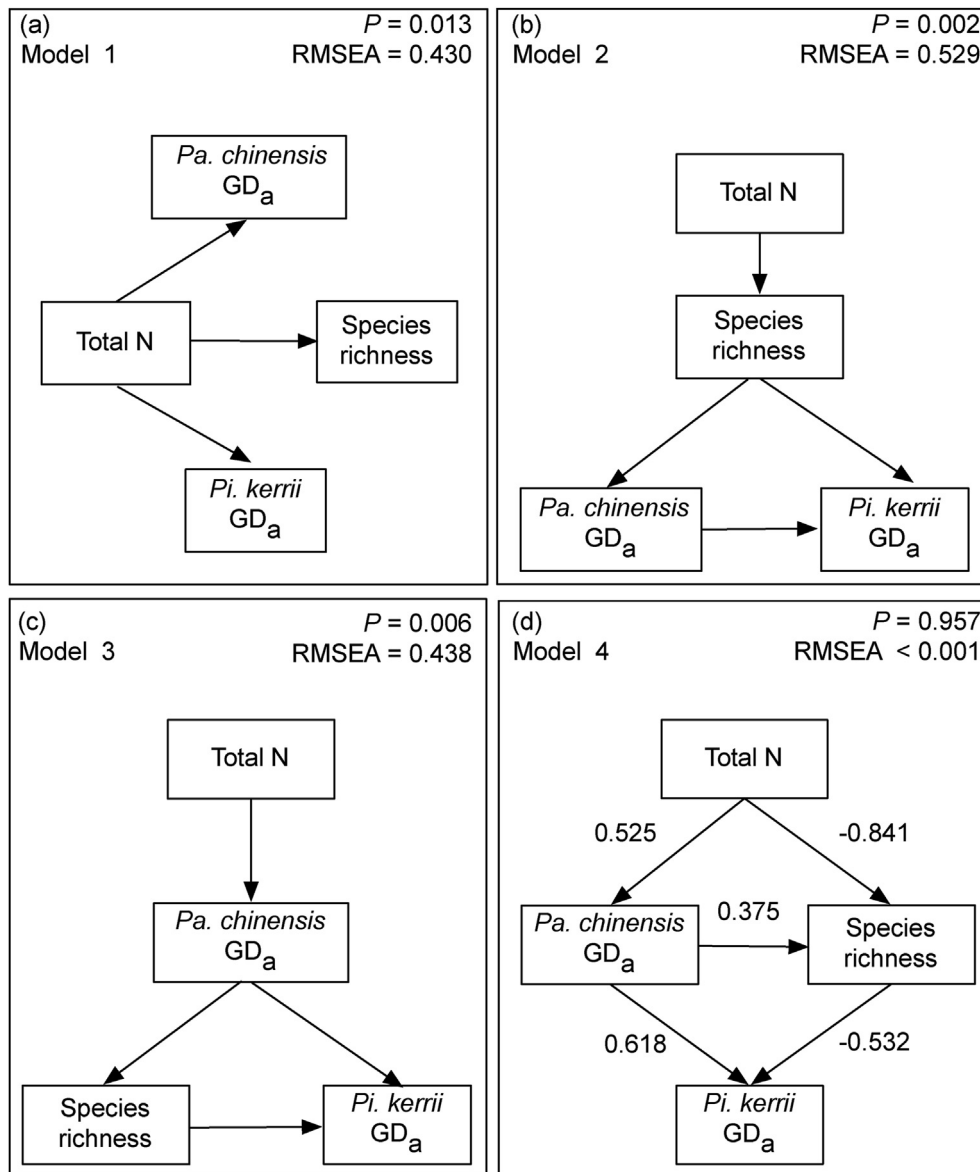
Fig. 2. Structural equation modelling of four alternative models exploring the mechanism underlying the connections between species diversity and genetic diversity. Model 4 was determined to be the best fit for the data with Chi-square $P = 0.957$ and RMSEA < 0.001. The numbers in Model 4 are standardized coefficients of direct effect. GD_a is adaptive genetic diversity and species richness was rarefied to the smallest sampling size across the plots.

Table 1
Species diversity, genetic diversity of *Parashorea chinensis* and *Pittosporopsis kerrii*, and soil nutrient levels in the plots.

Location	GD$_a$ (P.c)	GD$_a$ (P.k)	GD$_n$ (P.c)	GD$_n$ (P.k)	GD$_t$ (P.c)	GD$_t$ (P.k)	SD$_r$	SI	Ab. (P.c)	Ab. (P.k)	Ab.	TN (g/kg)	EP (mg/kg)
1	0.087	0.119	0.249	0.103	0.248	0.104	87	3.138	132	356	1059	1.77	3.32
2	0.102	0.178	0.261	0.102	0.260	0.104	89	3.567	87	46	736	1.90	6.27
3	0.093	0.124	0.259	0.081	0.258	0.082	96	3.284	162	278	1033	1.83	4.28
4	0.075	0.123	0.246	0.083	0.246	0.084	95	3.859	81	141	938	1.92	8.14
5	0.072	0.114	0.257	0.098	0.256	0.099	100	3.649	149	148	970	1.80	5.44
6	0.060	0.124	0.256	0.091	0.256	0.093	86	3.044	234	332	1132	1.69	4.17
7	0.093	0.135	0.258	0.077	0.258	0.078	109	3.957	39	102	794	1.74	3.22
8	0.104	0.194	0.253	0.080	0.253	0.082	65	3.072	117	158	654	2.34	13.21
9	0.094	0.156	0.254	0.083	0.254	0.084	85	3.247	108	172	709	1.99	12.76
10	0.138	–	0.253	–	0.252	–	83	3.258	144	231	922	2.26	8.27
11	0.078	0.163	0.258	0.096	0.258	0.097	69	2.744	131	232	707	1.98	7.08
12	0.081	0.159	0.259	0.107	0.259	0.109	76	3.182	85	234	799	1.88	12.29
13	0.067	0.130	0.257	0.101	0.256	0.102	78	3.131	63	152	538	2.16	15.76
14	0.086	0.202	0.256	0.110	0.255	0.112	67	2.779	123	174	622	2.02	8.00
15	0.091	0.135	0.257	0.091	0.257	0.090	71	2.775	174	271	858	2.04	6.69

Note: *P.c: Parashorea chinensis*; *P.k: Pittosporopsis kerrii*; GD$_a$: adaptive genetic diversity; GD$_n$, neutral genetic diversity; GD$_t$, total genetic diversity; SD$_r$: rarefied species richness; *SI*: Shannon's index; Ab.: abundance; TN: total nitrogen; EP: extractable phosphorus; −: data not available due to low-quality samples.

Table 2
Pairwise Pearson correlations between species diversity, genetic diversity of *Parashorea chinensis* and *Pittosporopsis kerrii*, and soil nutrient levels in the plots.

	GD$_a$ (P.c)	GD$_a$ (P.k)	GD$_n$ (P.c)	GD$_n$ (P.k)	GD$_t$ (P.c)	GD$_t$ (P.k)	SI	SD$_r$	Ab. (P.c)	Ab. (P.k)	Ab.	TN
GD$_a$ (P.k)	**0.524***											
GD$_n$ (P.c)	−0.102	0.219										
GD$_n$ (P.k)	−0.274	0.246	0.209									
GD$_t$ (P.c)	−0.080	0.231	**0.998****	0.208								
GD$_t$ (P.k)	−0.289	0.221	0.205	**0.999****	0.204							
SI	0.050	−0.380	−0.165	−0.387	−0.167	−0.379						
SD$_r$	−0.067	**−0.647***	−0.037	−0.384	−0.043	−0.369	**0.869****					
Ab. (P.c)	−0.099	−0.214	0.029	0.003	0.024	0.007	−0.497	−0.188				
Ab. (P.k)	−0.139	−0.379	−0.188	0.087	−0.193	0.098	**−0.549***	−0.211	**0.706****			
Ab.	−0.081	**−0.690****	−0.258	−0.192	−0.265	−0.175	0.222	0.506	**0.615***	0.607*		
TN	**0.525***	**0.580***	−0.180	−0.041	−0.166	−0.056	−0.357	**−0.644****	−0.155	−0.218	**−0.600****	
EP	0.022	0.394	−0.036	0.111	−0.033	0.102	−0.233	−0.537*	−0.384	−0.292	**−0.711****	**0.703****

Note: *P.c: Parashorea chinensis*; *P.k: Pittosporopsis kerrii*; GD$_a$: adaptive genetic diversity; GD$_n$, neutral genetic diversity; GD$_t$, total genetic diversity; SD$_r$: rarefied species richness; SI: Shannon's index; Ab.: abundance; TN: total nitrogen; EP: extractable phosphorus. Data marked in bold indicate significant correlation. *$P < 0.05$; **$P < 0.01$.

$P > 0.05$ and a root mean square error of approximation (RMSEA) below 0.08 (Hooper et al., 2008). Pearson correlation analysis was implemented using the SPSS 16.0 statistical software package (SPSS Inc., Chicago, IL). SEM analysis was undertaken in SPSS AMOS (IBM Ltd, Chicago). The significance was determined at $P < 0.05$.

3. Results

3.1. Soil properties and community characteristics

Across all 15 plots soil properties were highly variable (Table 1). The EP content varied five-fold and ranged from 3.22 to 15.76 mg/kg, while TN ranged from 1.69 to 2.34 g/kg. A total of 305 tree species with DBH >1 cm were recorded within the fifteen 1-ha plots (Table S1). ANOVA analysis revealed a significant difference in TN and EP across the plots (TN: F = 19.024, $P < 0.001$; EP: F = 18.123, $P < 0.001$).

An average of 100 tree species was recorded in each plot (Table S1), while the rarefied tree species richness ranged from 65 to 109. The total tree abundance among the plots varied from 680 to 1186, with an average of 902 individuals per plot (Table 1).

3.2. Genetic diversity of focal species

The adaptive diversity of *Pa. chinensis* across the 15 plots varied from 0.060 to 0.138, and that of *Pi. kerrii* varied from 0.114 to 0.202. Neither neutral nor total genetic diversity of the two focal species varied substantially across the plots (Table 1). Significant genetic differentiation was revealed in selective SNP loci among the plots using Fisher's exact test (*Pa. chinensis*: F$_{ST}$ = 0.3202, X^2 = Infinity, df = 148, $P < 0.001$; *Pi. kerrii*: F$_{ST}$ = 0.1627, X^2 = Infinity, df = 178, $P < 0.001$).

3.3. Effects of soil properties on species and genetic diversity

The Shapiro−Wilk test revealed that GD$_n$ and GD$_t$ of *Pa. chinensis* did not have a normal distribution and were therefore log-transformed for subsequent analysis. The results of Pearson correlation analysis between the variables measured in this study are shown in Table 2. A negative SGDC was revealed between SD$_r$ and the GD$_a$ of *Pi. kerrii* (r = −0.647, $P = 0.012$), and correlation between SD$_r$ and the GD$_a$ of *Pa. chinensis* was absent (r = −0.067, $P = 0.814$). Soil properties (TN) had opposing effects on GD$_a$ and SD$_r$. A greater concentration of soil nitrogen promoted the GD$_a$ of both *Pa. chinensis* (r = 0.525, $P = 0.044$) and *Pi. kerrii* (r = 0.580, $P = 0.030$), while increased nitrogen availability reduced SD$_r$ (r = −0.644, $P = 0.010$). Furthermore, positive correlations were revealed between the GD$_a$ of *Pa. chinensis* and *Pi. kerrii* (r = 0.524, $P = 0.050$). Spatial analysis revealed significant spatial autocorrelation in TN, EP and SD$_r$ across the plots, but absent in genetic diversity measures (Table S2); SLM analysis revealed that the effects of TN on SD$_r$ is significant even when the spatial effects were controlled (Table S2).

3.4. Structural equation models

SEM models 1−3 were not supported by the data (Chi-square $P < 0.05$ and RMSEA > 0.08) (Fig. 2a−c). Instead, the hierarchical

correlation model (model 4) was best supported by the data with Chi-square $P = 0.957$ and RMSEA < 0.001 (Fig. 2d). The hierarchical correlation model indicated that soil TN determined the level of GD_a in *Pa. chinensis* with a direct positive effect of 0.525, while soil TN was causally correlated with species richness (SD_r) with a direct negative effect of −0.841. Meanwhile, the increased GD_a of *Pa. chinensis* promoted species richness with a direct effect of 0.375. Both the GD_a in *Pa. chinensis* and the species richness of the community directly influenced the GD_a of *Pi. kerrii* but did so in opposing ways. A greater level of GD_a in *Pa. chinensis* promoted GD_a in *Pi. kerrii*, which was reduced by increased species richness. All the SEM models were not supported by the data when GD_a was substituted by either GD_n or GD_t of both focal species (Chi-square $P < 0.05$ and RMSEA > 0.08).

4. Discussion

4.1. Species-genetic diversity correlations

Our study showed that the adaptive GD of the understory-dominant species, *Pi. kerrii*, and SD_r (rarefied tree species richness) are negatively correlated, but that there is no significant correlation between the adaptive GD of the canopy-dominant species *Pa. chinensis*, the largest biomass in the community (Table 2). However, SEM analysis revealed a complex of hierarchical correlations. The GD_a of *Pa. chinensis* and SD_r are oppositely affected by soil nitrogen availability, whereas increasing the GD_a of *Pa. chinensis* promotes species diversity within the community. The GD_a of *Pa. chinensis* positively influences the GD_a of *Pi. kerrii*, which is negatively affected by SD_r (Fig. 2). Together with previously reported SGDCs for another understory-abundant tree species, *Beilschmiedia roxburghiana* (Lauraceae), in the same ecosystem (Xu et al., 2016), it seems that the SGDC is common in this speciose seasonal rainforest. However, the pattern of correlation (either positive or negative) depends on the ecological role of the focal species in the community. The GD_n or GD_t of both focal species were not correlated with soil or community properties (Table 2). When GD_n or GD_t of both focal species was used for the analysis, the SEM models were not supported (Chi-square $P < 0.05$ and RMSEA > 0.08), indicating that the observed SGDC pattern was driven by selective rather than neutral processes (Morrison-Whittle and Goddard, 2015).

4.2. Soil nitrogen availability had opposing effects on species and genetic diversity

Our SEM analysis suggested that the availability of soil nitrogen had a significant role in structuring SD and the adaptive GD of the canopy dominant species, *Pa. chinensis*, in Xishuangbanna tropical seasonal rainforest; the increased availability of soil nitrogen in this ecosystem reduced plant species richness and promoted the adaptive GD of *Pa. chinensis*. Previously, Silvertown et al. (2009) also reported opposing responses of GD and SD to elevated resource availability. Soil nitrogen has traditionally been considered the primary nutrient limiting plant growth in terrestrial ecosystems, particularly in temperate forests that usually have high nitrogen limitation (Hedin et al., 2003), where an increase in soil nitrogen promotes the growth of tree species. In Xishuangbanna tropical seasonal rainforest, Song et al. (2015) recorded greater total tree biomass in plots with a higher level of nitrogen availability. However, the increased growth of individuals could directly intensify inter-species competition for resources such as light, water, and other limiting nutrients, such as phosphorus, or space, at the very least. With intensified interspecific competition, the growth and establishment of some species could be reduced because species

with better nutrient acquisition capacity and faster growth would gain a competitive advantage at the expense of those with less efficient nutrient acquisition (Li et al., 2015). Meanwhile, in environments in which competition is high, species with a higher photosynthetic capacity could more flexibly respond to the spatial heterogeneity of the environment and gain an advantage over slow-growing plants (Westoby et al., 2002; Li et al., 2015). Therefore, increased nitrogen availability may have reduced species richness by intensifying competition.

Unlike its negative effect on species richness, the increased availability of soil nitrogen led to an increase in the GD_a of the dominant species, *Pa. chinensis*, possibly because the increased nitrogen promoted its growth (Song et al., 2015). This improved nutrient condition may weaken purifying selection, leading to the accumulation of more mutations and greater GD (Snell-Rood et al., 2010). Greater availability of a limiting nutrient may also relax important selective pressures operating in habitats with a lower availability of the nutrient, allowing the evolution and maintenance of more genotypes (Snell-Rood et al., 2010). In other words, increased nutrient availability might promote the survival of more genotypes that would otherwise be less competitive in habitats with lower nutrient levels.

4.3. Species diversity negatively affected the GD_a of Pittosporopsis kerrii

Our SEM analysis revealed SD negatively affects the adaptive genetic diversity of understory-abundant *Pi. kerrii*, which is analogous to our previous study on another understory-abundant species *Beilschmiedia roxburghiana* (Xu et al., 2016). The negative SGDCs may be explained by the "niche variation" hypothesis (Van Valen, 1965) — an increase in species diversity negatively affects the genetic diversity of species within a community for the reduced average niche breadth (Vellend and Geber, 2005). Meanwhile, in an ecosystem with a fixed number of individuals, SD may reduce GD by affecting population size (Vellend and Geber, 2005). As the number of species increases, the average population sizes of certain species would decrease through competitive exclusion, reducing the GD of the focal species in both neutral and non-neutral traits through genetic drift. However, in this study SD was correlated with adaptive genetic diversity rather than with neutral genetic diversity. The "niche variation" hypothesis seems a more likely explanation for the negative SGDC in the case of *Pi. kerrii*.

4.4. Increased GD_a in Parashorea chinensis promoted species co-existence

We also found that the increased adaptive genetic variation in the canopy-dominant species, *Pa. chinensis*, promotes the SD of co-existing species. This finding is consistent with the mass ratio hypothesis, which states that the effect of a species on an ecosystem is proportional to its relative abundance (in our case, biomass) in a given community (Grime, 1998). The genetic variation in a dominant species, particularly the adaptive genetic variation we measured, can affect species interactions, which includes many other subordinate species co-existing in the community (Crutsinger, 2016). The diverse genotypes of the dominant species may result in spatially heterogeneous species interactions, which can promote species co-existence by favouring certain plant species in different micro-environments (Vellend and Geber, 2005; Ehlers et al., 2016). Increased intraspecific genetic variation allows for evolutionary adaptation. If it benefits a competitively inferior species, it could promote species co-existence due to the local existence of specific genotypes. Increased soil nutrients (nitrogen) may also shift the balance between species facilitation and competition,

thereby changing patterns of community structure (Boyden et al., 2005). Improved soil nutrient conditions lead to stronger inter-specific competition as a result of higher productivity and greater demand for resources (Grime, 1979), thus reducing SD. However, facilitation and competition may co-occur in time and space (Walker and Chapin, 1987; Choler et al., 2001; Callaway et al., 2002), producing dynamic relationships between individuals and species. The increased genotypic diversity of the dominant species may enhance the supply of resources and modify the environment for other species (Callaway et al., 2002), thereby promoting species co-existence.

4.5. Increased GD_a in Parashorea chinensis promoted GD_a of Pittosporopsis kerrii

Increased adaptive genetic variation in the canopy-dominant species, *Pa. chinensis*, promoted the GD_a of the co-existing and understory-dominant species, *Pi. kerrii*, in Xishuangbanna tropical seasonal rainforest. There is evidence that the response of a plant to a neighbour may depend on the co-evolutionary history of the interacting genotypes (Thorpe et al., 2011). For example, some plants can recognize the genetic identity of neighbouring plants if they have a common history of co-existence (Ehlers et al., 2016). Thus, the existence of *Pa. chinensis* may have enhanced the supply of a limiting resource for *Pi. kerrii*. One hypothesis worth testing is that arbuscular mycorrhizae connections between the two tree species provide additional nutrients (e.g., phosphorus or carbon) to both in plots with higher nitrogen availability. It is increasingly recognized that arbuscular mycorrhizal fungi mediate interactions and co-existence in mixed plant species systems through the inter-species transfer of carbon, phosphorus, and nitrogen (Hart et al., 2003). Mycorrhizae are an important ecosystem component, promoting the absorption of nutrients and plant growth and improving the stress resistance and rhizosphere environment of plants. *Pa. chinensis* is believed to be associated with arbuscular mycorrhizae fungi, particularly in its seedling and juvenile stages, as the formation of mycorrhizal symbiosis is the key to its successful regeneration (Ingleby et al., 1998; Shi et al., 2003). It is likely that the survival of more *Pa. chinensis* genotypes may have facilitated the survival of more *Pi. kerrii* genotypes through genotype–genotype interactions (He and Lamont, 2014; Ehlers et al., 2016).

5. Concluding remarks

We have shown that a shared environmental factor (soil nitrogen) created opposing responses in SD and GD (of dominant canopy species). Further, SEM analysis revealed that the two levels of biodiversity are causally connected, as increased adaptive GD leads to increased SD by promoting co-existence. Our results revealed the significant ecological role of dominant species in competitive interactions and the regulation of community structure, and they highlight the important ecological connection between GD and SD. However, the pattern of the interactions depends on the identity of the species. Finally, our study demonstrated both the necessity of including multiple species and a gradient of limiting environmental factors in research exploring SGDCs in a system as well as the power of SEM to disentangle complex hierarchical correlations in ecosystems.

Data accessibility

Data are available as online supplementary material.

Author contributions

QML and THH designed the study, CNC and QML collected genetic data, CNC and THH analyzed performed genotyping and analyzed genetic diversity, and WMX and THH performed the correlation analysis. MC, LQS and LXL provided the plot census data, QML and TTH wrote the manuscript, and QML, THH, CNC and WMX contributed to revisions.

Declaration of competing interest

The authors declare that there are no conflicts of interest.

Acknowledgements

This research was supported by the Strategic Priority Research Program of Chinese Academy of Sciences, Grant No. XDB31000000, the National Natural Science Foundation of China (No. 31370267). The authors would like to thank the Xishuangbanna Station for Tropical Rain Forest Ecosystem Studies for assisting with the data collection and Wen-Fu Zhang for taxonomically identifying the tree species outside the 20-ha FDP.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.pld.2021.11.002.

References

Anselin, L., Syabri, I., Kho, Y., 2006. GeoDa, an introduction to spatial data analysis. Geogr. Anal. 38, 5–22. https://doi.org/10.1111/j.0016-7363.2005.00671.x.

Antonovics, J., 2003. Toward community genomics? Ecology 84, 598–601. https://doi.org/10.1890/0012-9658.

Barbour, M.A., Rodriguez-Cabal, M.A., Wu, E.T., et al., 2015. Multiple plant traits shape the genetic basis of herbivore community assembly. Funct. Ecol. 29, 1361–1370. https://doi.org/10.1111/1365-2435.12409.

Boyden, S., Binkley, D., Senock, R., 2005. Competition and facilitation between Eucalyptus and nitrogen-fixing *Falcataria* in relation to soil fertility. Ecology 86, 992–1001. https://doi.org/10.1890/04-0430.

Callaway, R.M., Brooker, R.W., Choler, P., et al., 2002. Positive interactions among alpine plants increase with stress. Nature 417, 844–848. https://doi.org/10.1038/nature00812.

Cao, M., Zhang, J.H., 1997. Tree species diversity of tropical forest vegetation in Xishuangbanna, SW China. Biodivers. Conserv. 6, 995–1006. https://doi.org/10.1023/A:1018367630923.

Catchen, J., Hohenlohe, P., Bassham, S., et al., 2013. Stacks: an analysis tool set for population genomics. Mol. Ecol. 22, 3124–3140. https://doi.org/10.1111/mec.12354.

Choler, P., Michalet, R., Callaway, R.M., 2001. Competition and facilitation on gradients in alpine communities. Ecology 82, 3295–3308. https://doi.org/10.1890/0012-9658.

Cleary, D.F.R., Fauvelot, C., Genner, M.J., et al., 2006. Parallel responses of species and genetic diversity to El Niño Southern Oscillation-induced environmental destruction. Ecol. Lett. 9, 304–310. https://doi.org/10.1111/j.1461-0248.2005.00876.x.

Crutsinger, G.M., 2016. A community genetics perspective: opportunities for the coming decade. New Phytol. 210, 65–70. https://doi.org/10.1111/nph.13537.

Ehlers, B.K., Damgaard, C.F., Laroche, F., 2016. Intraspecific genetic variation and species coexistence in plant communities. Biol. Lett. 12, 20150853. https://doi.org/10.1098/rsbl.2015.0853.

Excoffier, L., Lischer, H.E.L., 2010. Arlequin suite ver 3.5: a new series of programs to perform population genetics analyses under Linux and Windows. Mol. Ecol. Resour. 10, 564–567. https://doi.org/10.1111/j.1755-0998.2010.02847.x.

Grace, J.B., Anderson, M.T., Olff, H., et al., 2010. On the specification of structural equation models for ecological systems. Ecol. Monogr. 80, 67–87. https://doi.org/10.1890/09-0464.1.

Grime, J.P., 1979. Plant strategies and vegetation processes. John Wiley & Sons, Chichester.

Grime, J.P., 1998. Benefits of plant diversity to ecosystems: immediate, filter and founder effects. J. Ecol. 86, 902–906. https://doi.org/10.1046/j.1365-2745.1998.00306.x.

Hart, M.M., Reader, R.J., Klironomos, J.N., 2003. Plant coexistence mediated by arbuscular mycorrhizal fungi. Trends Ecol. Evol. 18, 418–423. https://doi.org/10.1016/S0169-5347(03)00127-7.

He, T., Lamont, B.B., 2014. Genetic and ecological consequences of interactions between three banksias in Mediterranean-type shrubland. J. Veg. Sci. 25, 617–626. https://doi.org/10.1111/jvs.12113.

277

He, T., Lamont, B.B., Krauss, S.L., et al., 2008. Covariation between intraspecific genetic diversity and species diversity within a plant functional group. J. Ecol. 96, 956—961. https://doi.org/10.1111/j.1365-2745.2008.01402.x.

Hedin, L.O., Vitousek, P.M., Matson, P.A., 2003. Nutrient losses over four million years of tropical forest development. Ecology 84, 2231—2255. https://doi.org/10.1890/02-4066.

Hooper, D., Coughlan, J., Mullen, M., 2008. Structural equation modelling: guidelines for determining model fit. Electron. J. Bus. Res. Meth. 6, 53—60.

Hu, Y.H., Sha, L.Q., Blanchet, F.G., et al., 2012. Dominant species and dispersal limitation regulate tree species distributions in a 20-ha plot in Xishuangbanna, southwest China. Oikos 121, 952—960. https://doi.org/10.1111/j.1600-0706.2011.19831.x.

Hughes, A.R., Inouye, B.D., Johnson, M.T., et al., 2008. Ecological consequences of genetic diversity. Ecol. Lett. 11, 609—623. https://doi.org/10.1111/j.1461-0248.2008.01179.x.

Ingleby, K., Munro, R.C., Noor, M., et al., 1998. Ectomycorrhizal populations and growth of *Shorea parvfolia* (Dipterocarpaceae) seedlings regenerating under three different forest canopies following logging. For. Ecol. Manag. 111, 171—1791. https://doi.org/10.1016/S0378-1127(98)00324-7.

Johnson, M.T., Agrawal, A.A., 2005. Plant genotype and environment interact to shape a diverse arthropod community on evening primrose (*Oenothera biennis*). Ecology 86, 874—885. https://doi.org/10.1890/04-1068.

Johnson, M.T.J., Stinchcombe, J.R., 2007. An emerging synthesis between community ecology and evolutionary biology. Trends Ecol. Evol. 22, 250—257. https://doi.org/10.1016/j.tree.2007.01.014.

Kahilainen, A., Puurtinen, M., Kotiaho, J.S., 2014. Conservation implications of species—genetic diversity correlations. Glob. Ecol. Conserv. 2, 315—323. https://doi.org/10.1016/j.gecco.2014.10.013.

Karlin, A.A., Guttman, S.I., Rathbun, S.L., 1984. Spatial autocorrelation analysis of heterozygosity and geographic distribution in populations of *Desmognathus fuscus* (Amphibia, Plethodontidae). Copeia 2, 343—356. https://doi.org/10.2307/1445190.

Lamy, T., Jarne, P., Laroche, F., et al., 2013. Variation in habitat connectivity generates positive correlations between species and genetic diversity in a metacommunity. Mol. Ecol. 22, 4445—4456. https://doi.org/10.1111/mec.12399.

Lamy, T., Laroche, F., David, P., et al., 2017. The contribution of species—genetic diversity correlations to the understanding of community assembly rules. Oikos 126, 759—771. https://doi.org/10.1111/oik.03997.

Lan, G.Y., Hu, Y.H., Cao, M., et al., 2008. Establishment of Xishuangbanna tropical forest dynamics plot: species compositions and spatial distribution patters. Chin. J. Plant Ecol. 32, 287—298. https://doi.org/10.3773/j.issn.1005-264x.

Lankau, R.A., Strauss, S.Y., 2007. Mutual feedbacks maintain both genetic and species diversity in a plant community. Science 317, 1561—1563. https://doi.org/10.1126/science.1147455.

Li, X., Rennenberg, H., Simon, J., 2015. Competition for nitrogen between *Fagus sylvatica* and *Acer pseudoplatanus* seedlings depends on soil nitrogen availability. Front. Plant Sci. 6, 302. https://doi.org/10.3389/fpls.2015.00302.

Li, H.J., Zhang, Z.B., 2007. Effects of mast seeding and rodent abundance on seed predation and dispersal by rodents in *Prunus armeniaca* (Rosaceae). For. Ecol. Manag. 242, 511—517. https://doi.org/10.1016/j.foreco.2007.01.063.

Mitchell, M.W., 1992. Complexity: the Emerging Science at the Edge of Order and Chaos, vol. 384. Simon & Schuster, New York, United States.

Morrison-Whittle, P., Goddard, M., 2015. Quantifying the relative roles of selective and neutral processes in defining eukaryotic microbial communities. ISME J. 9, 2003—2011. 10.1038/ismej.2015.18.

Nazareno, A.G., Bemmels, J.B., Dick, C.W., et al., 2017. Minimum sample sizes for population genomics: an empirical study from an Amazonian plant species. Mol. Ecol. Resour. 17, 1136—1147. 10.1111/1755-0998.12654.

Oksanen, J., Blanchet, G., Kindt, R., et al., 2015. vegan: community ecology package. R package version 2.3-0. http://CRAN.R-project.org/package=vegan.

Paine, R.T., 1969. A note on trophic complexity and community stability. Am. Nat. 103, 91—93.

Papadopoulou, A., Anastasiou, I., Spagopoulou, F., et al., 2011. Testing the species-genetic diversity correlation in the Aegean archipelago: toward a haplotype-based macroecology? Am. Nat. 178, 241—255. https://doi.org/10.1086/660828.

R Core Team, 2015. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna. URL. https://www.R-project.org/.

Raymond, M., Rousset, F., 1995. GENEPOP (version 1.2): population genetics software for exact tests and ecumenicism. J. Hered. 86, 248—249. https://doi.org/10.1093/oxfordjournals.jhered.a111573.

Shi, Z.Y., Chen, Y.L., Liu, R.J., et al., 2003. Preliminary research on arbuscular mycorrhizal fungi of Dipterocarpaceae in Xishuangbanna, Southern Yunnan. Chin. J. Plant Ecol. 27, 360—365. https://doi.org/10.17521/cjpe.2003.0053.

Silvertown, J., Biss, P.M., Freeland, J., 2009. Community genetics: resource addition has opposing effects on genetic and species diversity in a 150-year experiment. Ecol. Lett. 12, 165—170. https://doi.org/10.1111/j.1461-0248.2008.01273.x.

Snell-Rood, E.C., Van Dyken, J.D., Cruickshank, T., et al., 2010. Toward a population genetic framework of developmental evolution: the costs, limits, and consequences of phenotypic plasticity. Bioessays 32, 71—81. https://doi.org/10.1002/bies.200900132.

Song, C.Y., Xu, W.M., Li, Q.M., 2015. Effects of soil nitrogen content on tree diversity in Xishuangbanna tropical seasonal rain forest. Plant Divers. Resour. 37, 99—104. https://doi.org/10.7677/ynzwyj201514066.

Sun, X., Liu, D., Zhang, X., et al., 2013. SLAF-seq: an efficient method of large-scale de novo SNP discovery and genotyping using high-throughput sequencing. PLoS One 8, e58700. https://doi.org/10.1371/journal.pone.0058700.

Thorpe, A.S., Aschehoug, E.T., Atwater, D.Z., et al., 2011. Interaction among plants and evolution. J. Ecol. 99, 729—740. https://doi.org/10.1111/j.1365-2745.2011.01802.x.

Van Valen, L., 1965. Morphological variation and width of ecological niche. Am. Nat. 99, 377—390. https://doi.org/10.1086/282379.

Vander Wall, S.B., 2001. The evolutionary ecology of nut dispersal. Bot. Rev. 67, 74—117. https://doi.org/10.1007/BF02857850.

Vellend, M., Geber, M.A., 2005. Connections between species diversity and genetic diversity. Ecol. Lett. 8, 767—781. https://doi.org/10.1111/j.1461-0248.2005.00775.x.

Walker, L.R., Chapin, F.S., 1987. Interactions among processes controlling successional change. Oikos 50, 131—135. https://doi.org/10.2307/3565409.

Watanabe, K., Monaghan, M.T., 2017. Comparative tests of the species-genetic diversity correlation at neutral and nonneutral loci in four species of stream insect. Evolution 71, 1755—1764. https://doi.org/10.1111/evo.13261.

Westoby, M., Falster, D.S., Moles, A.T., et al., 2002. Plant ecological strategies: some leading dimensions of variation between species. Annu. Rev. Ecol. Evol. Syst. 33, 125—159. https://doi.org/10.1146/annurev.ecolsys.33.010802.150452.

Wright, S.J., 2019. Plant responses to nutrient addition experiments conducted in tropical forests. Ecol. Monogr. 89, e01382. https://doi.org/10.1002/ecm.1382.

Xu, Z.F., 1995. The types of ecosystems keystone species and their managing strategies. Acta Bot. Yunnan. 17, 331—335.

Xu, Z.F., Yu, P.H., 1982. The research of adaptability of the introduced dipterocarps to lower temperature. Acta Bot. Yunnan 4, 207—301.

Xu, W.M., Liu, L., He, T., et al., 2016. Soil properties drive a negative correlation between species diversity and genetic diversity in a tropical seasonal rainforest. Sci. Rep. 6, 20652. https://doi.org/10.1038/srep20652.

Ying, S.H., Shuai, J.R., 1990. Study on fruiting behaviour, seedling establishment and population age classes of *Parashorea chinensis*. Acta Bot. Yunnan. 12, 415—420.

Zacharias, M.A., Roff, J.C., 2001. Use of focal species in marine conservation and management: a review and critique. Aquat. Conserv. 11, 59—76. https://doi.org/10.1002/aqc.429.

Zhu, H., 1992. Research of community ecology on *Shorea chinensis* forest in Xishuangbanna. Acta Bot. Yunnanica 14, 237—258.