

Relative roles of local disturbance, current climate and palaeoclimate

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Relative roles of local disturbance, current climate and palaeoclimate in determining phylogenetic and functional diversity in Chinese forests

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Abstract

The main processes underlying the generation and maintenance of biodiversity include both local factors such as competition and abiotic filtering and regional forces such as palaeoclimate, speciation and dispersal. While the effects of regional and local drivers on species diversity are increasingly studied, their relative importance for other aspects of diversity, notably phylogenetic and functional diversity is so far little studied. Here, we link data from large Chinese forest plots to data on current and Last Glacial Maximum (LGM) climate as well as local disturbance regimes to study their relative roles in determining woody plant phylogenetic and functional diversity in this important hotspot for woody plant diversity. Local disturbance was the best predictor of functional diversity as represented by maximum canopy height (H_{\max}), probably reflecting the dominant role of competition for light in determining the forest H_{\max} structure. In contrast, the LGM-present anomaly in temperature was the factor with the strongest explanatory power for phylogenetic diversity, with modern climate also important. Hence, local contemporary and regional historical factors have highly contrasting importance for the geographic patterns of the functional and phylogenetic aspects of Chinese forest woody plant diversity. Importantly, contemporary factors are of overriding importance for functional diversity, while palaeoclimate has left a strong signature in the phylogenetic diversity patterns.

1 Introduction

How biodiversity is generated and maintained is a central issue in ecology (Ricklefs, 1987; Pennisi, 2005; De Aguiar et al., 2009; Tittensor et al., 2010). Traditionally, emphasis has been on local forces such as competition, abiotic filtering and predation (Chesson, 2000; Svenning et al., 2004; Chen et al., 2010), but historical factors (e.g., palaeoclimate) and related regional processes (speciation, extinction and dispersal)

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are increasingly also considered (Dynesius and Jansson, 2000; Sandel et al., 2011; Kissling et al., 2012).

Many studies have considered the roles of local factors in determining diversity and structure in tropical, subtropical, and temperate forests (Svenning et al., 2004; Chen et al., 2010; Zhu et al., 2010; Wang et al., 2011). For instance, in one tropical forest, spatial location, environmental factors and past land use were all found to have important impacts on species composition (Svenning et al., 2004). Moreover, strong effects of current climate have been found in studies spanning larger geographic extents (Wang et al., 2009a, b). At such scales important imprints of historical-regional factors have also been found (Latham and Ricklefs, 1993; Ricklefs et al., 1999; Greve et al., 2011; Kissling et al., 2012; Rakotoarinivo et al., 2013).

However, these studies mainly focused on species richness, which ignores ecological and evolutionary differences among species. During the past decade, forest ecologists have increasingly used phylogenetic and functional information to provide novel insights into studies on community ecology (Webb et al., 2002; Kunstler et al., 2012; Mi et al., 2012; Swenson, 2013). Overall, phylogenetic patterns should reflect the imprints of evolutionary and biogeographic history on community structure (Kellermann et al., 2012a, b; Kissling et al., 2012). In contrast, functional traits should be directly linked to ongoing ecological processes (Swenson, 2013), while phylogenetic patterns would only indirectly (via niche conservatism) or not all (Purschke et al., 2013) relate to these.

China is a global hotspot for plant diversity (López-Pujol et al., 2006) and harbors a broad range of forest types (Qian and Ricklefs, 1999); its temperate forests are the most diverse on Earth (Qian and Ricklefs, 2000). The high species richness has been attributed to high levels of topographic heterogeneity, strong connectivity to the tropics, and more stable palaeoclimate with less influence of the Pleistocene glaciations than in other temperate areas such as much of North America (Qian and Ricklefs, 1999; Qian and Ricklefs, 2000). Previous studies have investigated woody plant species richness patterns in forests across China and did find important roles of both current and historical factors (Qian and Ricklefs, 1999; Wang et al., 2009b). However, large-scale vari-

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ations in phylogenetic and functional woody plant community structure across China have hitherto remained been unstudied, but is the focus of the present study. Overall, one may predict that phylogenetic structure should primarily reflect current or palaeoclimate via climatic niche conservatism (Wiens and Graham, 2005; Losos, 2008) or palaeoclimatic effects on diversification (Dynesius and Jansson, 2000). Climatic niche conservatism may also result in palaeoclimatic effects via dispersal-lagged climate-change-induced range dynamics (Hortal et al., 2011). In contrast, functional community structure may be more strongly related to contemporary ecological processes, e.g., succession (Purschke et al., 2013).

Additionally, assembly mechanisms may differ among organism groups due to differences in dispersal ability or other functional traits (Sandel et al., 2011; Lindström and Langenheder, 2012). In northeastern China, tree species richness was found to be mainly limited by climate, while shrub richness was more correlated to local factors (Wang et al., 2009a). Therefore, trees and shrubs may also exhibit different phylogenetic and functional patterns for across Chinese forests, but this has so far not been studied.

Here, we linked data on woody plant communities in Chinese forests to data on local disturbance (representing successional dynamics), current climate, and palaeoclimate (climate shifts between the LGM and now) to assess their relative roles in determining functional and phylogenetic diversity in these ecosystems. We also tested if these relations differed between the two main growth forms, trees and shrubs.

2 Material and methods

2.1 Data

2.1.1 Forest communities

Forest community data was mainly collected from Chinese Forest Biodiversity Monitoring Network (CForBio, <http://www.cfbiodiv.org>), which aims to study mechanisms underlying biodiversity and community structure in Chinese forests, with additional data from other published studies. In total, data were included from 11 forest plots across China (Table A1, Fig. 1). The plots were located in forest types ranging from temperate forests to subtropical and tropical forest, spanning tree diversities from 8 to 342 woody species. All woody individuals with diameter at breast height (DBH) ≥ 1 cm were measured and identified to species when possible. Here, we used the species list and species abundance data from each plot, representing a total of 1102 species and 495 815 individuals, among which gymnosperms constitute 16 species and 23 940 individuals.

2.1.2 Phylogenetic tree

A phylogenetic tree (Fig. A1) including the 1102 species was constructed by the plant phylogeny database Phylomatic (Webb and Donoghue, 2005), which uses the Angiosperm Phylogeny Group III (2009) classification. The BLADJ algorithm was used to estimate phylogenetic branch lengths using Phylocom 4.1 (Webb et al., 2008). To investigate the difference between trees and shrubs, we also built two phylogenetic trees using the same method, with one including 570 species of trees and the other including 167 species of shrubs. Species-level information on growth form (shrub or tree) came from Flora of China (<http://www.efloras.org/>).

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2.1.3 Functional trait data

Functional community structure was computed based on a single functional trait of key importance in plant communities, maximum canopy height (H_{\max}). This was the only trait broadly available for the study species; H_{\max} of each species was recorded from Flora of China, and, in total, we found H_{\max} information for 958 species ($n = 559$ tree spp. and 161 shrub spp.). A similarity distance matrix for H_{\max} of all species was then constructed, comparing the H_{\max} values for all pairs of species using Euclidian distance. Subsequently, we conducted a cluster analysis (complete linkage method which finds similar clusters) of this distance matrix and constructed a dendrogram (Fig. A2) based on the results of cluster analysis. Finally, two similar functional trees were computed just for trees and shrubs.

2.1.4 Environmental data

Data on current climate came from the WorldClim database (<http://www.worldclim.org>). Here, we considered mean annual temperature (MAT), maximum temperature of warmest month (MTWM), minimum temperature of coldest month (MTCM), mean annual precipitation (MAP), precipitation of wettest month (PWM) and precipitation of driest month (PDM). We represented palaeoclimate factors using the MAT anomaly (present-day MAT – LGM MAT) and the velocity of MAT (the ratio of the temporal MAT gradient to the spatial MAT gradient, Loarie et al., 2009; Sandel et al., 2011). Both were computed based on the mean of the Community Climate System Model version 3 (CCSM3) and Model for Interdisciplinary Research on Climate version 3.2 (MIROC3.2) palaeoclimatic simulations for the Last Glacial Maximum (LGM, 0.021 Mya). CCSM3 is a coupled climate model, which has components representing the atmosphere, ocean, sea ice and land surface connected by a flux coupler (Collins et al., 2006). MIROC3.2 includes a T42 global atmospheric spectral model and a medium-resolution ocean model (K-1 Model Developers, 2004). Both of these models have been widely used in

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recent macroecological studies (Sandel et al., 2011; Kissling et al., 2012; Rakotoarinivo et al., 2013; Smith et al., 2013). All climate variables were processed in ArcMap 10.1.

Local disturbance was presented by the proportion of light-demanding species (Molino and Sabatier, 2001). Species were scored as light-demanding ($n = 346$ spp.) primarily based on their habitat descriptions (occurrence in open forest or in disturbed, anthropogenic habitats) in Flora of China (Feng et al., 2013). Finally, to account for the varying plot areas (Table A1), plot area was also included as an explanatory variable in the modelling.

2.2 Methods

The Net Relatedness Index (NRI) (Webb et al., 2002) was used to quantify phylogenetic community structure (NRI_{PHY}). The formula is:

$$NRI = -1 \times \frac{MPD_{obs} - \text{mean}MPD_{rnd}}{sdMPD_{rnd}} \quad (1)$$

where MPD_{obs} is the observed mean phylogenetic distance (MPD) of a plot, $\text{mean}MPD_{rnd}$ is the mean MPD of the null models (shuffle distance matrix labels), and $sdMPD_{rnd}$ is the standard deviation (SD) of MPD of the null models. Functional diversity was calculated in the same way as NRI (Swenson and Enquist, 2009), but using the functional H_{max} -based dendrogram described above (NRI_{FUN}). Both abundance weighted and presence-absence based NRI_{PHY} and NRI_{FUN} were computed (indicated by $_ab$ and $_pr$ subscripts). As phylogenetic outliers may strongly influence phylogenetic community structure (Letcher et al., 2012; Feng et al., 2013), NRI_{PHY} was furthermore computed including both gymnosperms and angiosperms or only angiosperms (indicated by $_gym$ and $_ang$ subscripts).

To avoid including large number of correlated variables in the later analyses, we conducted a correlation analysis and removed redundant climate variables. Spearman correlation between each diversity index and explanatory variable was used to assess pairwise relationships. Generalized Linear Models (GLMs) with Gaussian error was

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applied to fit the relationship between each diversity index and all combinations of 1 or 2 explanatory variables. More complex models could not be fit with the available sample size. Model explanatory power was represented by pseudo- R^2 , while the small-sample-size corrected version of the Akaike Information Criterion (AIC_c) was used to select the best model for each diversity index. The overall multi-model support for a given explanatory variable was estimated as the summed Akaike weights (w) for all GLMs including this variable. We used Moran's I test to check for spatial auto-correlation (SAC) in the residuals of all GLMs.

The statistical calculations were performed in the R 2.15.1 (R Development Core Team, 2010) using the packages picante (Kembel et al., 2010), spdep (Bivand, 2007), pscl (Jackman, 2010) and MuMIn (Barton, 2010).

3 Results

There were high correlations with groups of the environmental variables representing palaeoclimate and representing current climate (Table A2). In the following, we therefore used MAT to represent current temperature (correlations between MAT and MTWM and MTCM were 0.69 and 0.98, respectively) and MAP to represent current precipitation (correlations between MAP and PWM and PDM were 0.96 and 0.93, respectively). The residuals of most of the GLMs had no spatial autocorrelation, except for a few weakly supported models, so models accounting for spatial dependence were not implemented.

Considering bivariate rank correlations, functional community structure (NRI_{FUN}) was only significantly correlated with proportion of light-demanding species (LDSR), no matter if species abundances were considered or not, and always so that functional clustering increased with increasing proportion of LDSR (Table 1, Figure 2). In contrast, phylogenetic structure (NRI_{PHY}) was significantly and positively correlated with the LGM-present MAT anomaly in most cases, i.e., phylogenetic clustering tended to increase with increasing Late Quaternary temperature change. NRI_{PHY} was also sig-

nificantly correlated with current MAT and LGM-present MAT velocity in some cases, except for $NRI_{PHY_gym_pr}$ which had no significant relations with any variables (Table 1, Fig. 2).

Considering single-predictor GLMs, NRI_{FUN} was also best explained by LDSR, while NRI_{PHY} considering angiosperms was best explained by LGM-present MAT anomaly and current MAT. Again, functional clustering increased with LDSR, while phylogenetic clustering increased with increasing Late Quaternary temperature shift. No significant relations were found for NRI_{PHY} with gymnosperms included (Table 2).

Considering both one- and two-predictor GLMs, LDSR had the strongest support for functional community structure, while LGM-present MAT anomaly was the most important factor for NRI_{PHY} considering only angiosperms (Table 3), and again with similar relations as indicated by the bivariate correlations and single-predictor GLMs. No particular variable was strongly supported for NRI_{PHY} with gymnosperms included, although LGM-present MAT anomaly was among the most supported (Table 3).

Tree and shrub communities showed different functional and phylogenetic patterns (Table 4). Generally, for NRI_{FUN} the best and only important predictor was LDSR for trees and current MAP and MAT for shrubs. Although no significant relationships for growth-form-specific phylogenetic structure to any of the explanatory variables were found, LGM-present MAT anomaly again tended to be among the more important for phylogenetic structure of shrubs, but not for trees (Table 4).

4 Discussion

For woody plant communities in forests across China, phylogenetic and functional community structure show highly divergent relations to potential driving factors, with the former most strongly constrained by palaeoclimate and the latter most strongly determined by contemporary local ecological dynamics. Hence, these two key aspects of woody plant diversity appear to be predominantly shaped by divergent assembly mechanisms acting on very different spatiotemporal scales. Growth-form specific relations

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were generally weaker and less consistent, perhaps reflecting reduced species-wise sample sizes as well as growth-form specific dynamics.

Functional structure in this study was only represented by maximum plant height (H_{\max}). Plant height is a key component of plant ecological strategies (Westoby, 1998), because it reflects the ability to compete for light, especially in dense, tall vegetation such as forests, and may also be correlated with other traits such as canopy area, leaf mass per area, leaf area ratio, metabolic rates, and dispersal ability (Enquist et al., 1998; Falster and Westoby, 2003; Moles et al., 2009; Thomson et al., 2011). Nevertheless, it is important to note that other aspects of functional diversity may very well show other geographic patterns and ecological relationships (Wright et al., 2007; Swenson and Weiser, 2010). In the present case, functional NRI was most correlated with the proportion of light-demanding species (LDSR), an indicator of local-scale disturbance dynamics (Molino and Sabatier, 2001; Feng et al., 2013). In a smaller study area (8107 hectares), Feng et al. (2013) also found LDSR to be well linked with functional diversity in a subtropical forest landscape in southern China and concluded that this might reflect the important role of competition for light in determining forest structure. Across Chinese forests, there was increasing functional clustering and thus decreasing variability in H_{\max} with increasing LDSR. Notably, the standard deviation of H_{\max} of the 30% most abundant species in the four plots with the highest LDSR was 7.6, while it was 10.8 in the four plots with the lowest LDSR, even after excluding the TS plot (with the lowest LDSR and the highest H_{\max} standard deviation, 40.3) due to its low number of species ($n = 8$ in total). Studies from other areas and vegetation types have also found functional clustering to increase with disturbance (Cianciaruso et al., 2012; Purschke et al., 2013).

A global study of plant height patterns showed that precipitation in the wettest month was the best predictor of height (Moles et al., 2009), which is partly consistent with our finding as the annual precipitation (highly correlated with the precipitation in the wettest month) was the second best predictor for H_{\max} -defined functional NRI. Furthermore, the trend towards increasing clustering with increasing temperature and precipitation

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(Table 1) also agreed with Moles et al. (2009) who found that cold, dry, low productivity systems tended to have species with a wide range of height strategies, perhaps reflecting more shady conditions and increased competition for light under warm, wet conditions.

5 Long-term historical factors have been reported to be well correlated with various aspects of diversity at large geographic scales (Jansson, 2003; Kissling et al., 2012; Sandel et al., 2011; Rakotoarinivo et al., 2013). Notably, several studies have found phylogenetic community structure to be strongly shaped by historical factors (Kissling et al., 2012). As a key example, Kissling et al. (2012) find that global patterns in phylogenetic structure for country-level palm assemblages is strongly linked to deep-time
10 Cenozoic climate change, while there are also imprints of Quaternary climate change within some biogeographic regions. Notably, a strong increase in clustering with increasing LGM-present MAT anomaly is found within South America. Hortal et al. (2011) found a similar relation for scarab beetles within Europe, and a consistent pattern emerged for Chinese forest woody-plant communities in the present study. Consider-
15 ing only angiosperms, we also found an increase phylogenetic clustering with LGM-present MAT anomaly. Such a pattern may reflect strong filtering on phylogenetically conserved traits by the Pleistocene glaciations (Hortal et al., 2011). While eastern Asia was less affected by the Pleistocene glaciations than Europe or North America, these nevertheless caused massive vegetation changes and retraction of forests (Yu et al.,
20 2000; Liu et al., 2003, 2013). The much weaker and often inconsistent patterns that resulted when gymnosperms were included probably reflect the potentially strong effects of such phylogenetic outlier groups on phylogenetic community structure (Letcher et al., 2012; Feng et al., 2013).

25 Trees and shrubs communities showed substantially different patterns in terms of functional structure, which was in line with previous studies about species diversity (Wang et al., 2009a; Sandel et al., 2011) and further emphasized the importance of considering different taxonomic and functional groups regarding assembly mechanisms (Lindström and Langenheder, 2012). High correlation between LDSR and H_{\max}

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defined functional NRI was only found in tree communities, while MAP was the best predictor of this measure for shrub communities. Wright (1992) argued that understory shrub diversity is critically affected by dry season rainfall, which may explain the particular importance of MAP for shrub functional NRI. For growth-form-specific phylogenetic structure, we did not find significant relations with any of the explanatory variables. The partially inconsistent and often weak relations for the growth-form-specific diversity measures may simply reflect the lower species-wise sample size for these subsets and thus greater sensitivity to stochastic processes.

Our study shows that functional and phylogenetic structure of woody-plant communities in Chinese forests are shaped by divergent processes acting on very different spatiotemporal scales. Functional structure was more determined by contemporary local dynamics, while palaeoclimate was more important for phylogenetic structure. These differences are consistent with theoretical expectations and the few existing empirical studies (Kissling et al., 2012; Purschke et al., 2013), pointing to their potential wider generality. Many further studies will be needed for assessing this. Further, functional diversity was in the present study represent by a single – albeit very important – functional trait, namely maximum stem height. Other aspects of functional diversity may well reflect different determining factors (cf. e.g., Wright et al., 2007; Swenson and Weiser, 2010). As both phylogenetic structure and functional traits may affect forest ecosystem functioning and ecosystem services, our findings illustrate that these may be shaped by both local contemporary and long-term regional processes.

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Table 1. Spearman correlations (r_s) between each diversity index and each explanatory variable. NRI_{FUN} : functional (H_{max}) NRI, and NRI_{PHY} : phylogenetic NRI, based on either presence-absence ($_{\text{pr}}$) or abundances ($_{\text{ab}}$) with gymnosperms ($_{\text{gym}}$) or only considering angiosperms ($_{\text{ang}}$). Significant values are given in bold; *, significant at $p < 0.05$; **, significant at $p < 0.01$.

r_s	Velocity	Anomaly	MAT	MAP	LDSR	Area
$\text{NRI}_{\text{FUN}_{\text{pr}}}$	0.02	-0.04	0.40	0.48	0.64*	-0.40
$\text{NRI}_{\text{FUN}_{\text{ab}}}$	0.09	0.08	0.38	0.57	0.65*	-0.51
$\text{NRI}_{\text{PHY}_{\text{ang}_{\text{pr}}}}$	0.57	0.72*	-0.69*	-0.49	-0.35	0.11
$\text{NRI}_{\text{PHY}_{\text{ang}_{\text{ab}}}}$	0.61*	0.82**	-0.66*	-0.32	-0.38	0.05
$\text{NRI}_{\text{PHY}_{\text{gym}_{\text{pr}}}}$	0.32	0.27	-0.13	-0.22	-0.18	0.27
$\text{NRI}_{\text{PHY}_{\text{gym}_{\text{ab}}}}$	0.45	0.65*	-0.16	0.35	-0.03	0.34

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Table 2. Pseudo- R^2 for single predictor GLMs of each diversity index against each explanatory variable. Significant values are given in bold; *, significant at $p < 0.05$; **, significant at $p < 0.01$.

	Velocity	Anomaly	MAT	MAP	LDSR	Area
NRI_{FUN_pr}	0.00	0.01	0.22	0.34	0.67**	0.08
NRI_{FUN_ab}	0.00	0.00	0.24	0.44*	0.50*	0.06
$NRI_{PHY_ang_pr}$	0.20	0.45*	0.61**	0.36	0.19	0.08
$NRI_{PHY_ang_ab}$	0.29	0.59**	0.41*	0.09	0.12	0.03
$NRI_{PHY_gym_pr}$	0.07	0.13	0.11	0.14	0.07	0.16
$NRI_{PHY_gym_ab}$	0.24	0.28	0.00	0.13	0.02	0.17

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Table 3. Summed Akaike weights (w) for each predictor variable based on all possible single- and two-predictor GLMs. Variables with $w \geq 0.50$ are given in bold.

	Velocity	Anomaly	MAT	MAP	LDSR	Area
H_{\max_pr}	0.05	0.05	0.06	0.09	0.95	0.10
H_{\max_ab}	0.06	0.08	0.12	0.32	0.54	0.09
$\text{NRI}_{\text{PHY_ang_pr}}$	0.06	0.52	0.45	0.46	0.06	0.06
$\text{NRI}_{\text{PHY_ang_ab}}$	0.08	0.82	0.16	0.11	0.18	0.05
$\text{NRI}_{\text{PHY_gym_pr}}$	0.11	0.15	0.13	0.16	0.11	0.19
$\text{NRI}_{\text{PHY_gym_ab}}$	0.21	0.33	0.12	0.17	0.08	0.15

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Table 4. Pseudo- R^2 for single-predictor GLMs of each diversity index for the two functional groups trees and shrubs against each explanatory variable. *, Significant values are given in bold; * significant level at 0.05.

	Velocity	Anomaly	MAT	MAP	LDSR	Area
$\text{NRI}_{\text{FUN}}^{\text{Tree}}_{\text{ab}}$	0.03	0.12	0.03	0.03	0.21	0.06
$\text{NRI}_{\text{FUN}}^{\text{Shrub}}_{\text{ab}}$	0.00	0.02	0.03	0.14	0.05	0.00
$\text{NRI}_{\text{FUN}}^{\text{Tree}}_{\text{pr}}$	0.02	0.07	0.00	0.07	0.45*	0.02
$\text{NRI}_{\text{FUN}}^{\text{Shrub}}_{\text{pr}}$	0.04	0.06	0.40*	0.45*	0.14	0.00
$\text{NRI}_{\text{PHY_ang}}^{\text{Tree}}_{\text{ab}}$	0.02	0.08	0.10	0.27	0.03	0.08
$\text{NRI}_{\text{PHY_ang}}^{\text{Shrub}}_{\text{ab}}$	0.16	0.21	0.16	0.07	0.12	0.04
$\text{NRI}_{\text{PHY_ang}}^{\text{Tree}}_{\text{pr}}$	0.00	0.01	0.01	0.00	0.11	0.24
$\text{NRI}_{\text{PHY_ang}}^{\text{Shrub}}_{\text{pr}}$	0.08	0.23	0.12	0.00	0.08	0.03

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Table A1. General information of 11 forest plots in China. No.species: number of species in each plot. Anomaly: LGM-present MAT anomaly. MAT: mean annual temperature. MAP: mean annual precipitation. LDSR: proportion of light demanding species. NRI_{FUN} : functional (H_{max})NRI, and NRI_{PHY} : phylogenetic NRI, both based on either presence-absence ($_{pr}$) or abundances ($_{ab}$) with gymnosperms ($_{gym}$) or only considering angiosperms ($_{ang}$).

	ALS	BSZ	CBS	DHS	DJY	GTS	JH	LS	TS	TYS	XSBN
No.species	68	152	50	198	98	158	48	45	8	21	342
Longitude	101.03	119.2	128.08	112.54	103.45	118.12	127.74	128.89	87.47	112.15	101.58
Latitude	24.54	27.76	42.38	23.17	30.73	29.25	43.96	47.18	43.43	36.69	21.61
Area (hm ²)	6	5	25	20	5	24	42	9	8	1.96	20
Velocity	0.3	2.23	4.35	0.63	0.58	1.88	0.85	2.28	0.27	0.67	0.39
Anomaly	2.65	5.8	5.6	2.4	3.4	5	5.65	5.55	2.9	4	2.2
MAT	13.2	11.4	2.3	20.9	15	14.4	2.6	0.8	2.5	6.5	21.9
MAP (mm yr ⁻¹)	1116	2147	693	1698	1202	1935	671	648	239	588	1575
LDSR	0.1	0.32	0.04	0.43	0.29	0.37	0.05	0.18	0	0.1	0.13
$NRI_{FUN_{pr}}$	-0.23	1.33	-1.13	2.32	2.33	2.13	-2.29	-2.19	-1.32	-0.15	-2.92
$NRI_{FUN_{ab}}$	1.12	1.41	-1.54	0.62	1.48	0.34	-1.77	-1.49	-4.78	-0.5	-2.29
$NRI_{PHY_{ang_{pr}}}$	-0.36	1.71	4.77	0.43	2.62	0.08	5.2	2.99	1.64	3.6	-0.75
$NRI_{PHY_{ang_{ab}}}$	1.7	2.3	3.38	-0.66	0.79	0.66	3.44	1.88	-0.6	2.94	-0.74
$NRI_{PHY_{gym_{pr}}}$	-0.34	0.56	2.93	0.98	2.65	0.17	3.19	0.78	0.24	2.3	0.87
$NRI_{PHY_{gym_{ab}}}$	1.74	2.41	2.25	-0.4	0.98	0.65	2.43	0.35	-2.69	-2.75	-0.49

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Table A2. Matrix of correlation coefficients among the 10 environmental variables. The bold value in each column means the most correlated variable with that column.

CorCoe	Velocity	Anomaly	MAT	MAP	MTWM	MTCM	PWM	PDM	LDSR	Area
Velocity	1	0.74	-0.42	0.03	-0.17	-0.44	0.02	0.12	0	0.21
Anomaly	0.74	1	-0.63	-0.04	-0.32	-0.64	-0.02	0.1	-0.03	0.29
MAT	-0.42	-0.63	1	0.76	0.69	0.98	0.77	0.58	0.63	-0.1
MAP	0.03	-0.04	0.76	1	0.5	0.77	0.96	0.93	0.82	0.01
MTWM	-0.17	-0.32	0.69	0.5	1	0.55	0.52	0.4	0.6	0.33
MTCM	-0.44	-0.64	0.98	0.77	0.55	1	0.76	0.61	0.62	-0.2
PWM	0.02	-0.02	0.77	0.96	0.52	0.76	1	0.82	0.79	0.03
PDM	0.12	0.1	0.58	0.93	0.4	0.61	0.82	1	0.79	0.07
LDSR	0	-0.03	0.63	0.82	0.6	0.62	0.79	0.79	1	-0.1
Area	0.21	0.29	-0.07	0.01	0.33	-0.2	0.03	0.07	-0.1	1

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Fig. 1. Locations of the 11 forest plots: Liangshui (LS), Jiaohe (JH), Changbaishan (CBS), Taiyueshan (TYS), Dujiangyan (DJY), Ailaoshan (ALS), Xishuangbanna (XSBN), Dinghushan (DHS), Gutianshan (GTS), Baishanzu (BSZ).

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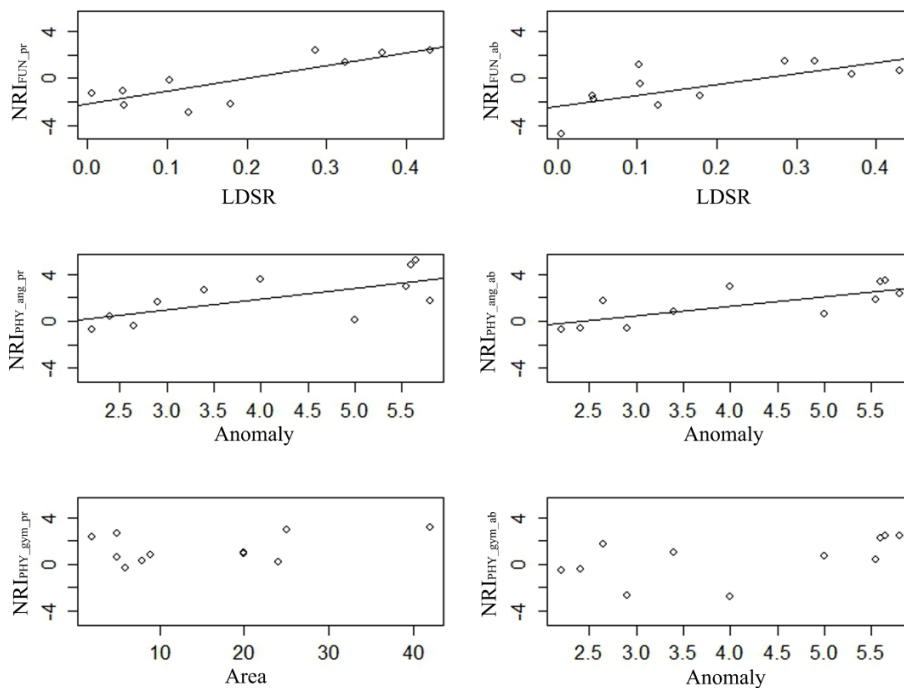
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Fig. 2. Scatter plots of each diversity index against its best predictor. Linear regression fits are given for significant relationships.

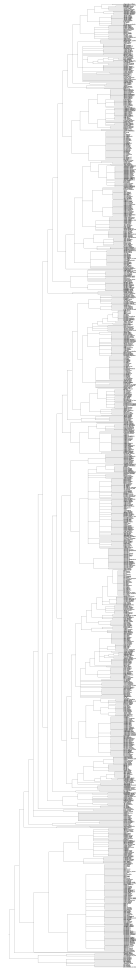


Fig. A1. A phylogeny tree including 1102 species.

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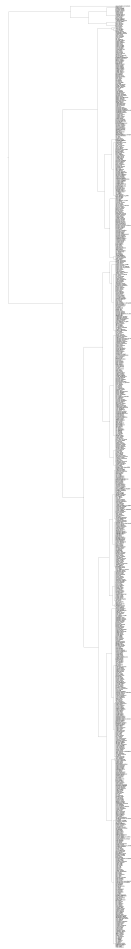


Fig. A2. A functional dendrogram represented by maximum canopy height including 958 species.

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