

Environmental and spatial contributions to seedling and adult tree assembly across tropical, subtropical and subalpine elevational gradients

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Abstract

Aims

Quantifying the relative importance of the mechanisms that drive community assembly in forests is a crucial issue in community ecology. The present study aims to understand the ways in which niche-based and spatially based processes influence community assembly in areas in different climatic conditions and how these processes change during the transition from seedling to adult.

Methods

In this study, we investigated how taxonomic and phylogenetic beta diversity in seedling and adult stages of forest trees change across three elevational transects in tropical, subtropical and subalpine forests in Southwest China, and the relationships of these changes to the environment and inter-site distances. We quantified the relative contribution of environmental conditions and spatial distribution to taxonomic and phylogenetic beta diversity of both seedling and adult life stages along each elevational transect. We also quantified the taxonomic and phylogenetic similarity between seedlings and adult trees along elevations.

Important Findings

Taxonomic and phylogenetic beta diversity of both seedlings and adult trees increased with an increase in both environmental distance and spatial distance in all three transects. On both taxonomic and phylogenetic levels, the effects of environmental filtering and spatial disposition varied between life stages and among forest types. Phylogenetic similarity between seedlings and adult trees increased with elevation, although the taxonomic similarity did not show clear elevational patterns. Our results suggest that the relative contribution of niche-based and space-based processes to taxonomic and phylogenetic assemblages varies across major plant life stages and among forest types. Our findings also highlight the importance of ontogenetic stages for fully understanding community assembly of long-lived tree species.

Keywords: beta diversity, dispersal limitation, environmental filtering, phylogeny

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INTRODUCTION

Identifying the mechanisms driving community assembly is a central objective of community ecology (Hubbell 2001; Leibold

2008; Myers *et al.* 2013; Tilman 2004). Theories emphasizing niche-based processes, which incorporate environmental filtering, suggest that community composition across ecological gradients should show strong correlations with

environmental changes (Chesson 2000; Leibold *et al.* 2004). Conversely, theories emphasizing spatial processes highlight innate dispersal limitation in community assembly processes (Bell 2005; Hu *et al.* 2012b). Measures of beta diversity quantify turnover along environmental and spatial gradients and have the potential to estimate the relative importance of these two ecological processes in community assembly (Anderson *et al.* 2011; Kraft *et al.* 2011).

Several studies have combined niche-based and space-based explanations into an integrative approach which has clearly demonstrated the importance of both kinds of processes in shaping community dynamics (Girdler and Barrie 2008; Tuomisto *et al.* 2003). At large biogeographic scales (e.g. continental or global), both broader spatial distances and increased habitat heterogeneity limit the distribution of species (Wiens 2011). In Western Amazonia, differences in composition of tree species among plots can be better explained by environmental variation than by dispersal limitation (Tuomisto *et al.* 2003). However, the distribution of species in the Panama Canal watershed has been primarily affected by dispersal limitation and then shaped by environmental heterogeneity (Chust *et al.* 2006). Moreover, the relative contributions of both niche-based and spatial processes change with spatial scale. For example, in tropical tree community assemblages, stronger environmental filtering occurs at broader spatial scales (Yang *et al.* 2014).

The response of forest communities to environmental filtering and spatial arrangement varies with ontogeny (development from seedling to adult), especially when we compare the seedling stage to adult tree life stages (Lasky *et al.* 2015; Perez-Ramos and Maranon 2012). The different relative importance of environmental filtering on tree assemblages may reflect changes in the environmental requirements of each life stage (Bertrand *et al.* 2011; Jin *et al.* 2015). So, dispersal limitation may be strongest at the earlier life stages of trees, resulting from limitations in long-distance dispersal of seeds. Hu *et al.* (2012a) showed that in a seasonal tropical forest in China, environmental variables (topography and soil characters) played an increasingly important role as tree size increased. In contrast, spatial processes had greater influence among small trees, and this decreased with increasing tree size. In Neotropical lowland forest, spatially dependent processes (i.e. dispersal limitation) had a greater effect on species assemblages of young trees (Arieira *et al.* 2016). For community assembly in a subtropical forest, the importance of environmental filtering increased, and that of dispersal limitation decreased, with tree life stages (Yang *et al.* 2016). Most studies, however, have sampled only young trees or juvenile stages, with little attention given to the understory tree seedlings (diameter at breast height [DBH] < 1 cm), even though tree seedlings play a key role in forest regeneration (Bace *et al.* 2012). Moreover, we lack knowledge of how ontogenetic shifts in environmental and spatial contributions to tree assembly vary across contrasting climatic regimes.

Most previous studies have focused on taxonomic beta diversity by investigating taxonomic turnover or assemblage

dissimilarity (Anderson *et al.* 2011; Kraft *et al.* 2011; Myers *et al.* 2015). By using a species-centered point of view, species are treated independently, which conveys little information regarding the ecological similarity or evolutionary history of the species (Chave *et al.* 2007; Swenson 2011). Given the potential limitations of taxonomic beta diversity measures, phylogenetic beta diversity measures provide more refined information regarding the ecological and evolutionary relationships among the species within the assemblages being compared. For example, tropical forests with high taxonomic beta diversity but low phylogenetic beta diversity may indicate the presence of many closely related species (Qian *et al.* 2013). Moreover, changes in phylogenetic structure with increased tree size may indicate the variation of assembly mechanisms across life stages (Swenson *et al.* 2007). The inclusion of phylogenetic beta diversity in community structure investigations is essential to fully understand the evolutionary processes driving the organization of communities (Fortunel *et al.* 2014; Graham and Fine 2008; Swenson 2011).

Elevational transects offer ideal systems for exploring the ways in which ecological processes respond to changing environments. With increases in elevation, different suites of environmental conditions exist within short spatial distances of each other; an upward shift of 100 m is approximately equivalent to a pole-ward shift of 100 km with respect to temperature change (Jump *et al.* 2009; Tello *et al.* 2015). Accordingly, steeper environmental gradients may be more suitable for detecting environmentally driven patterns in species composition. They may also mitigate larger-scale spatial changes in spatial distribution as species' displacements or, indeed, whole communities shift in search of suitable habitat (Qian *et al.* 2014). In addition, elevational gradients avoid many underlying issues associated with latitudinal co-varying environmental conditions (Körner 2007). Elevational gradients, therefore, are ideal for investigating the roles of ecological and evolutionary processes in structuring species assemblages in local communities.

Here, we investigate the ontogenetic changes in taxonomic and phylogenetic beta diversity of seedlings and adult tree species in tropical, subtropical and subalpine forests across elevational gradients in Southwest China. The goal of this study is to quantify the relative contribution of environmental variables and spatial drivers to the taxonomic and phylogenetic beta diversity of the two selected age classes along three elevational transects. We hypothesized that the relative contribution of environmental filtering and spatial drivers decrease from tropical to subalpine environment in structuring taxonomic and phylogenetic beta diversity. We also expected that the influence of these processes increase from seedling to adult stages.

MATERIALS AND METHODS

Study site

Yunnan province (21°09'–29°15'N and 97°32'–106°12'E), located in southwest China, is one of the most biodiverse regions in China and belongs to the Indo-Burma biodiversity

hotspot (Myers et al. 2000; Yang et al. 2004). Yunnan adjoins the eastern Asia monsoon region in the east, the tropical monsoon region of southern Asia in the south and west, and the Indo-China and Tibetan plateau region in the northwest. This region is divided according to temperature into tropical, subtropical and temperate climate zones. It is a highland province with a terraced terrain stretching from the northwest (6740 m a.s.l.) to the southeast (76 m a.s.l.). The variation in elevation promotes a variety of microclimates (Wu et al. 1987).

From 2011 to 2012, we established three transects: the tropical transect located in Xishuangbanna National Nature Reserve, the subtropical transect located in Ailaoshan National Nature Reserve and the subalpine transect located in Yulong Snow Mountain Nature Reserve (Fig. 1). Each transect included four elevation zones: 800 m, 1000 m, 1200 m and 1400 m in Xishuangbanna; 2000 m, 2200 m, 2400 m and 2600 m in Ailaoshan; and 3200 m, 3400 m, 3600 m and 3800 m in Yulong Snow Mountain. Within each elevation zone, we set up five replicate plots of 20 m × 20 m that were spaced at least 200 m from each other. Anthropogenic and natural disturbances, such as large canopy gaps in the plots, were avoided. To survey seedlings, in 2013 and 2014, five 1 m × 1 m seedling plots were established at the four corners and the center of the each plot producing a total of 100 plots for each elevational transect.

Data collection

Within each 20 m × 20 m plot, all trees with a DBH equal to or greater than 5 cm were measured, tagged and identified.

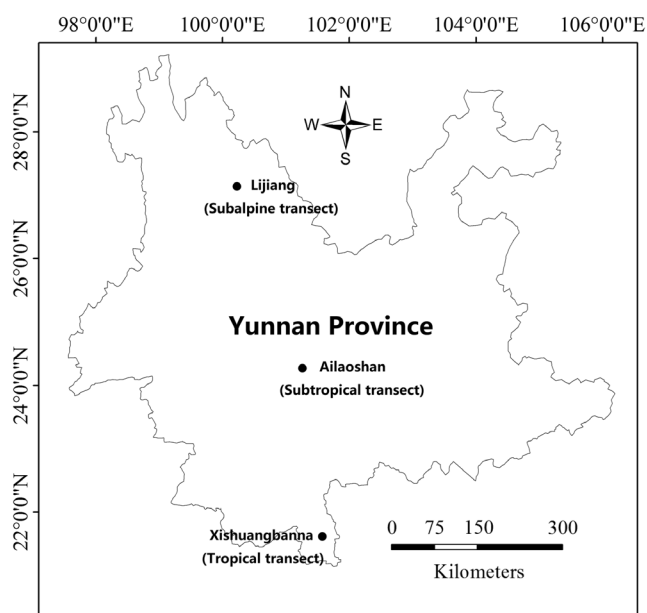


Figure 1: elevational transects in Yunnan Province. Elevational transects were located in tropical (Xishuangbanna; 800 m, 1000 m, 1200 m and 1400 m), subtropical (Ailaoshan; 2000 m, 2200 m, 2400 m and 2600 m), and subalpine (Lijiang; 3200 m, 3400 m, 3600 m and 3800 m) Yunnan Province, China. The map was generated using ArcGIS 10.1 (www.esri.com).

We defined the individuals with DBH equal to or greater than 10 cm as adults. Within each 1 m × 1 m seedling plot, all individuals with a stem diameter less than 1 cm (hereafter referred to as seedlings) were measured, tagged and identified to species. The seedling data collected from the five 1 m × 1 m seedling plots in each plot were pooled before analysis. For adults, we recorded 2067 individuals from 212 species, and for seedlings we recorded 1843 individuals from 218 species.

For each plot, we determined elevation from GPS coordinates using GARMIN GPSMAP 60CSX (Garmin Corporation, China), and both slope and aspect were calculated from a HRB DQY-1 geologic compass (Harbin Optical Instrument Factory, China). We measured soil moisture at the end of both the dry season (April 2014) and rainy season (October 2014) using a conductivity probe (Theta probe MPM-160B, ICT International Proprietary Limited, Armidale, Australia). For each seedling plot, we measured the soil moisture 5 cm below the ground at five randomly selected points and calculated the average soil moisture in each plot. We generated five environmental variables: (i) elevation, (ii) soil moisture in the dry season, (iii) soil moisture in the rainy season, (iv) slope, and (v) aspect (sine-transformed).

Data analysis

Phylogenetic tree reconstruction.

We used a new tool for reconstructing phylogenies of seed plants (S.PhyloMaker), based on an updated megaphylogeny of vascular plants (PhytoPhylo), to reconstruct our phylogenetic tree (S.PhyloMaker and PhytoPhylo are available in R; Qian and Jin 2015). We first standardized the spelling and nomenclature of our species list according to The Plant List (TPL, www.theplantlist.org). All names in the species list for each transect that are considered synonyms in TPL were replaced with their accepted names in TPL. Then we assigned a family name to each species in our species list. We used the R package “S.PhyloMaker” with Scenario 3 to generate a phylogenetic tree of our species list (see details in S.PhyloMaker package; Qian and Jin 2015). Following the BLADJ algorithm approach implemented in the software Phylocom (Webb et al. 2008), we constructed the phylogenetic tree of our species list by adding species to the appropriate family or genus.

Taxonomic and phylogenetic beta diversity across spatial and environmental gradients.

For each pair of plots, we calculated a taxonomic similarity index and a phylogenetic similarity index of seedlings and adult trees. To calculate taxonomic similarity, we used the Sørensen index (Sørensen 1948) which is one of the most commonly used taxonomic similarity indices based on the presence or absence of shared species. To quantify phylogenetic diversity, we utilized the widely used similarity index, PhyloSor. Both Sørensen and PhyloSor indices are incidence-based. We used these indices because Sørensen and PhyloSor are analogs of each other (Bryant et al. 2008; Swenson 2011) making them comparable within this study. Bryant et al. (2008) define these indices as:

$$\text{Sørensen} = (2 \times S_{ij}) / (S_i + S_j)$$

and

$$\text{PhyloSor} = (2 \times \text{BL}_{ij}) / (\text{BL}_i + \text{BL}_j)$$

Where S_{ij} is the number of species shared between localities i and j , S_i and S_j are the numbers of species in localities i and j , BL_{ij} is the total length of the branches shared between localities i and j , and BL_i and BL_j are the total branch lengths in localities i and j , respectively.

Values of both Sørensen index and PhyloSor index range from 0 (no similarity) to 1 (complete similarity). Taxonomic dissimilarity (i.e. $1 - \text{Sørensen}$) and phylogenetic dissimilarity (i.e. $1 - \text{PhyloSor}$) are used here as measures of taxonomic beta diversity and phylogenetic beta diversity, respectively.

We used multiple regression on distance matrices (MRM) to partition variation both in taxonomic and phylogenetic beta diversity into fractions explained by environmental and spatial distance in both seedling and adult tree stages (Legendre *et al.* 1994; Lichstein 2007). MRM is similar to a partial Mantel's test and can be used to examine the correlation between the dependent distance matrix and the independent distance matrices. We constructed the spatial distance matrix by calculating the spatial distance between each pair of plots using the latitude/longitude coordinates and altitude in the center of each plot. An environmental distance matrix was constructed using the Euclidean distance between each pair of plots based on the five environmental factors (all factors were standardized by subtracting the mean value of the variable and dividing by one standard deviation before analyses).

We used linear regression models to quantify the degree of taxonomic and phylogenetic beta diversity across environmental and spatial gradients (Qian *et al.* 2013). A slope (an estimate) of the regression model represents the strength of the taxonomic or phylogenetic beta diversity. The steeper the slope, the greater the taxonomic or phylogenetic beta diversity across environmental and spatial distances.

Taxonomic and phylogenetic similarities between seedlings and adult trees.

We used the Sørensen index and the PhyloSor index to calculate the taxonomic similarity and phylogenetic similarity between seedling and adult assemblages within each elevational zone. All trees or seedlings from the five plots in the same elevation were pooled and treated as a single large plot in this analysis. We used linear regression modeling to quantify the bivariate relationships of taxonomic and phylogenetic similarity with elevation.

The above statistical analyses were performed using the R packages "ecodist", "vegan" and "picante" (Dixon 2003; Goslee and Urban 2007; Kembel *et al.* 2010; R Development Core Team 2013).

RESULTS

In general, relatively high taxonomic beta diversity and low phylogenetic beta diversity were found at both seedling and adult stages across all three transects (Figs. 2 and 3). The tropical transect had similar taxonomic and phylogenetic beta diversity patterns to the subtropical and subalpine transects. In general, the taxonomic beta diversity within seedling assemblages was lower than in adult assemblages, except in the subtropical transect, which showed higher taxonomic beta diversity at the seedling stage (Fig. 1b and c).

For taxonomic beta diversity, in tropical and subalpine transects, environmental distance alone explained much more taxonomic beta diversity than spatial distance at the adult stage when compared to the seedling stage (tropical 0.2 vs. 0.14, subalpine 0.17 vs. 0.05, respectively). In the subtropical transect, by contrast, environmental distance explained more variability in seedling beta diversity than for adult trees (seedlings 0.06, adult trees 0.02). Spatial distance explained much more variation in taxonomic beta diversity at the seedling stage than at the adult stage in the tropical and subtropical transects (tropical 0.10 vs. 0.04, and subtropical 0.07 vs. <0.01, respectively), but in the subalpine transect, spatial distance explained more variance at the adult stage than at the seedling stage (seedlings 0.05, adult trees <0.01).

For phylogenetic beta diversity, in subalpine transects, environmental distance explained much more variation at the adult stage than at the seedling stage (0.14 vs. 0.02, respectively), but in the tropical transect, the reverse was true (seedlings 0.17, adult trees 0.12). Spatial distance explained much more variation in phylogenetic beta diversity at the adult stage than at the seedling stage in tropical and subalpine transects, but in the subtropical transect the reverse was true (seedlings 0.08, adult trees <0.01) (Table 2).

The taxonomic and phylogenetic similarity values between seedling and adult assemblages for all elevations in our study varied across all three transects. Phylogenetic similarities are consistently higher than taxonomic similarities (Fig. 4), but there is no significant relationship between species similarity and elevation. There is a significant relationship between phylogenetic similarity and elevation with seedling and adult assemblages more closely correlated at higher elevations.

DISCUSSION

We investigated taxonomic and phylogenetic beta diversity in different life stages of trees across three elevational transects in tropical, subtropical, and subalpine forest types in China. Our results show that the degrees (i.e. regression slopes in Figs. 2 and 3) of taxonomic and phylogenetic beta diversity varied between seedling and adult stages, reflecting changes in the niche-based (i.e. environmental distance) and stochastic (spatial distance) ecological processes across different life stages. These changes may be explained by biogeographic and evolutionary history,

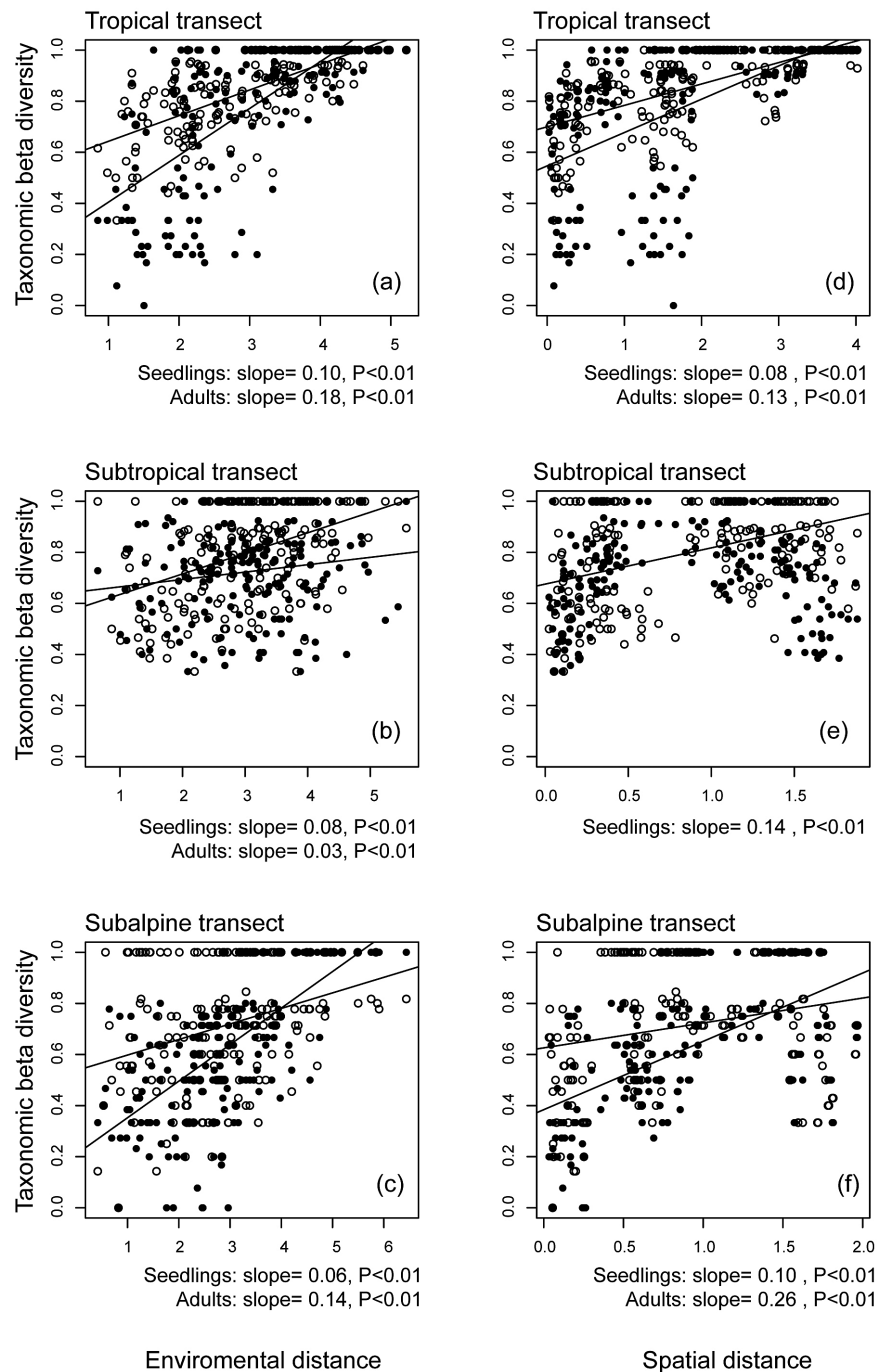


Figure 2: relationships between taxonomic beta diversity and environmental and spatial distance in three transects. Open circles are seedlings, closed circles are adult trees. (a–c) are relationships between taxonomic beta diversity and environmental distance in tropical, subtropical and subalpine transects, and (d–f) are relationships between taxonomic beta diversity and spatial distance in tropical, subtropical and subalpine transects, respectively.

as well as the combined effect of environmental filtering, dispersal limitation and anthropogenic disturbance.

Results relating to phylogenetic distance will by necessity involve evolutionary explanations (Graham and Fine 2008). Two mechanisms could produce the observed patterns. Turnover across sites may reflect active evolutionary

habitat-partitioning *in situ*, resulting in closely related species turning over across adjacent sites (Fine and Kembel 2011). Alternatively, and perhaps more likely, the regional species-set in each location represents the consequences of relatively recent evolutionary radiations and, accordingly, contains closely related species—in other words, they are based on

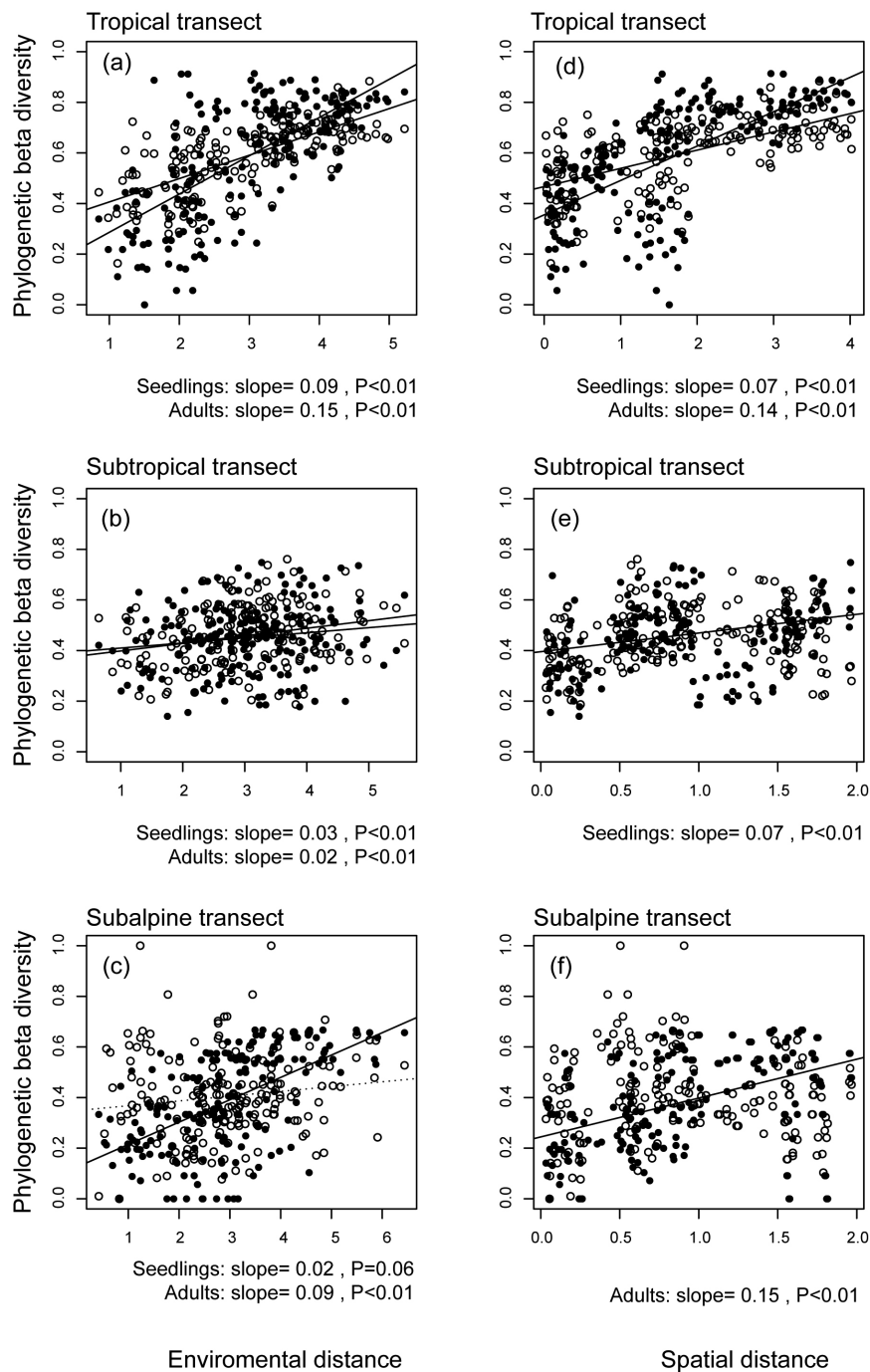


Figure 3: relationships between phylogenetic beta diversity and environmental and spatial distance in three transects. Open circles are seedlings, closed circles are adult trees. (a–c) are relationships between phylogenetic beta diversity and environmental distance in tropical, subtropical and subalpine transects, and (d–f) are relationships between phylogenetic beta diversity and spatial distance in tropical, subtropical and subalpine transects, respectively.

biogeographic contingency. These species then assort themselves across elevations either based on niche-based processes (i.e. environmental filtering) or spatial-based processes (i.e. dispersal limitation; Myers *et al.* 2013). In this study, the significant influence of environmental distance on phylogenetic beta diversity may indicate that environmental filtering selects

more closely related species which tend to be more ecologically similar due to evolutionary conservatism (Losos 2008; Wiens *et al.* 2010). These results are in line with those of the few other studies in which taxonomic and phylogenetic beta diversity have been compared. In a North American study, the spatial turnover of plant species was predominantly due

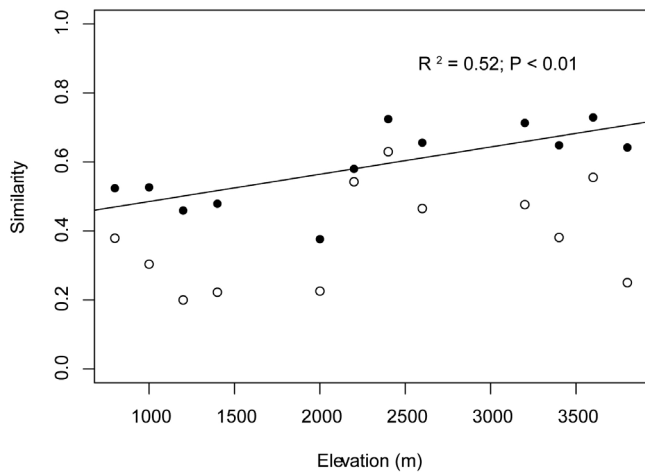


Figure 4: taxonomic and phylogenetic similarity between seedlings and adult trees along the elevational gradient sampled (open circles: taxonomic similarity; closed circles: phylogenetic similarity, R -squared = 0.52, F statistic= 10.69, P value < 0.01).

to the turnover of phylogenetically related species (Qian et al. 2013). This finding also has been reported in birds (Graham et al. 2009).

Closely related species generally have similar environmental requirements (Losos 2008), so environmental filtering should select phylogenetically related species at both seedling and adult stages. As this environmental filtering strengthens with increasing elevation, more phylogenetically related species are likely to be selected (Qian et al. 2014). Our results comport with this expectation, as across all elevations, phylogenetic similarity between adult and seedling assemblages rose significantly with elevation, although there was no such relationship for taxonomic similarity (Fig. 4).

This study region experienced a warm and humid environment ca. 20 million years ago with a diverse ancient tropical vegetation (Wu et al. 1987). Subsequently, the progressive southeasterly uplift of the Tibetan Plateau drove climatic changes and, as a result, significant changes in the flora and vegetation types (Jacques et al. 2014). Consequently, northern Yunnan (Lijiang) became a refuge for Palearctic species, whereas the more southerly site (Xishuangbanna) became a refuge for palaeotropical floristic species, with our subtropical site in Central Yunnan (Ailaoshan) representing a transitional zone (Li et al. 2015; Yan et al. 2009). Our study revealed an inconsistent relative contribution of environmental and spatial distances to beta diversity in tropical, subtropical and subalpine transects (Table 1 and 2). Previous studies have suggested that changes in dominance patterns reflect differing ecological mechanisms within different forests perhaps explained by a multifaceted biogeographic history (Condit et al. 2002; De Cáceres et al. 2012; Myers et al. 2013).

In this regard, our results agree with several previous studies, which have shown that the spatial effect was a key driver of tree species distributions from saplings to mature trees in Malaysian tropical forests (He et al. 1997; Seidler and Plotkin

2006). We found that the relative contribution of spatial distance decreased from the seedling to the adult tree stage in the tropical and subtropical transects (Table 1), consistent with a previous study in the same Xishuangbanna tropical forest. Hu et al. (2012a) showed that the effect of spatial processes decreased with increasing tree size (DBH \geq 1cm) at small spatial scales. This pattern highlights the importance of distance-dependent processes (e.g. dispersal) on the variation in community composition at the early stage of tree life history in tropical forests (Arieira et al. 2016). Conversely, in subalpine transects, we found that the composition of adult species between assemblages showed stronger spatial dependence (Table 1). Some spatially structured ecological factors that we did not measure such as soil nutrients may have had a strong effect on the survival of tree species into their later stages (Gilbert and Bennett 2010; Smith and Lundholm 2010), possibly accounting for the fact that spatial distance explained more of the variability in species composition in the adult than in the seedling stage.

Conflicting results across transects might, in large part, be associated with climatic and topographic drivers of ambient environmental conditions. For instance, some studies were conducted in areas with more complex and steeper gradients (Yang et al. 2015), while other studies were conducted in less extreme environmental gradients (Kanagaraj et al. 2011; Seidler and Plotkin 2006). Communities with different proportions of long-distance dispersed species may result in different rates of turnover for different life stages (Yang et al. 2016). Species that are capable of long-distance dispersal consistently showed less spatial clustering. These species (such as those dispersed by wind or frugivorous birds) may have seedlings far from the parent tree, but only the seedlings establishing in suitable habitat survived to more mature stages (Metz 2012), and suitable habitat is always spatial correlated (Harms et al. 2001). In contrast, species with relatively short dispersal capabilities (such as those dispersed by gravity) will likely exhibit the consequences of dispersal limitation across all life stages. Accordingly, taxonomic beta diversity will increase with life stage for communities with a large proportion of long-distance dispersal species and, in contrast, will be more stable across life stages for communities with a large proportion of short dispersal distance species. In this regard, we found contrasting result between subtropical transect and the other two transects (Table 1). There are also many other mechanisms that might lead to the unmatched species composition between adult trees and seedlings. Conspecific negative density dependence has been widely recorded in many kinds of forests and results in a lack of conspecific seedlings close to their parent trees (Johnson et al. 2012). Recruit limitation can also lead to an absence of conspecific seedlings in the understory (Hurt and Pacala 1995). Moreover, canopy closure may exclude shade intolerant seedlings in the understory (Comita and Hubbell 2009; Rieger et al. 2009).

When the various effects of environmental and spatial distance that we observed tracked the latitudes of our study plots

Table 1: variation in taxonomic beta diversity explained by environmental and spatial distances across seedling and adult tree communities in three elevational transects using multiple regressions on distance matrices

Location	Response distance matrix	Combination of environmental and spatial distance	Environmental distance	Spatial distance
Tropical transect	Seedling	0.32***	0.14***	0.10***
	Adult tree	0.27***	0.2***	0.04***
Subtropical transect	Seedling	0.11***	0.06***	0.07***
	Adult tree	<0.01	0.02	<0.01
Subalpine transect	Seedling	0.05**	0.05***	<0.01*
	Adult tree	0.26***	0.17***	0.05***

*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$. "Combination of environmental and spatial distance" represents the variation explained by both environmental and spatial components; "environmental distance" represents the variation explained purely by the environmental component; "spatial distance" represents the variation explained purely by the spatial component.

Table 2: variation in phylogenetic beta diversity explained by environmental and spatial distances across seedling and adult tree assemblages in three elevational transects using multiple regressions on distance matrices

Transect location	Response distance matrix	Combination of environmental and spatial distance	Environmental distance	Spatial distance
Tropical transect	Seedling	0.31***	0.17***	0.07***
	Adult tree	0.35***	0.12***	0.14***
Subtropical transect	Seedling	0.05***	0.01**	0.08***
	Adult tree	<0.01	0.02	<0.01
Subalpine transect	Seedling	<0.01	0.02	0.01
	Adult tree	0.18***	0.14***	0.02**

*** $P < 0.001$, ** $P < 0.01$. "Combination of environmental and spatial distance" represents the variation explained by both environmental and spatial components; "environmental distance" represents the variation explained purely by the environmental component; "spatial distance" represents the variation explained purely by the spatial component.

(that is: tropical to subtropical to subalpine) then we regard this as an 'expected' result because of the significant changes in climate (exacerbated by altitude) that this sequence of sites encompasses. When other patterns emerged, these may either reflect taxonomic idiosyncrasies of the plots (as discussed above) or historical and on-going anthropogenic impacts which may be overwhelming the 'natural' patterns that might otherwise be observed (Passy and Blanchet 2007; Vellend *et al.* 2007). The types and intensity of on-going use of the forests differ substantially. All forests have been used in the past for extraction of forest products from selective log removal to gathering of medicinal and culinary herbs, fungi and other minor forest products (Yang *et al.* 2004; Zhang and Cao 1995). This process is on-going, especially in the subalpine forest sites. These subalpine sites also continue to be used for grazing by horses, sheep and yaks (Feng *et al.* 2006).

In summary, we investigated the taxonomic and phylogenetic beta diversity of adult tree and seedling assemblages within forests across tropical, subtropical and subalpine elevational transects in southwest China. We demonstrated that environmental conditions, as well as spatial variables, shape the taxonomic and phylogenetic beta diversity among these three transects. Our results highlight the importance of phylogeny for fully understanding the pattern of seedling to adult transformation along an environmental gradient.

We suggest long-term monitoring of tree species composition among different life stages to improve understanding of the ecological processes that drive these patterns of community structure.

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REFERENCES

- Anderson MJ, Crist TO, Chase JM, et al. (2011) Navigating the multiple meanings of β diversity: a roadmap for the practicing ecologist. *Ecol Lett* **14**:19–28.
- Arieira J, Penha J, Nunes da Cunha C, et al. (2016) Ontogenetic shifts in habitat-association of tree species in a neotropical wetland. *Plant Soil* **404**:219–36.
- Bace R, Svoboda M, Pouska V, et al. (2012) Natural regeneration in Central-European subalpine spruce forests: Which logs are suitable for seedling recruitment? *Forest Ecol Manag* **266**:254–62.
- Bell G (2005) The co-distribution of species in relation to the neutral theory of community ecology. *Ecology* **86**:1757–70.
- Bertrand R, Gegout JC, Bontemps JD (2011) Niches of temperate tree species converge towards nutrient-richer conditions over ontogeny. *Oikos* **120**:1479–88.
- Bryant JA, Lamanna C, Morlon H, et al. (2008) Microbes on mountainsides: Contrasting elevational patterns of bacterial and plant diversity. *Proc Natl Acad Sci USA* **105**:11505–11.
- Chave J, Chust G, Thébaud C (2007) The importance of phylogenetic structure in biodiversity studies. In: Storch D, et al. (eds.), *Scaling Biodiversity*. Cambridge Press, 151–67.
- Chesson P (2000) Mechanisms of maintenance of species diversity. *Annu Rev Ecol Syst* **31**:343–66.
- Chust G, Chave J, Condit R, et al. (2006) Determinants and spatial modeling of tree β -diversity in a tropical forest landscape in Panama. *J Veg Sci* **17**:83–92.
- Comita LS, Hubbell SP (2009) Local neighborhood and species' shade tolerance influence survival in a diverse seedling bank. *Ecology* **90**:328–34.
- Condit R, Pitman N, Leigh EG Jr, et al. (2002) Beta-diversity in tropical forest trees. *Science* **295**:666–9.
- De Cáceres M, Legendre P, Valencia R, et al. (2012) The variation of tree beta diversity across a global network of forest plots. *Glob Ecol Biogeogr* **21**:1191–202.
- Dixon P (2003) VEGAN, a package of R functions for community ecology. *J Veg Sci* **14**:927–30.
- Feng J, Wang X, Xu C, et al. (2006) Altitudinal patterns of plant species diversity and community structure on Yulong mountains, Yunnan, China. *J Mt Sci* **24**:110–6.
- Fine PVA, Kembel SW (2011) Phylogenetic community structure and phylogenetic turnover across space and edaphic gradients in western Amazonian tree communities. *Ecography* **34**:552–65.
- Fortunel C, Paine CET, Fine PVA, et al. (2014) Environmental factors predict community functional composition in Amazonian forests. *J Ecol* **102**:145–55.
- Gilbert B, Bennett JR (2010) Partitioning variation in ecological communities: do the numbers add up? *J Appl Ecol* **47**:1071–82.
- Girdler EB, Barrie BTC (2008) The scale-dependent importance of habitat factors and dispersal limitation in structuring great lakes shoreline plant communities. *Plant Ecol* **198**:211–23.
- Goslee SC, Urban DL (2007) The ecodist package for dissimilarity-based analysis of ecological data. *J Stat Softw* **22**:1–19.
- Graham CH, Fine PV (2008) Phylogenetic beta diversity: linking ecological and evolutionary processes across space in time. *Ecol Lett* **11**:1265–77.
- Graham CH, Parra JL, Rahbek C, et al. (2009) Phylogenetic structure in tropical hummingbird communities. *Proc Natl Acad Sci USA* **106**:19673–8.
- Harms KE, Condit R, Hubbell SP, et al. (2001) Habitat associations of trees and shrubs in a 50-ha neotropical forest plot. *J Ecol* **89**:947–59.
- He FL, Legendre P, LaFrankie JV (1997) Distribution patterns of tree species in a Malaysian tropical rain forest. *J Veg Sci* **8**:105–14.
- Hu YH, Lan GY, Sha LQ, et al. (2012a) Strong neutral spatial effects shape tree species distributions across life stages at multiple scales. *PLoS One* **7**:e38247.
- Hu YH, Sha LQ, Blanchet FG, et al. (2012b) Dominant species and dispersal limitation regulate tree species distributions in a 20-ha plot in Xishuangbanna, southwest China. *Oikos* **121**:952–60.
- Hubbell SP (2001) *The Unified Neutral Theory of Biodiversity and Biogeography (mpb-32)*. Princeton, NJ: Princeton University Press.
- Hurttt GC, Pacala SW (1995) The consequences of recruitment limitation: reconciling chance, history and competitive differences between plants. *J Theor Biol* **176**:1–12.
- Jacques FM, Su T, Spicer RA, et al. (2014) Late Miocene southwestern Chinese floristic diversity shaped by the southeastern uplift of the Tibetan plateau. *Palaeogeogr Palaeoclimatol* **411**:208–15.
- Jin Y, Qian H, Yu M (2015) Phylogenetic structure of tree species across different life stages from seedlings to canopy trees in a subtropical evergreen broad-leaved forest. *PLoS One* **10**:e0131162.
- Johnson DJ, Beaulieu WT, Bever JD, et al. (2012) Conspecific negative density dependence and forest diversity. *Science* **336**:904–7.
- Jump AS, Mátyás C, Peñuelas J (2009) The altitude-for-latitude disparity in the range retractions of woody species. *Trends Ecol Evol* **24**:694–701.
- Körner C (2007) The use of 'altitude' in ecological research. *Trends Ecol Evol* **22**:569–74.
- Kanagaraj R, Wiegand T, Comita LS, et al. (2011) Tropical tree species assemblages in topographical habitats change in time and with life stage. *J Ecol* **99**:1441–52.
- Kembel SW, Cowan PD, Helmus MR, et al. (2010) Picante: R tools for integrating phylogenies and ecology. *Bioinformatics* **26**:1463–4.
- Kraft NJ, Comita LS, Chase JM, et al. (2011) Disentangling the drivers of β diversity along latitudinal and elevational gradients. *Science* **333**:1755–8.
- Lasky JR, Bachelot B, Muscarella R, et al. (2015) Ontogenetic shifts in trait-mediated mechanisms of plant community assembly. *Ecology* **96**:2157–69.
- Legendre P, Lapointe FJ, Casgrain P (1994) Modeling brain evolution from behavior: a permutational regression approach. *Evolution* **48**:1487–99.
- Leibold MA (2008) Ecology: return of the niche. *Nature* **454**:39–41.
- Leibold MA, Holyoak M, Mouquet N, et al. (2004) The metacommunity concept: a framework for multi-scale community ecology. *Ecol Lett* **7**:601–13.
- Li R, Kraft NJB, Yang J, et al. (2015) A phylogenetically informed delineation of floristic regions within a biodiversity hotspot in Yunnan, China. *Sci Rep* **5**:9396.
- Lichstein JW (2007) Multiple regression on distance matrices: a multivariate spatial analysis tool. *Plant Ecol* **188**:117–31.

- Losos JB (2008) Phylogenetic niche conservatism, phylogenetic signal and the relationship between phylogenetic relatedness and ecological similarity among species. *Ecol Lett* **11**:995–1003.
- Metz MR (2012) Does habitat specialization by seedlings contribute to the high diversity of a lowland rain forest? *J Ecol* **100**:969–79.
- Myers JA, Chase JM, Jiménez I, *et al.* (2013) Beta-diversity in temperate and tropical forests reflects dissimilar mechanisms of community assembly. *Ecol Lett* **16**:151–7.
- Myers JA, Chase JM, Crandall RM, *et al.* (2015) Disturbance alters beta-diversity but not the relative importance of community assembly mechanisms. *J Ecol* **103**:1291–9.
- Myers N, Mittermeier RA, Mittermeier CG, *et al.* (2000) Biodiversity hotspots for conservation priorities. *Nature* **403**:853–8.
- Passy SI, Blanchet FG (2007) Algal communities in human-impacted stream ecosystems suffer beta-diversity decline. *Divers Distrib* **13**:670–9.
- Perez-Ramos IM, Maranon T (2012) Community-level seedling dynamics in Mediterranean forests: uncoupling between the canopy and the seedling layers. *J Veg Sci* **23**:526–40.
- Qian H, Hao Z, Zhang J (2014) Phylogenetic structure and phylogenetic diversity of angiosperm assemblages in forests along an elevational gradient in Changbaishan, China. *J Plant Ecol* **7**:154–65.
- Qian H, Jin Y (2015) An updated megaphylogeny of plants, a tool for generating plant phylogenies, and an analysis of phylogenetic community structure. *J Plant Ecol* **9**:233–9.
- Qian H, Swenson NG, Zhang J (2013) Phylogenetic beta diversity of angiosperms in North America. *Glob Ecol Biogeogr* **22**:1152–61.
- R Development Core Team (2013) R: A Language and Environment for Statistical Computing [Internet]. Vienna, Austria: R foundation for statistical computing. <http://www.r-project.org> (19 November 2017, date last accessed).
- Rueger N, Huth A, Hubbell SP, *et al.* (2009) Response of recruitment to light availability across a tropical lowland rain forest community. *J Ecol* **97**:1360–8.
- Sørensen T (1948) A method of establishing groups of equal amplitude in plant sociology based on similarity of species and its application to analyses of the vegetation on Danish commons. *Biologiske Skrifter* **5**:1–34.
- Seidler TG, Plotkin JB (2006) Seed dispersal and spatial pattern in tropical trees. *PLoS Biol* **4**:e344.
- Smith TW, Lundholm JT (2010) Variation partitioning as a tool to distinguish between niche and neutral processes. *Ecography* **33**:648–55.
- Swenson NG (2011) Phylogenetic beta diversity metrics, trait evolution and inferring the functional beta diversity of communities. *PLoS One* **6**:e21264.
- Swenson NG, Enquist BJ, Thompson J, *et al.* (2007) The influence of spatial and size scale on phylogenetic relatedness in tropical forest communities. *Ecology* **88**:1770–80.
- Tello JS, Myers JA, Macía MJ, *et al.* (2015) Elevational gradients in β -diversity reflect variation in the strength of local community assembly mechanisms across spatial scales. *PLoS One* **10**:e0121458.
- Tilman D (2004) Niche tradeoffs, neutrality, and community structure: a stochastic theory of resource competition, invasion, and community assembly. *Proc Natl Acad Sci USA* **101**:10854–61.
- Tuomisto H, Ruokolainen K, Yli-Halla M (2003) Dispersal, environment, and floristic variation of western Amazonian forests. *Science* **299**:241–4.
- Vellend M, Verheyen K, Flinn KM, *et al.* (2007) Homogenization of forest plant communities and weakening of species-environment relationships via agricultural land use. *J Ecol* **95**:565–73.
- Webb CO, Ackerly DD, Kembel SW (2008) Phylocom: software for the analysis of phylogenetic community structure and trait evolution. *Bioinformatics* **24**:2098–100.
- Wiens JJ (2011) The niche, biogeography and species interactions. *Philos Trans R Soc Lond B Biol Sci* **366**:2336–50.
- Wiens JJ, Ackerly DD, Allen AP, *et al.* (2010) Niche conservatism as an emerging principle in ecology and conservation biology. *Ecol Lett* **13**:1310–24.
- Wu Z, Zhu Y, Jiang H (1987) *The Vegetation of Yunnan*. Beijing: Scientific Press.
- Yan LC, Shi JP, Zhu H, *et al.* (2009) The studies on floristics of seed plants in Ailaoshan region, Yunnan China. *J Trop Subtrop Botany* **17**:283–91.
- Yang J, Swenson NG, Zhang GC, *et al.* (2015) Local-scale partitioning of functional and phylogenetic beta diversity in a tropical tree assemblage. *Sci Rep* **5**:12731.
- Yang J, Zhang G, Ci X, *et al.* (2014) Functional and phylogenetic assembly in a Chinese tropical tree community across size classes, spatial scales and habitats. *Funct Ecol* **28**:520–9.
- Yang QS, Shen GC, Liu HM, *et al.* (2016) Detangling the effects of environmental filtering and dispersal limitation on aggregated distributions of tree and shrub species: life stage matters. *PLoS One* **11**:e0156326.
- Yang YM, Tian K, Hao JM, *et al.* (2004) Biodiversity and biodiversity conservation in Yunnan, China. *Biodivers Conserv* **13**:813–26.
- Zhang J, Cao M (1995) Tropical forest vegetation of Xishuangbanna, SW China and its secondary changes, with special reference to some problems in local nature conservation. *Biol Conserv* **73**:229–38.