

# Phylogenetic structure and phylogenetic diversity of angiosperm assemblages in forests along an elevational gradient in Changbaishan, China

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## Abstract

### Aims

Understanding what drives the variation in species composition and diversity among local communities can provide insights into the mechanisms of community assembly. Because ecological traits are often thought to be phylogenetically conserved, there should be patterns in phylogenetic structure and phylogenetic diversity in local communities along ecological gradients. We investigate potential patterns in angiosperm assemblages along an elevational gradient with a steep ecological gradient in Changbaishan, China.

### Methods

We used 13 angiosperm assemblages in forest plots (32 × 32 m) distributed along an elevational gradient from 720 to 1900 m above sea level. We used Faith's phylogenetic diversity metric to quantify the phylogenetic alpha diversity of each forest plot, used the net relatedness index to quantify the degree of phylogenetic relatedness among angiosperm species within each forest plot and used a phylogenetic dissimilarity index to quantify phylogenetic beta diversity among forest plots. We related the measures of phylogenetic structure and phylogenetic diversity to environmental (climatic and edaphic) factors.

### Important Findings

Our study showed that angiosperm assemblages tended to be more phylogenetically clustered at higher elevations in Changbaishan. This finding is consistent with the prediction of the phylogenetic niche conservatism hypothesis, which highlights the role of niche constraints in governing the phylogenetic structure of assemblages. Our study also showed that woody assemblages differ from herbaceous assemblages in several major aspects. First, phylogenetic clustering dominated in woody assemblages, whereas phylogenetic overdispersion dominated in herbaceous assemblages; second, patterns in phylogenetic relatedness along the elevational and temperature gradients of Changbaishan were stronger for woody assemblages than for herbaceous assemblages; third, environmental variables explained much more variations in phylogenetic relatedness, phylogenetic alpha diversity and phylogenetic beta diversity for woody assemblages than for herbaceous assemblages.

**Keywords:** elevational diversity gradient, herbaceous plants, net relatedness index, phylogenetic alpha diversity, phylogenetic beta diversity, woody plants

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## INTRODUCTION

Species diversity and composition vary among regions and local communities (Ricklefs 2004). Understanding what drives

the variation can provide insights into the mechanisms of community assembly (Cavender-Bares *et al.* 2009) but is a great challenge to ecologists (Ricklefs 2004). A large number of hypotheses have been proposed to explain contemporary

distributions of species diversity (Palmer 1994), but they may be put into two broad classes: niche-based deterministic versus neutrality-based stochastic hypotheses. Niche-based theories predict that factors such as interspecific interactions (e.g. competition, facilitation and predation) and environmental conditions play a primary role in structuring species assemblages in local communities, causing species assemblages to differ among different habitat types (Hutchinson 1957; Tokeshi 1990). Alternatively, neutrality-based theories emphasize the role of stochastic events, such as dispersal limitation and local extinction, in structuring species assemblages in local communities, causing random fluctuations of species composition among local communities and spatial dependency in species composition even under homogeneous environments (Hubbell 2001). Many studies have shown that both deterministic and stochastic processes play a role in structuring species assemblages but that their relative importance depends on prevailing environmental conditions (Chase 2007). In particular, deterministic processes are expected to play a greater role under a harsher environment (Chase and Myers 2011).

The decrease of species diversity along a latitudinal gradient from the equator to the poles is the most conspicuous species diversity pattern on earth (Rosenzweig 1995). It has been >200 years since the latitudinal diversity gradient was first described (Humboldt and Bonpland 1807), but its causes remain poorly understood (Mittelbach et al. 2007). It has been widely believed that the increase of harshness in environments, particularly temperature, toward the poles is responsible, at least in part, for the origin of the decreasing gradient in species diversity along a latitudinal gradient. In other words, the latitudinal gradient of species diversity is considered a result of niche-based processes (Condamine et al. 2012).

Paleobotanical data have shown that most plant lineages originated during the time when the planet was predominately under tropical environments (Behrensmeyer et al. 1992; Graham 1999). During the global cooling process initiated in the early Eocene, temperature decreased more quickly at higher latitudes so that the gradient of temperature from the equator to the poles became steeper. The climate cooling process forced tropical species at higher latitudes to migrate into lower (warmer) latitudes, to evolve into species that could tolerate colder temperatures or to go extinct. Because ecological traits (e.g. cold tolerance) are thought to be phylogenetically conserved (Latham and Ricklefs 1993), a hypothesis known as phylogenetic niche conservatism (i.e. the tendency of the niche of species within a lineage to be stable over evolutionary time; Wiens et al. 2010) and because an evolutionary event can rarely produce a lineage that is able to survive and reproduce in novel climatic conditions such as freezing temperature (Latham and Ricklefs 1993; Ricklefs 2006; Wiens and Donoghue 2004), fewer lineages have crossed ecophysiological barriers to distribute into harsher (e.g. colder) environments (Ricklefs 2006). The phylogenetic niche conservatism hypothesis predicts not only a decreasing trend in species diversity but also an increasing trend in phylogenetic relatedness among

species within assemblages along a latitudinal gradient from the equator to the poles. For the latter, the phylogenetic niche conservatism hypothesis predicts that species co-occurring within an assemblage should be more phylogenetically related (i.e. more phylogenetic clustering) at a higher latitude (Qian et al. 2013). In other words, species co-occurring in an assemblage should be less phylogenetically related (i.e. more phylogenetic overdispersion or evenness) at a lower latitude.

Similar to the latitudinal diversity gradient is the elevational diversity gradient, which was initially documented by Carolus Linnaeus 230 years ago (Linnaeus 1781). The two types of gradients may differ substantially in some aspects (Rahbek 1995), but many temperature-related variables (such as growing degree days, mean annual temperature, length of the growing season and minimum temperature of the coldest month) change in similar ways along both elevational and latitudinal gradients, and primary factors driving elevational diversity gradients are thought to be the same as those driving latitudinal diversity gradients. For example, temperature is commonly considered a primary driver of species diversity patterns along both latitudinal (Mittelbach et al. 2007; Qian and Ricklefs 2011) and elevational gradients (Sanders et al. 2007). An elevational gradient may have advantage over a latitudinal gradient for testing some temperature-related macroecological hypotheses partly because the geographical distance of the same length of the temperature gradient is much shorter along an elevational gradient, compared with that along a latitudinal gradient. For example, an upward shift of 100 m is approximately equivalent to a polarward shift of 100 km in the temperate zone with respect to temperature change (Jump et al. 2009; Stephenson and Das 2011). Thus, an elevational temperature gradient is much steeper than a latitudinal temperature gradient for a given geographical distance. A steeper environmental gradient is more appropriate for testing a species diversity pattern driven by environmental filtering because the steeper the environmental gradient, the more that environmental filtering will sort species based on their niche requirements (Willis et al. 2010) and because a steeper environmental gradient could avoid or reduce lags of species migration or community shifts for suitable habitats during climate change (Bertrand et al. 2011). In addition, many potential underlying causes that covary along latitudinal gradients do not covary along elevational gradients (Körner 2007). Thus, macroclimatic variation along elevational gradients can provide an excellent natural laboratory to investigate the role of temperature as an environmental filtering factor in structuring species assemblages in local communities.

Phylogenetic relatedness among species within local assemblages has been investigated along several elevational gradients but contrasting patterns have emerged. For example, species in local assemblages tend to be more phylogenetically related (i.e. greater phylogenetic clustering) at higher elevations for ants in the Smoky Mountains in the USA (Machac et al. 2011), biofilm bacteria in Laojun Mountain in China (Wang et al. 2012), bees in the Alps in Germany (Hoiss et al.

2012), bumblebees and butterflies in western Swiss Alps (Pellissier *et al.* 2013a, 2013b) and hummingbirds in the Andes in Ecuador (Graham *et al.* 2009). The results of these studies are consistent with the prediction of the phylogenetic niche conservatism hypothesis. However, along an elevational gradient in the Colorado Rocky Mountains in the USA, Bryant *et al.* (2008) found contrasting patterns for soil bacteria and angiosperms: toward a higher elevation, soil bacteria tend to be more phylogenetically related (more clustering), whereas angiosperms tend to be less phylogenetically related (more overdispersion). Similarly, Kluge and Kessler (2011) reported contrasting patterns in phylogenetic relatedness for epiphytic and terrestrial ferns along an elevational gradient in Costa Rica: epiphytic ferns tended to be more phylogenetically related with elevation, whereas terrestrial ferns tended to be less phylogenetically related with elevation. Because there are only few studies that have investigated the tendency of phylogenetic relatedness along elevational gradients, drawing a general conclusion on the elevational pattern of phylogenetic relatedness requires more studies. The first major goal of the present study was to investigate the tendency of phylogenetic relatedness among angiosperm species in local forest communities along an elevational gradient in Changbaishan, China. Because climate and soil are key environmental factors structuring species assemblages in local plant communities (Gurevitch *et al.* 2002; Liu *et al.* 2013), we also examined relations of phylogenetic relatedness and phylogenetic alpha diversity with climatic and edaphic variations among forests along the elevational gradient.

When environmental filtering plays a primary role in determining the difference in species composition between local communities, one would expect that there would be not only a non-random phylogenetic structure within a local community but also a non-random phylogenetic structure in the turnover of species between local communities (i.e. a phylogenetic turnover beyond the one expected from the turnover of species independent of the phylogeny; Hardy *et al.* 2012). In other words, patterns of within-assemblage phylogenetic structure would ultimately lead to patterns in phylogenetic turnover between assemblages, i.e. phylogenetic beta diversity (Graham and Fine 2008; Zhang *et al.* 2013). Phylogenetic beta diversity measures phylogenetic distances among communities in a phylogenetic framework. Research of phylogenetic beta diversity links local processes (e.g. environmental filtering) to regional and evolutionary processes (e.g. ecological trait evolution) and thus addresses the question of how ecological and evolutionary factors interact to influence variations in species compositions in communities across a spatial extent or along an environmental gradient. Although elevational gradients are excellent systems for investigating phylogenetic beta diversity with respect to environmental gradient due to their steeper environmental gradients over short geographical distances, compared with latitudinal and longitudinal gradients, few studies have investigated phylogenetic beta diversity along elevational gradients. The second major goal

of the present study was to relate phylogenetic beta diversity to environmental (climatic and edaphic) distances between local angiosperm assemblages along the elevational gradient of Changbaishan.

Previous studies have shown that macroecological patterns for woody plants often differ substantially from those for herbaceous plants (e.g. Hawkins *et al.* 2011; Ricklefs and Latham 1992). Ricklefs and Latham (1992) suggest that large woody plants have climate-dominated niches, whereas herbaceous plants have edaphic and microhabitat-dominated niches. Accordingly, we analyzed data separately for woody and herbaceous plants.

## MATERIALS AND METHODS

### Study area and sites

Our study area is Changbaishan (also known as Changbai Mountain), which is located on the border between China and North Korea. Changbaishan is of volcanic origin (Zhao 1987) and is a cone-shaped mountain with its highest peak being 2749 m above sea level (at 42°00'N and 128°10'E). The vast majority of Changbaishan is located within Changbaishan National Nature Reserve in China, which is 1965 km<sup>2</sup> in area (located between 41°41' and 42°51'N in latitude, 127°43' and 128°16'E in longitude and 720 to 2691 m in elevation). Forest vegetation covers all elevations <1950 m, above which there is alpine tundra vegetation (Qian *et al.* 1999).

An elevational gradient was set on the northern slope of Changbaishan from 720 m (42.423 N, 128.096 E) to 1900 m (42.060 N, 128.073 E) in elevation within Changbaishan National Nature Reserve. Along the gradient, thirteen 32 × 32 m forest plots were set with an interval of ~100 m in elevation. The sites selected for each forest plot had little to no previous human disturbance. All angiosperm species within each forest plot were identified, and life forms (woody vs. herbaceous) of the species were documented. The forest plot located at the lowest elevation of the gradient was composed of numerous broadleaved tree species (e.g. *Acer mono*, *Fraxinus mandshurica*, *Juglans mandshurica*, *Phellodendron amurense*, *Quercus mongolica*, *Tilia amurensis*, *T. mandshurica* and *Ulmus japonica*) mixed with *Pinus koraiensis*; the forest plot located at the highest elevation of the gradient was composed of few tree species and dominated by *Betula ermanii*.

### Phylogenetic supertree and phylogenetic metrics

We used Phylomatic (Webb and Donoghue 2005) to build a phylogenetic supertree, which was based on Angiosperm Phylogeny Group's (2009) system. We assigned each species to a family of Angiosperm Phylogeny Group (2009) and used a maximally resolved supertree of angiosperms (available at <http://www.phylodiversity.net>) to build a phylogenetic supertree for all angiosperm species found in the 13 forest plots. Branch lengths were estimated with the BLADJ algorithm (Webb *et al.* 2008) based on family ages in a dated version of megatree of Davies *et al.* (2004) implemented in Phylomatic.

Given the scarcity of comprehensive, time-calibrated phylogenies within families and genera, we followed previous studies (e.g. Hardy et al. 2012) to treat genera as polytomies within families and species as polytomies within genera. In addition to building a phylogenetic supertree with both woody and herbaceous angiosperm species, we also built a phylogenetic supertree with only woody species and a phylogenetic supertree with only herbaceous species. These two supertrees were used respectively when phylogenetic metrics were calculated separately for woody and herbaceous species (see below).

We used Faith's phylogenetic diversity (PD) metric (Faith 1992) to quantify the phylogenetic alpha diversity of each forest plot as the total phylogenetic branch length joining the basal node (i.e. the angiosperm node in our case) to the tips of all the species in the forest plot. Faith's PD has the advantage of being phylogenetic diversity metric in conservation research (Faith 1992; Forest et al. 2007; Morlon et al. 2011; Rodrigues and Gaston 2002). Values of the PD for each plot were calculated using both woody and herbaceous species as well as using either life form.

We used the net relatedness index (NRI; Webb 2000) to quantify the degree of phylogenetic relatedness among species within each forest plot. NRI measures the standardized effect size of the mean phylogenetic distance (MPD), which estimates the average phylogenetic relatedness between all possible pairs of taxa in an assemblage. NRI is defined as follows (Webb 2000):  $NRI = -1 \times (MPD_{\text{observed}} - MPD_{\text{randomized}}) / (sdMPD_{\text{randomized}})$ , where  $MPD_{\text{observed}}$  is the observed MPD,  $MPD_{\text{randomized}}$  is the expected MPD of the randomized assemblages ( $n = 1000$ ) and  $sdMPD_{\text{randomized}}$  is the standard deviation of the MPD for the randomized assemblages. A positive NRI value indicates that MPD is lower than that expected by chance (i.e. species more closely related than expected) and that phylogenetic clustering of species occurs. Conversely, a negative NRI value results when the observed MPD is greater than that expected by chance (i.e. species more distantly related than expected by chance) and thus indicates phylogenetic overdispersion or evenness. Values of the NRI for each forest plot were calculated separately for woody and herbaceous species.

For each pair of forest plots, we calculated a phylogenetic Sørensen (PhyloSor) similarity index as follows:  $PhyloSor = 2 \times BL_{ij} / (BL_i + BL_j)$ , where  $BL_{ij}$  is the total length of the branches shared between forest plots  $i$  and  $j$ ,  $BL_i$  and

$BL_j$  are the total branch lengths in forest plots  $i$  and  $j$ , respectively (Bryant et al. 2008). Values of PhyloSor range from 0 (no similarity) to 1 (complete similarity). Phylogenetic dissimilarity (i.e.  $1 - \text{PhyloSor}$ ) is considered a measure of phylogenetic beta diversity. Values of PhyloSor between forest plots were calculated separately for woody and herbaceous species.

### Environmental variables

We used the following climatic variables to quantify climatic conditions of each forest plot: annual mean temperature, temperature seasonality, minimum temperature of the coldest month, temperature annual range, annual precipitation, precipitation of the driest month and precipitation seasonality. Data for these variables were obtained from the WorldClim database (Hijmans et al. 2005; available at <http://www.worldclim.org/>). The spatial resolution of the climatic data is 1 km, which is shorter than the shortest geographical distance separating the forest plots by a factor of 3.4 on average (the 13 forest plots were distributed along a gradient of 44 km). We subjected the seven climatic variables to a principal components analysis based on their correlation matrix. The first principal component (PC1) accounted for a high amount (93.2%) of the variation in the seven climatic variables (Table 1) and was strongly correlated with each of the seven climatic variables (see online supplementary Table S1). As a result, we used the climate PC1 to represent the seven original climatic variables.

Soils for each of the forest plots were characterized with the contents of organic matter, nitrogen, phosphorus and potassium. Soil data were obtained from the study by Hao et al. (2002). We subjected the four edaphic variables to a second principal components analysis based on their correlation matrix. The first two principal components (soil PC1 and PC2) accounted for a high amount (94.7%) of the variation in the four edaphic variables (Table 1). Accordingly, we used them to represent the four original edaphic variables.

### Data analysis

We used Pearson's correlation coefficient to quantify the relationships between pairwise variables. We conducted a series of partial regressions (Legendre and Legendre 1998) to partition the variance in PD or NRI into four fractions: uniquely explained by climate PC1, uniquely explained by soil PC1 and PC2, explained jointly by the climate and soil PCs and

**Table 1:** the first three principal components (PCs) of each of the two principal component analyses for climatic and soil variables

	Climate			Soil		
	PC1	PC2	PC3	PC1	PC2	PC3
Eigenvalue	6.523	0.364	0.084	3.186	0.601	0.146
Proportion of variance	93.190	5.195	1.207	79.655	15.016	3.646
Cumulative % of variance	93.190	98.385	99.592	79.655	94.671	98.317
Broken-stick eigenvalue	2.593	1.593	1.093	2.083	1.083	0.583



explained by neither climate nor soil. We also conducted a series of partial regressions to partition the variance in PhyloSor into four fractions: uniquely explained by climatic distance, uniquely explained by edaphic distance, explained jointly by climatic and edaphic distances and explained by neither distance. Climatic distance was measured as absolute values of differences in climate PC1 between paired forest plots, and edaphic distance between paired forest plots was calculated as the Euclidean distance based on soil PC1 and PC2.

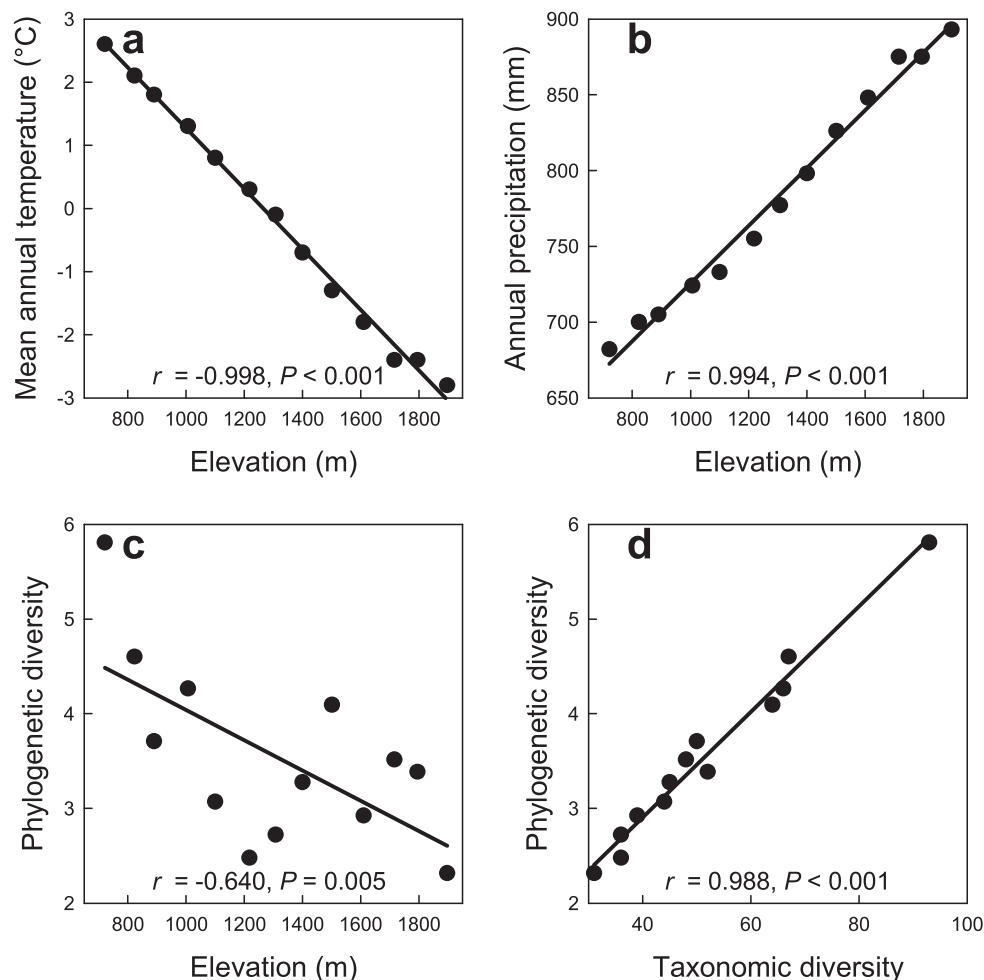
Because of the non-independence in spatially autocorrelated or pairwise data, the number of degrees of freedom can increase the rate of the Type I error, and thus the significance of statistical tests based on traditional  $P$  values can be inflated. We determined  $P$  values based on a randomization approach. Specifically, we performed a random permutation ( $n = 999$ ) for each analysis, and obtained error probabilities by using the  $z$  standard deviate, where  $z = \text{abs}((\text{observed coefficient} - \text{mean of permuted coefficient}) / \text{standard deviation of permuted coefficient})$ ; (Crawley 2002). The  $z$  standard deviate is

normally distributed (Crawley 2002) so that the error probability can be assessed from statistical tables or appropriate curves or functions (e.g. a  $z$  score  $> 1.96$  translates into a  $P$  value  $< 0.05$  for a two-tailed test). Randomizations were performed with R software (R Development Core Team 2009).

## RESULTS

A total number of 191 angiosperm species were found in the 13 forest plots, of which 72 were woody plants and 119 were herbaceous plants. Taxonomic diversity (species richness) of woody plants was strongly and negatively correlated with elevation ( $r = -0.918$ ,  $P < 0.001$ ). However, species richness of herbaceous plants was weakly and negatively correlated with elevation ( $r = -0.171$ ,  $P = 0.267$ ).

The elevational gradient of Changbaishan was strongly correlated with both mean annual temperature ( $r = -0.998$ ,  $P < 0.001$ ; Fig. 1a) and annual precipitation ( $r = 0.994$ ,  $P < 0.001$ ; Fig. 1b). Phylogenetic diversity was moderately and negatively correlated with elevation ( $r = -0.640$ ,  $P = 0.005$ ;



**Figure 1:** bivariate plots of elevation (a, b), mean annual temperature (a), annual precipitation (b), phylogenetic diversity (1000 million years) (c, d) and taxonomic diversity (number of angiosperm species) (d) for forest communities along an elevational gradient in Changbaishan.

Fig. 1c) and was strongly and positively correlated with taxonomic diversity ( $r = 0.998$ ,  $P < 0.001$ ; Fig. 1d).

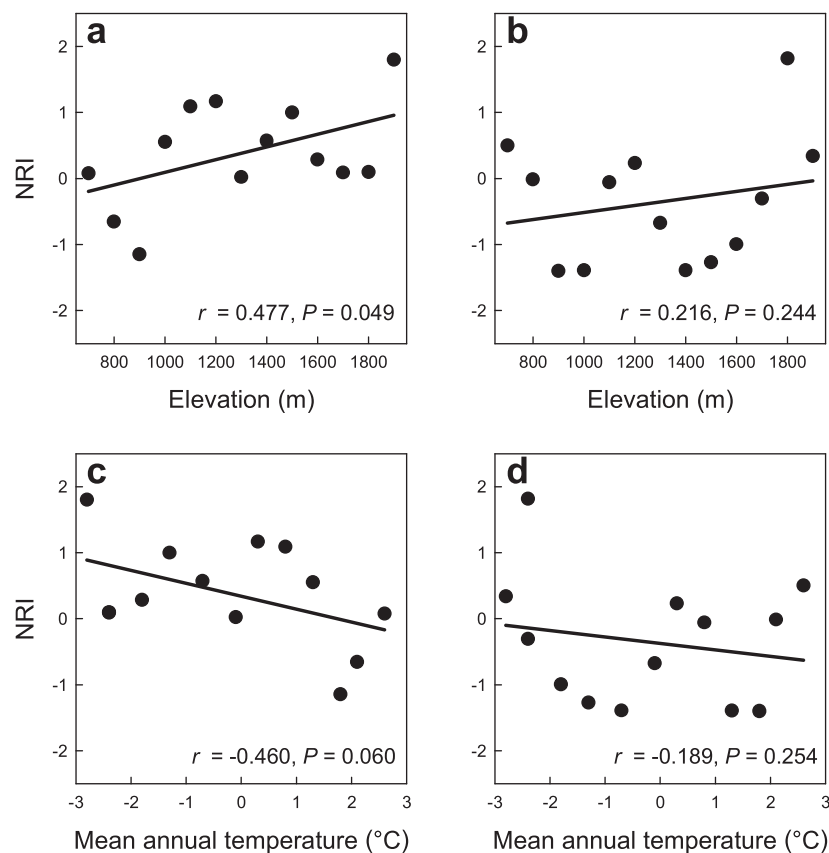
Of the 13 forest plots, 11 (84.6%) had positive values of NRI for woody plants, indicating that a vast majority of the woody angiosperm assemblages was phylogenetically clustered. In contrast, 9 (69.2%) of the 13 forest plots had negative values of the NRI for herbaceous plants, indicating that a vast majority of the herbaceous angiosperm assemblages were phylogenetically overdispersed. The mean ( $\pm$  SD) values of the NRI for the 13 forest plots were  $0.380 (\pm 0.784)$  and  $-0.355 (\pm 0.961)$ , respectively, for woody and herbaceous plants. The NRI tended to increase with elevation for both woody and herbaceous plants (Fig. 2a and b), indicating that species in local forest communities in Changbaishan were more phylogenetically related at higher elevations, although this trend was statistically significant only for woody plants ( $P < 0.05$ ). The trend of the NRI along the temperature gradient of Changbaishan mirrored that along the elevational gradient (Fig. 2c and d), although the relationship between the NRI and temperature was only marginally significant ( $P = 0.06$ ) for woody plants.

Climate (represented by climate PC1) and soil (represented by soil PC1 and PC2) together explained a great amount (87.6%) of the variance in the PD for woody plants. Climate

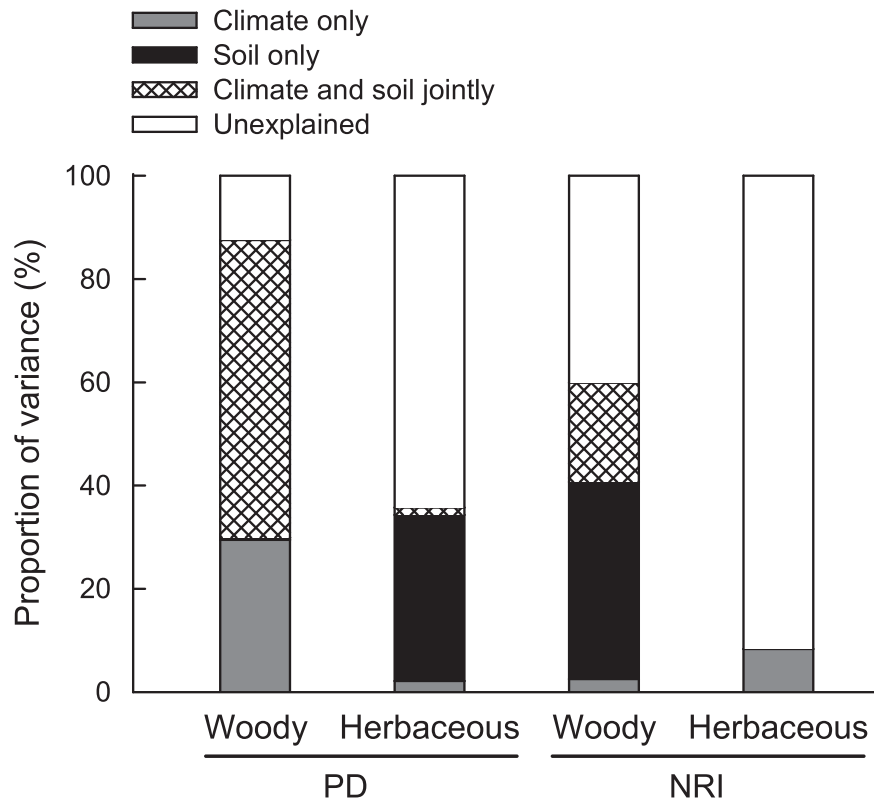
explained 29.5% of the variance independently and 57.7% of the variance jointly with soil, whereas soil independently explained only 0.4% of the variance in the PD for woody plants (Fig. 3). In contrast, for herbaceous plants, climate and soil together explained only 35.7% of the variance in the PD, the vast majority of which was explained by soil alone (Fig. 3).

Climate and soil together explained 59.9% and 8.3% of the variance in the NRI for woody and herbaceous plants, respectively. For woody plants, soil explained much more variance in the NRI than climate; in contrast, soil explained no variance in the NRI for herbaceous plants (Fig. 3).

Phylogenetic beta diversity was significantly and positively correlated with both climatic and edaphic distances between forest plots along the elevational gradient in Changbaishan but was correlated with climatic distance more strongly than with edaphic distance (Fig. 4). Climatic and edaphic distances together explained 78.6% and 22.9% of the variance in phylogenetic beta diversity for woody and herbaceous plants, respectively (Fig. 5). For both life forms, nearly half of the explained variance was explained jointly by climate and edaphic distances between forest plots, and climatic distance explained much more variance in phylogenetic beta diversity than edaphic distance (Fig. 5).



**Figure 2:** relations of NRI with elevation and mean annual temperature for (a, c) woody and (b, d) herbaceous plants in forest communities along an elevational gradient in Changbaishan.

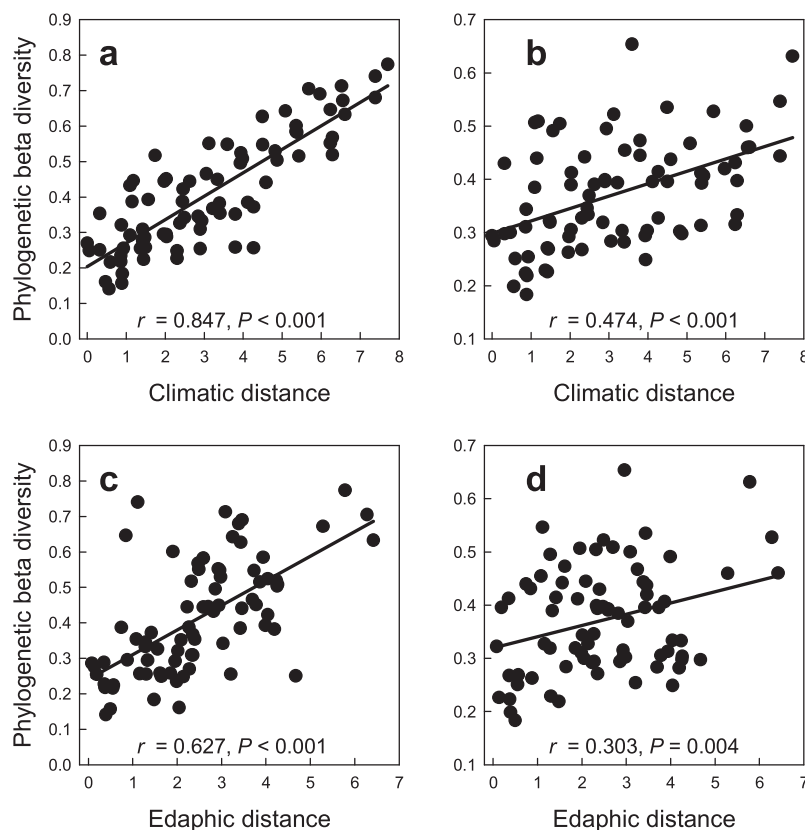


**Figure 3:** variance in phylogenetic alpha diversity (Faith's PD) and NRI explained only by climate PC1, only by soil PC1 and PC2, or jointly by climate PC1 and soil PC1 and PC2 for woody and herbaceous plants in forest communities along an elevational gradient in Changbaishan.

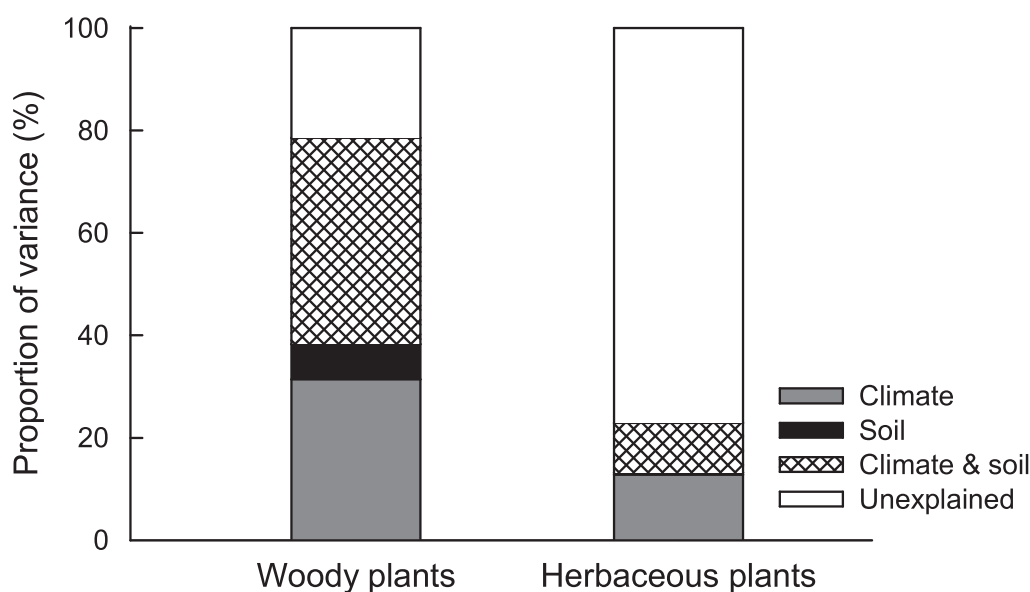
## DISCUSSION

We analyzed a data set with 13 angiosperm assemblages along an elevational gradient in Changbaishan. This elevational gradient is ideal for investigating climate-driven compositional and phylogenetic patterns of angiosperm assemblages at least for two reasons. First, the vegetation of the forest plot located at the lowest end of the gradient represents the typical low-elevation forest vegetation of a broad region in which Changbaishan is located and the site located at the highest end of the gradient is near the alpine treeline, which is the highest elevation for trees to grow in Changbaishan. The forest vegetation near the alpine treeline highly resembles the forest vegetation located near the arctic treeline in the Russian Far East in terms of forest structure and dominant species (Krestov 2003; Qian *et al.* 2003). Thus, the elevational forest gradient of Changbaishan is similar to a long latitudinal forest gradient of ~3000 km from mid to high latitudes in northeastern Asia. Second, unlike many high mountains with hump-shaped patterns in precipitation along their elevational gradients, which may result in complicated patterns of species diversity such as a hump-shaped pattern in species diversity (Vetaas and Grytnes 2002), gradients of both temperature and precipitation are not only monotonic but also linear along the elevational gradient of Changbaishan (Fig. 1).

Our study showed that angiosperm assemblages tend to be more phylogenetically clustered at higher elevations in Changbaishan. Our finding is contrary to that of Bryant *et al.* (2008), who showed that angiosperm assemblages tend to be more phylogenetically overdispersed at higher elevations in Colorado Rocky Mountains, USA. The gradient of angiosperm species richness from the lowest to highest elevations differs between Changbaishan and Colorado Rocky Mountains: angiosperm richness in Changbaishan followed a monotonic pattern (data not shown), whereas angiosperm richness in Colorado Rocky Mountains follows a hump-shaped pattern (Bryant *et al.* 2008). A hump-shaped pattern in species richness may suggest that some key factors driving species composition and richness also follow a hump-shaped pattern along the elevational gradient of Colorado Rocky Mountains. It is not clear if the hump-shaped pattern in angiosperm richness is responsible to some degree for the pattern of phylogenetic structure observed by Bryant *et al.* (2008) in Colorado Rocky Mountains. Our finding is also contrary to those of Culmsee and Leuschner (2013) and González-Caro *et al.* (2014). The former showed that the phylogenetic structure of angiosperm assemblages is overdispersion at high elevations in tropical Asia (Malesia) and the latter showed that phylogenetic evenness occurs at low temperatures, whereas phylogenetic clustering occurs at high temperatures in tropical South America



**Figure 4:** relations of phylogenetic beta diversity with climatic and edaphic distances for (a, c) woody and (b, d) herbaceous plants in forest communities along an elevational gradient in Changbaishan.



**Figure 5:** variance in phylogenetic beta diversity (measured as  $1 - \text{PhyloSor}$ ) explained only by climate PC1, only by soil PC1 and PC2, or jointly by climate PC1 and soil PC1 and PC2 for woody and herbaceous plants in forest communities along an elevational gradient in Changbaishan.

(Colombia). Nevertheless, the pattern of phylogenetic relatedness along the elevational gradient of Changbaishan is consistent with those found in most of the other studies on the

elevational pattern of phylogenetic relatedness (e.g. [Graham et al. 2009](#); [Li et al. 2014](#); [Machac et al. 2011](#); [Pellissier et al. 2013a, 2013b](#); [Wang et al. 2012](#)), supporting the prediction



of the phylogenetic niche conservatism hypothesis for phylogenetic community assembly along temperature gradients. Future studies should investigate the mechanisms that have caused the contrasting relationships between phylogenetic relatedness and elevation.

Our study showed that woody assemblages differ from herbaceous assemblages in several major phylogenetic aspects. First, phylogenetic clustering dominated in woody assemblages, whereas phylogenetic overdispersion dominated in herbaceous assemblages; second, patterns in phylogenetic relatedness along the elevational and temperature gradients of Changbaishan were stronger for woody assemblages than for herbaceous assemblages; third, environmental variables explained much more variations in phylogenetic relatedness, phylogenetic alpha diversity and phylogenetic beta diversity for woody assemblages than for herbaceous assemblages. A phylogenetic clustering pattern is commonly explained as a result of environmental filtering (Bryant *et al.* 2008; Webb *et al.* 2002) because ecological traits are generally phylogenetically conserved and thus more closely related species are expected to be more ecologically similar (Webb *et al.* 2002). Conversely, a phylogenetic overdispersion pattern is commonly explained as a result of interspecific interactions (Cavender-Bares *et al.* 2004; Helmus *et al.* 2007; Machac *et al.* 2011) because more closely related species are expected to have widely overlapping niches and thus to compete with one another strongly for similar resources, a process known as limiting similarity, which would lead to co-occurrence of distantly related species within a local assemblage. A lack of phylogenetic structure suggests that neutral processes structure local communities (Kembel and Hubbell 2006). The fact that both woody and herbaceous plants in our study showed the tendency of increasing phylogenetic clustering toward the highest elevation (and thus coldest temperature) in the gradient of Changbaishan may suggest that the environmental filtering process has played a primary role in structuring species into communities for both woody and herbaceous plants, although phylogenetic clustering may result from other processes (Cavender-Bares *et al.* 2009). A phylogenetic overdispersion pattern may result from the limiting similarity process in some cases (e.g. Graham *et al.* 2009), but it may result from other processes as well. It is not clear if the overall phylogenetic overdispersion pattern observed for herbaceous assemblages in the present study resulted from biotic interactions.

We believe that the fact that herbaceous plants showed a different pattern in phylogenetic structure and weaker relationships with environments, compared with woody plants, is to a large extent because of their microhabitat conditions and life history traits. Woody plants in general and trees in particular are on average much larger than herbaceous plants, and thus stems and buds of woody plants are more easily damaged by cold temperature in winter. In contrast, herbaceous species can be protected from cold temperature by being annual, by the production of underground buds and stems, or by snow

cover during winter. Extensive snow cover, which occurs in all forests in Changbaishan, creates a thermally isolating layer and can significantly alter temperatures at smaller spatial scales (Bartlett *et al.* 2004). Moreover, snow cover is generally thicker at higher elevations in Changbaishan (Chi *et al.* 1981), which would presumably further weaken the temperature gradient under the snow cover from the lowest to highest elevations, compared with the temperature gradient in air above snow cover. The microclimatic decoupling between the soil surface in forest understories and air temperatures can amount to 2–8°C due to factors such as shading, snow cover and evapotranspiration (Graae *et al.* 2012). Ricklefs and Latham (1992) suggest that large woody plants have climate-dominated niches, whereas herbaceous plants have edaphic and microhabitat-dominated niches. The temperature filtering process presumably has played a greater role in structuring species into local communities for woody plants than for herbaceous species. This would lead to a weaker relationship between phylogenetic diversity and climate for herbaceous plants, compared with that in woody plants. Furthermore, because herbaceous plants experience on average warmer winter temperatures than woody plants do in the same forest communities, phylogenetic structure is expected to reveal less phylogenetic clustering for herbaceous plants than for woody plants. This may partly explain why herbaceous assemblages have on average a lower degree of phylogenetic clustering (i.e. a higher degree of phylogenetic overdispersion) than do woody plants in our study.

Our study found that a vast majority (85%) of the woody angiosperm assemblages examined are phylogenetically clustered (i.e. NRI > 0). This pattern has arisen probably because Changbaishan is located near the middle of a full latitudinal gradient from tropical forests at the equator to boreal forests at the arctic treeline. Because temperatures in forests at the alpine treeline are limiting temperatures for trees to grow and because the forest at the alpine treeline of Changbaishan resemble the forest at the arctic treeline in the Russian Far East (Krestov 2003; Qian *et al.* 2003), the highest degree of phylogenetic relatedness (i.e. the largest value of the NRI) observed in our study for woody angiosperms may represent the highest degree of phylogenetic clustering along a latitudinal gradient of forests in eastern Asia.

Both temperature and precipitation change monotonically from the lowest to the highest elevations in Changbaishan. Because they are strongly correlated ( $r = -0.997$ ), their relative effects on phylogenetic structure and phylogenetic diversity cannot be distinguished. However, because (i) precipitation increases with elevation and because species-rich areas such as tropical rain forest areas usually are areas with high amounts of precipitation, (ii) precipitation in tropical forests can be more than four times as high as the precipitation at the highest elevation of forests in Changbaishan and (iii) a high precipitation usually facilitates species richness, patterns of taxonomic and phylogenetic diversity and phylogenetic relatedness observed in this study are unlikely to

be driven by the precipitation gradient in Changbaishan. We believe that temperature is a primary force driving phylogenetic relatedness patterns observed in this study.

Many previous studies on beta diversity have considered both geographical distance and environmental distance as drivers of beta diversity (e.g. Condit et al. 2002; Qian and Ricklefs 2007, 2012). Geographical distance has been commonly used as a proxy of dispersal limitation. We did not consider geographical distance in our analyses of phylogenetic beta diversity because we do not consider geographical distance as a dispersal limitation in our study system. This is because our study system is a transect from the lowest to the highest elevations on one side of a cone-shaped mountain. Nearly all angiosperm species found in our sample plots are widely distributed in all aspects of the cone-shaped mountain but are largely restricted to their respective elevational zones. Furthermore, the longest geographical distance separating any two forest plots in the present study is only ~44 km. Thus, we believe that distributions of most, if not all, species found in our sample plots along the elevational gradient in Changbaishan are primarily determined by environmental factors.

In sum, our study demonstrated that angiosperm species in local communities tend to be more phylogenetically related at higher elevations and in lower temperatures. This finding is consistent with the prediction of the phylogenetic niche conservatism hypothesis, although it is contrary to the findings of previous studies on the relationship between angiosperm phylogenetic relatedness and elevation. Variations in environments among local communities explained more variations in phylogenetic structure and phylogenetic alpha and beta diversity for woody plants than for herbaceous plants.

## SUPPLEMENTARY MATERIAL

Supplementary material is available at *Journal of Plant Ecology* online.

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