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A trait-based approach reveals the importance of biotic filter for elevational herb richness pattern

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Abstract

Aim: To evaluate how a biotic filter (overstorey cover [OC]) shapes an elevational herb richness pattern and to test whether intermediate elevations represent more suitable habitats for herb species due to the minimal biotic and moderate abiotic filtering that occurred there.

Location: Dongling Mountain, China.

Taxon: Herbs.

Methods: We sampled herb richness along a 1,000-m vertical transect (OC and elevation covary) and four horizontal transects (across the OC gradient with no change in elevation). Functional traits related to shade (leaf mass per area [LMA] and leaf stem ratio [LSR]) and freezing tolerance (leaf thickness [LT] and hair density [HD]) were collected based on vegetation sampling plots. We divided the richness data into below- and above-timberline groups and then assessed the most important driver for each group. By estimating the variations in species richness and functional diversity along horizontal transects, we examined how these parameters responded to OC while controlling for associated differences in elevation.

Results: Herb richness showed a unimodal relationship with elevation, with a peak around the timberline. Below the timberline, herb richness was better predicted by OC and showed a positive relationship with the functional diversity of LMA and LSR. The frost period performed better in predicting herb richness above the timberline, and herb richness was positively related to the functional diversity of HD.

Main conclusions: The results support our hypothesis and highlight the importance of OC in shaping herb richness patterns. Below the timberline, OC acts as a filter, sorting species based on their ability to tolerate shade, whereas the frost period limits richness above the timberline and favours species that can tolerate low temperatures. Therefore, we suggest that biotic interactions, as well as environmental and geographical factors, should be considered the main drivers of elevational plant richness patterns.

KEYWORDS

“hump-shaped” richness pattern, biotic and abiotic filtering, community assembly, elevational gradient, functional diversity, herb community

1 | INTRODUCTION

Explaining spatial variations in species richness is one of the central issues in ecology and biogeography (Nogues-Bravo, Araújo, Romdal, & Rahbek, 2008). It is widely assumed that richness patterns result from the interplay of abiotic and biotic processes (Rahbek, 2005); however, understanding the determinants of these patterns remains a challenge. Elevational gradients represent ideal systems for exploring the mechanisms driving richness patterns (Graham et al., 2014), as particular elevational gradients are embedded in single biogeographic regions and thus represent natural experiments that eliminate the effects of large-scale climate variation (Körner, 2000). Additionally, studies on elevational gradients can be repeated worldwide (Sundqvist, Sanders, & Wardle, 2013).

It was long thought that richness simply declined with elevation (MacArthur, 1972); however, many studies have demonstrated that this is often not the case. Rahbek (2005) showed that more than half of the taxa worldwide exhibit the greatest richness at intermediate elevations, and when the effect of area was standardized, this “hump-shaped” richness pattern was enhanced. One of the leading explanations for this phenomenon is that mid-elevations represent more suitable habitats than other elevations because they offer favourable climatic conditions (moderate temperatures and the highest water availability, e.g. Kluge, Kessler, & Dunn, 2006), the highest productivity (Wu et al., 2013) and less human disturbance (Nogues-Bravo et al., 2008); such benign environments would allow more species to persist. However, this hypothesis mainly focuses on abiotic, area-related or energy-related factors, whereas the role of biotic interactions has seldom been emphasized.

Biotic interactions are considered a significant filter in the structuring of plant communities (Grime, 1973). In forests specifically, the importance of overstorey species in determining herb richness has been demonstrated by both correlative and experimental studies. Overstorey species have been referred to as biotic modifiers because they can reduce microclimatic variability in the understorey (Mölder, Bernhardt-Römermann, & Schmidt, 2008), and the litter they produce increases soil nutrient availability (Collins & Pickett, 1988). Furthermore, an important effect of overstorey species is the reduction of light availability to the understorey, which limits the photosynthesis of understorey species. This light-mediated plant–plant interaction could act as a filter to constrain species according to their functional abilities, where species with thinner leaves and/or more biomass allocation to leaves may benefit from dense cover because they can harvest more light (Boardman, 1977), whereas shade-intolerant species are excluded.

In this study, we hypothesize that this biotic filter (light-mediated plant–plant interaction) shapes herb richness at low elevations and is responsible for the observed “hump-shaped” richness pattern (Figure 1). According to this hypothesis, overstorey species might exhibit maximum vigour at low elevations, where the cover is densest and only small subsets of species can tolerate the resulting low-light availability conditions. As elevation increases, overstorey species lose their vigour due to increasing abiotic stress, and species richness

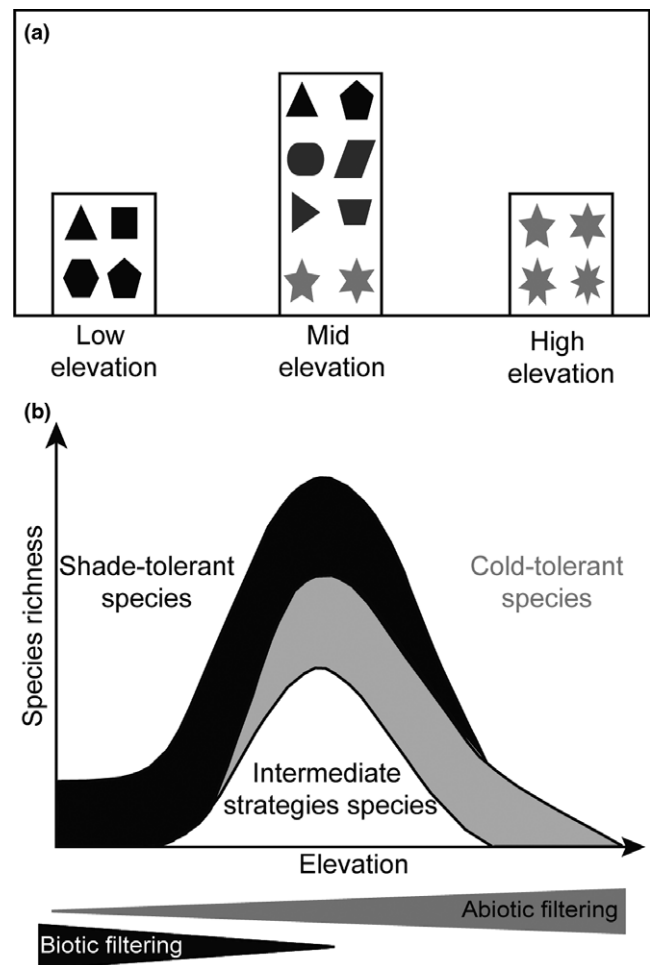


FIGURE 1 Conceptual model of how overstorey cover (biotic filtering) and frost period (abiotic filtering) shape elevational herb richness patterns (adapted from Grime, 1973). (a) Trait compositions at different elevations. Shapes represent different functional strategies. (b) Variations in herb richness along the elevational gradient; colours correspond to different strategy types: shade-tolerant (black), cold-tolerant (grey), or an intermediate strategy (white). The long triangle at the bottom of the figure represents the variation in the strength of biotic and abiotic filtering along the elevational gradient

increases because shade-intolerant species are relieved of the light limitation. However, at high elevations, low temperatures may filter out species that lack the ability to persist under cold conditions. Hence, the peak of herb richness occurs at mid-elevations because these elevations offer maximum light availability and moderate temperatures. This hypothesis is derived from Grime (1973) and has been confirmed by many experimental and observational studies (Fraser, Jentsch, & Sternberg, 2014; Gibb et al., 2015; Helm, Kalamees, & Zobel, 2014; Klanderud, Vandvik, & Goldberg, 2015) but has rarely been applied to the explanation of elevational richness patterns.

A precise description of the processes-shaping elevational richness patterns is challenging because multiple biotic and abiotic factors covary with elevation, which increases the difficulty of separating correlation from causation (Sundqvist et al., 2013). An alternative is to use a trait-based approach, which builds on the

**TABLE 1** Predictions of changes in individual functional diversity along an elevational gradient (adapted from Coyle et al., 2014). The solid black line represents the expected variation in the individual functional diversity

Trait	Functional importance	Functional diversity	
Leaf mass per area (LMA)	Related to photosynthetic rates (Pérez-Harguindeguy et al., 2013)	Species with high photosynthetic rates are advantageous in shaded environments, leading to a low LMA. Functional diversity of LMA will increase with elevation.	
Leaf stem ratio (LSR)	Related to carbon assimilation (Reich, Tjoelker, Walters, Vanderklein, & Buschena, 1998)	Shaded environments favour species with higher allocations to leaves and should lead to a high LSR. Functional diversity of LSR will increase with elevation.	
Leaf thickness (LT)	Thick leaves are an adaptation to frost (Pérez-Harguindeguy et al., 2013)	Low-temperature environments favour thick leaves, functional diversity of LT will decrease with elevation.	
Hair density (HD)	High hair density provides protection against frost (Ehleringer & Mooney, 1978)	Species with high hair density were allowed to persist in cold conditions, functional diversity of HD will decrease with elevation.	

assumption that species can join a community only if they possess functional traits for adapting to specific abiotic or biotic stressors (McGill, Enquist, Weiher, & Westoby, 2006). For example, under drought conditions, plants tend to exhibit small leaf areas to reduce transpiration, which leads to lower functional diversity of leaf area. Conversely, wet conditions permit a wider range of functional strategies and therefore result in higher functional diversity than do drought conditions.

Functional traits differentially represent an organism's ability to obtain resources, compete, and tolerate environmental stress (Ricotta & Moretti, 2011). Therefore, the variation in functional diversity based on certain traits can indicate the processes that play vital roles in the assembly of communities. We expect that biotic filtering at low elevations influences traits that are important for shade adaptation, thus driving trait convergence to an optimal state and leading to a lower diversity of such traits, while abiotic filtering at high elevations removes species that are unable to overcome the challenges of low temperatures and, in turn, decreases the diversity of traits involved in frost tolerance.

Herbaceous understorey vegetation is considered important for maintaining forest ecosystem services because it accounts for most

of the plant richness and affects nutrient cycling (Gilliam, 2007). Paradoxically, there is a paucity of studies on the response of herb richness to elevation (Sproull, Quigley, Sher, & González, 2015; Tang & Fang, 2004; Willinghöfer, Cicuzza, & Kessler, 2012). In this study, we therefore linked herb richness and functional traits to explore the underlying reason for the elevational pattern of herb richness and developed a set of predictions about changes in individual functional diversity along an elevational gradient (Table 1). We predicted that light limitation resulting from overstorey species is the most important driver of richness for herb communities below the timberline, whereas the herb richness pattern above the timberline is shaped by low temperatures.

2 | MATERIALS AND METHODS

2.1 | Study site

We collected data on Dongling Mountain, 100 km northwest of Beijing, China (Figure 1a,b). The location of the study area is 40°00'–40°03' N and 115°26'–115°30' E. The region has a typically warm, temperate and continental monsoon climate, with a mean annual

precipitation of 550 mm and a mean annual temperature of 6.4°C at 1,150 m (data from January 1992 to December 2002). The area spans an elevational gradient from 1,000 m to 2,303 m. The natural vegetation of the region is generally divided into two primary elevation-based habitat types: montane forest (1,000–2,200 m) and sub-alpine meadow (1,500–2,300 m). The montane forests are usually dominated by oak (*Quercus wutaishanica*, 1,000–1,800 m), birch (*Betula platyphylla*, 1,300–1,800 m; *Betula costata*, 1,800–2,200 m) and poplar (*Populus davidiana*, 1,200–1,600 m).

Species richness and functional traits were studied along one vertical transect and four horizontal transects (Figure 2c). All transects were distributed along the north slope of Dongling Mountain, with an elevational gradient of 1,300–2,300 m; the natural forest below 1,300 m was abandoned because it had been logged in the 1960s. The transect slope and aspect were maintained as constant as possible to control for the effects of topography.

2.2 | Vegetation sampling

For the vertical transects (1,300–2,300 m), 40 sites were chosen in elevation steps of 25 m, and each site contained three plots (10 × 10 m). Three quadrats (1 × 1 m) were randomly chosen within each plot to perform an inventory of herbaceous vegetation, and the species present in each quadrat were recorded. To eliminate the influence of the overstorey composition on herb diversity, our montane forest surveys focused only on the forests dominated by *Betula platyphylla*.

The horizontal transects were systematically located at elevational intervals of 200 m from 1,500 to 2,100 m. For each horizontal transect, three sites were selected along the overstorey cover (OC)

gradient (Figure S1 in Appendix S1), characterized by open area, sparse cover or dense cover. In the horizontal transects located at 1,500 and 1,700 m, the forest was dominated by *Betula platyphylla*, whereas at 1,900 and 2,100 m, the forest was dominated by *Betula costata*. The open area sites were defined as areas with an open canopy and a size >250 m² (50 × 50 m); we set this limit to ensure that the plots in the open areas were at least 10 m from the forest edge to avoid transition zones. We defined the sparse cover sites as areas with woody cover >40% and <60% and the dense cover sites as areas with >95% woody cover (Figure S2 in Appendix S1). The sites within the same horizontal transects were located 50–500 m apart from each other, depending on local conditions. We established three plots (consistent with the vertical transect) at each site, and the plots in each horizontal transect were always laid out parallel to each other.

2.3 | Trait collection

The selection and measurement of functional traits were conducted according to Pérez-Harguindeguy et al. (2013). Trait data measurements were recorded between July and August when herb leaves were fully expanded. Considering that individuals within a species may exhibit different trait values in different environmental conditions, 20 plots (10 × 10 m, based on vegetation sampling data) were selected along the vertical transect at elevation steps of 50 m. Plots were selected to ensure complete coverage of the elevational gradient (1,325–2,275 m) and to capture the natural variation in functional traits along the elevational gradient. In each horizontal transect, we selected three plots for trait collection (one per site, based on vegetation sampling data). Within each plot, three quadrats

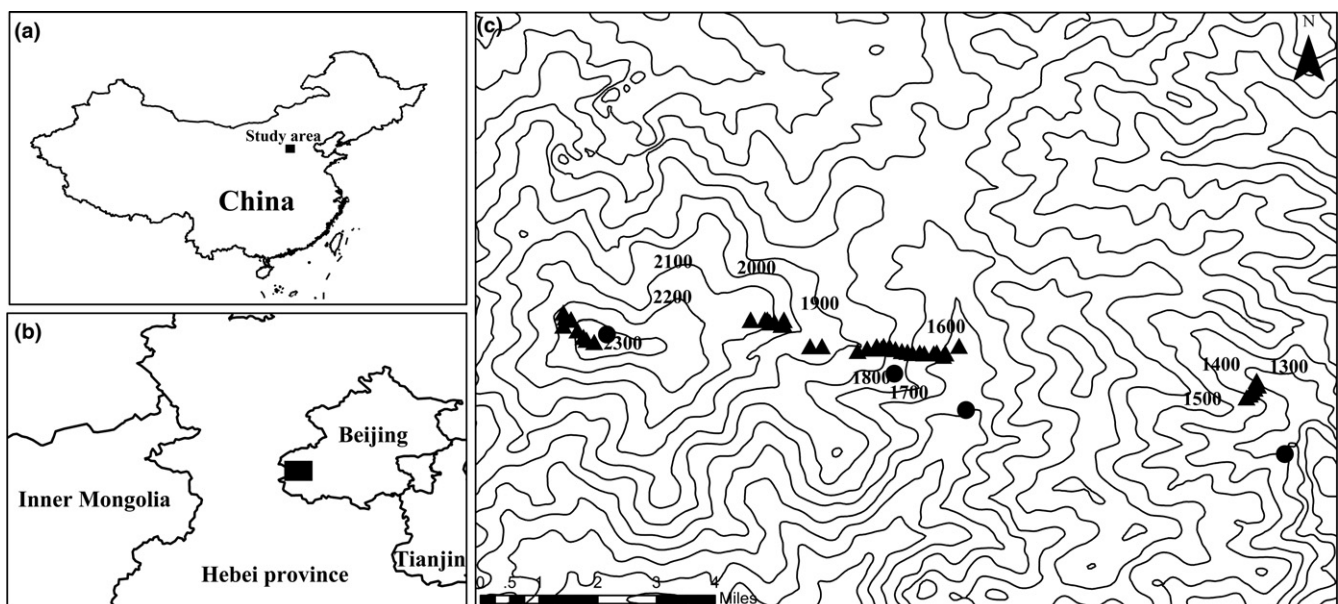


FIGURE 2 Map of the study area on Dongling Mountain: (a) location of the study area in China, (b) location of the study area in Beijing, and (c) location of the 40 sampling sites on Dongling Mountain. The black rectangle represents the study area; the black triangles represent the vertical transect sampling sites; the black circles represent individual horizontal transects; the solid line in (c) represents contours. The contour map data were downloaded from <http://www.gscloud.cn/>



(1 × 1 m, the same as for the herb sampling) were randomly selected for the inventory of herb species leaf traits. For each species in each quadrat, leaves were collected from one healthy-looking individual. For robust comparisons across species and elevations, traits were measured on the least-shaded, mature, healthy leaves when possible; leaves with obvious symptoms of pathogen or herbivore attack were excluded. Five leaves from each individual were selected for the measurement of leaf traits whenever possible. Within 20 trait-sampling plots, we recorded a total of 126 herb species that collectively accounted for 82% of the total species (across the entire 120 plots). We measured 1,036 individuals or an average of 8 individuals for each species.

We cut three equal-area, disc-shaped pieces from each leaf, placed all pieces in the oven (80°C for 48 hr), and then quantified the leaf mass per area (LMA) by taking the average value (YARIO-ELIII Elementar, Germany). Leaf thickness (LT) was measured three times per leaf, from the leaf base to the tip (Microcalliper, China). Finally, class divisions (five classes) were used to quantify hair density (HD) because this trait is relatively subjective. For each species in each quadrat, one intact mature individual was dried in an oven at 80°C for 48 hr, and the dried samples were then hand-separated into leaf blade and stem (including leaf sheath and inflorescences) components and weighed to quantify the leaf stem ratio (LSR) (Analytical Balance, China).

2.4 | Abiotic conditions

Temperatures were collected in each elevational transect from August 2016 to July 2017, using 10 Microdaq data-loggers (HoboPro RH/Temp). We deployed the data-loggers at elevation intervals of 100 m; the data-loggers were installed 10 cm below-ground to avoid artificial destruction. Temperature data were collected every 30 min. For each plot below the timberline, light availability was measured once in July 2017, when the overstorey layer species had completed leaf expansion. Measurements were performed with a digital camera (Canon 700D, Japan) with a fish-eye lens held horizontally 30 cm directly above the herb layer cover. Measurements were primarily taken on cloudy days between 7 a.m. and 9 a.m. because direct radiation can negatively affect the measurement of relative differences in radiation. The obtained photographs were analysed, using Winphot 5 (Ter Steege, 1996) to calculate the total site factor, which was measured as the proportion of solar radiation in a subplot relative to that in an open area.

2.5 | Statistical analysis

We measured functional diversity using the mean trait distance (MTD) of all species pairs that occurred in a plot (Clarke & Warwick, 1998). MTD is appropriate for this study because it has been shown to have the ability to discriminate community assembly processes and is mathematically independent of species richness (Coyle et al., 2014). We calculated MTD for each trait individually; the species-level traits were calculated using the species means for the entire

plot along the elevational gradient, and the distance between species was calculated as the Euclidean distance between species trait values.

To further eliminate the influence of the species pool, a constrained null model was used to simulate random assembly (Schweiger, Klotz, Durka, & Kuehn, 2008); the null distribution of individual functional diversity was generated for each plot by randomly shuffling trait values 1,000 times across the entire species pool and recalculating functional diversity each time. During each iteration, the species richness in each plot was kept constant (Kluge & Kessler, 2011). Then, we compared the observed empirical community values with the values of a null distribution model. Standardized effect sizes (SES) were calculated for the functional diversity of each trait, using the mean and standard deviations of the null distributions of functional diversity and are defined as follows:

$$\text{MTD}_{\text{obs},k} = \frac{2!(S-2)!}{S!} \sum_{i=1}^{S-1} \sum_{j=i+1}^S d_{ij}$$

$$\text{SES}_k = (\text{MTD}_{\text{obs},k} - \overline{\text{MTD}_{\text{null},k}}) / s_{\text{D}} \text{MTD}_{\text{null},k}$$

where $\text{MTD}_{\text{obs},k}$ is the observed mean distance of trait k ; S is the number of species in a plot; and d_{ij} is the trait distance between species i and j . $\text{MTD}_{\text{null},k}$ is the mean of the null distributions of trait k , and $s_{\text{D}} \text{MTD}_{\text{null},k}$ is the standard deviation.

The frost period was calculated as the length of time during which temperatures $\leq 0^\circ\text{C}$ occurred across the 12 months of the study. Actual evapotranspiration (AET) was calculated, and it was thus strongly related to net primary productivity. We calculated AET based on Turc's formula (Kluge et al., 2006):

$$\text{AET} = P / [0.9 + (P/L)^2]^{\frac{1}{2}}$$

$$L = 300 + 25T + 0.05T^3,$$

where P is soil moisture, and T is the mean annual temperature. The equal-elevation band area data were obtained from Shuttle Radar Topography Mission (STRM) 30 m digital elevation data (<http://srtm.csi.cgiar.org/>). We divided the range of elevation into 20 bands (50 m for each band) between 1,300 and 2,300 m. The surface area of each equal-elevation band (area) was calculated in ArcGIS 9.3.

To evaluate the importance of OC and frost period for herb richness, we used a multi-model information theoretic approach (Letten, Ashcroft, Keith, Gollan, & Ramp, 2013). To avoid overfitting and collinearity among variables, we pre-selected the explanatory variable based on our hypothesis and the strength of the species richness prediction, which was estimated using a generalized linear model (GLM). For the data obtained above the timberline, frost period and area showed high collinearity (Pearson's $|r| > 0.70$; Dormann et al., 2013). We excluded area from the model because (a) we hypothesized that frost period would be more important for shaping herb richness above the timberline; and the importance of area is only supported by a few studies (b) area

exhibited weaker (higher Akaike information criterion [AIC]) explanatory power than the frost period. Finally, the explanatory variables that exhibited a significant relationship with species richness and a weak correlation with other explanatory variables were selected for further analysis.

Models containing all possible combinations of explanatory variables were calculated and were then ranked according to their AIC values. We constructed the best-fitting subset by summing the Akaike weights of the highest ranked model until the sum exceeded 0.95. The relative importance of each variable was then calculated as the sum of the Akaike weights ($w + [j]$), where the explanatory variable occurred in the best fitting subset (Burnham & Anderson, 2002).

To reduce the risk of a false causal link between OC and species richness resulting from covariance of OC and elevation, we assessed how OC was correlated with species richness and individual functional diversity along the horizontal transects. In each horizontal transect, we used a paired *t*-test to explore the differences in species richness among the different cover levels. The Wilcoxon signed-rank test was used for comparisons of individual functional diversity because the data did not meet the assumptions of normality.

Spatial autocorrelation is a quality inherent to biogeographical data (Rahbek, 2005) because adjacent locations tend to be more similar due to various ecological properties and processes. This interdependence among data may affect the *p*-value and model selection in GLMs. To mitigate this problem, we tested spatial autocorrelations using Moran's *I* tests and removed the effects of spatial autocorrelations via simultaneous autoregression (SAR).

To investigate whether the richness patterns below and above the timberline are determined by different factors, we divided the vertical transect data into two groups: below the timberline (1,300–1,800 m) and above the timberline (1,800–2,300 m). Then, we conducted separate overall analyses for each of these groups (as above); each explanatory variable was included in a separate model. The analyses were performed, using R (R Development Core Team, 2014) and the Picante, Spdep, Vegan and MuMIn packages (Barton, 2012; Kembel et al., 2010; Oksanen, Blanchet, Kindt, Oksanen, & Suggests, 2013).

3 | RESULTS

3.1 | Elevational patterns of species richness and functional diversity

A total of 154 herb species from 42 families were observed along the 1000-m elevational gradient (Table S1 in Appendix S2). The families with the highest richness included Compositae (29), Liliaceae (15), and Ranunculaceae (18). Along the vertical transect, the observed species richness showed a “hump-shaped” pattern (Figure 3), with a peak approximately at the timberline, at 1,800 m ($P = 0.00$, $R^2 = 0.49$, $n = 120$), while a decrease was observed above the timberline.

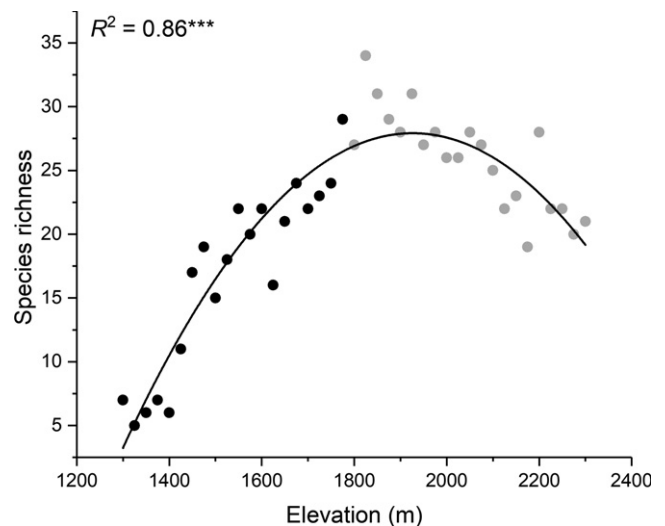


FIGURE 3 Elevational patterns of herb richness below (black circle) and above (grey circle) the timberline (based on vertical transect data). Adjusted R^2 and significance values are shown (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$)

Strong trends were observed in the individual functional diversity for plots across the entire vertical transect. The functional diversity of LSR and LMA increased along the entire vertical transect (Figure 4a,b); however, separate analyses show that LSR and LMA have different elevational patterns between below and above the timberline: when we only considered the data below the timberline, both LSR and LMA showed a positive relationship with elevation, whereas for the dataset above the timberline, neither LSR nor LMA significantly changed along the elevational gradient. In contrast, the functional diversity of LT and HD decreased with elevation (Figure 4c,d).

We examined the relationships between species richness and functional diversity in different elevational groups (Figure S1 in Appendix S3), and the results showed that the functional diversities of LSR and LMA positively correlated with species richness below the timberline, whereas above the timberline, functional diversity of HD showed positive relationships with species richness.

3.2 | Determinants of species richness at different elevation ranges

The models for species richness in each dataset showed spatial autocorrelation of residuals (Table S1 in Appendix S3). However, the signs and significance values obtained using SARs were almost identical to those obtained using GLMs. One explanation for these results may be that our data were insensitive to spatial autocorrelation. As expected, some of the explanatory variables selected for the GLM analysis were highly correlated, necessitating the exclusion of the weaker variable (greater AIC) of each collinear pair (Table S2 in Appendix S3).

When considering all plots, the frost period exhibited significant relationships with species richness (Table 2). When the plot dataset

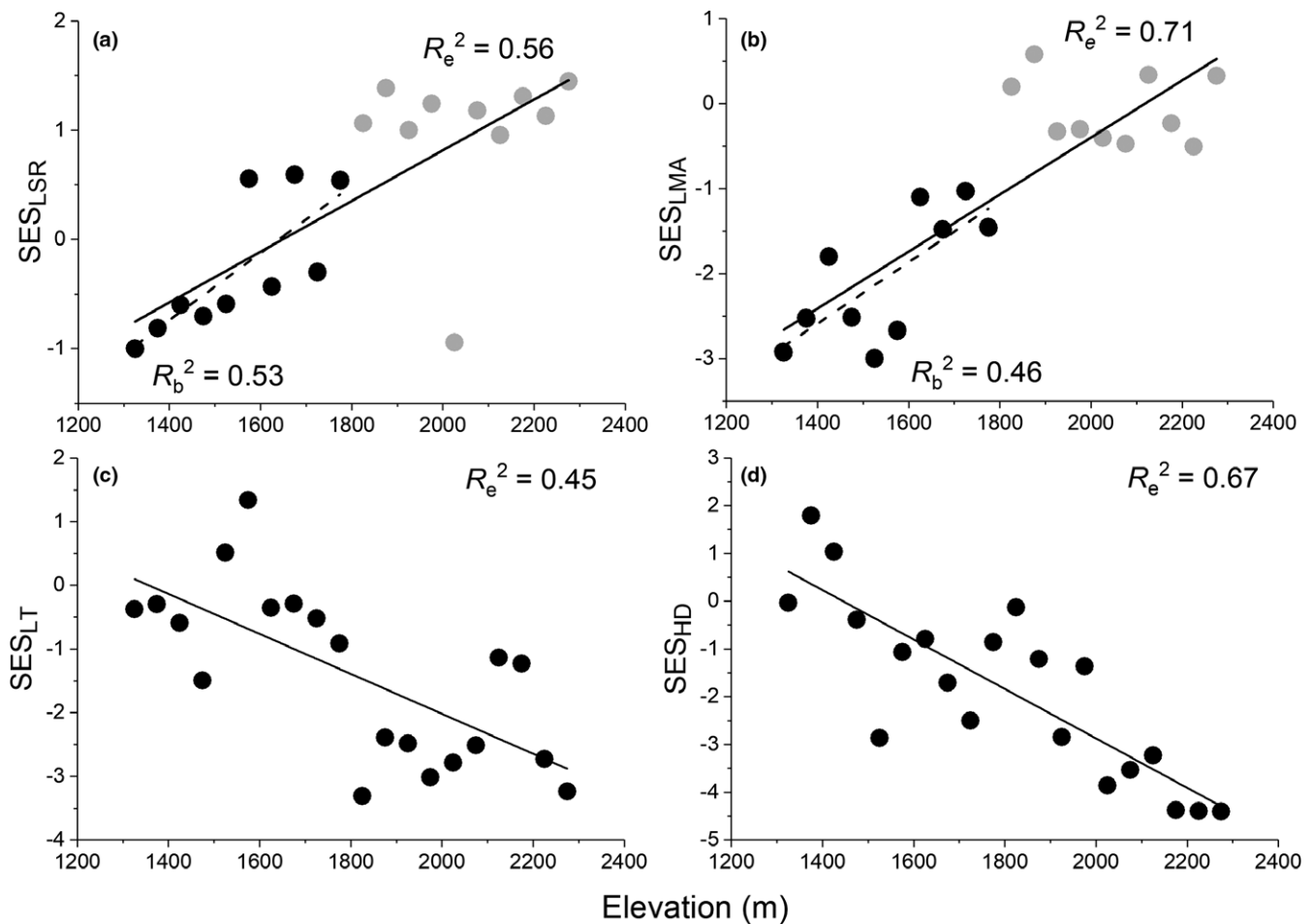


FIGURE 4 Elevational patterns of individual functional diversity (based on vertical transect data), measured as the standardized effect size. (a) Functional diversity of LSR; (b) functional diversity of LMA; (c) functional diversity of LT; (d) functional diversity of HD. We divided the dataset in half to obtain below- (black circle) and above-timberline (grey circle) groups and conducted separate analyses for the overall dataset and the below-timberline dataset. The solid line represents the trend line of the entire dataset; the dashed line represents the trend line of the dataset below the timberline. R_e^2 is the goodness of fit for the entire dataset; R_b^2 is for the dataset below timberline (based on the vertical transect data). $p < 0.001$ for all regressions

was divided into two elevational groups (below and above the timberline, each including 60 plots), the results showed that the groups were influenced by different factors. For the dataset below the timberline, species richness exhibited significant positive relationships with total site factor, area and frost period, with total site factor emerging as the more important predictor. For the dataset above the timberline, the frost period showed a significant negative relationship with species richness.

3.3 | Patterns of species richness and functional diversity along the horizontal transects

The results of the horizontal transect analysis were consistent with those of the vertical transect analysis. Herb richness changed negatively with total site factor (Figure 5a). Moreover, a pairwise comparison confirmed that species richness in open areas was significantly higher than that in sites under sparse or dense cover in all horizontal transects (Figure S3 in Appendix S1). Richness was also significantly

higher at sites under sparse cover than at sites under dense cover, except at 1,900 m. Furthermore, the functional diversity of LSR and LMA decreased along the cover gradient (Figure 5b,c).

4 | DISCUSSION

By analysing the variation in functional diversity and herb richness along vertical and horizontal transects, we obtained robust evidence that overstorey species can shape elevational herb richness patterns via the regulation of understorey light availability. Additionally, the results suggested that at high elevations, richness was reduced due to a long frost period. Because intermediate elevations offer the lowest light limitation and moderate temperatures, these elevations may support the coexistence of more species. In the following sections, we will discuss the role of biotic filtering in shaping elevational richness patterns and compare our findings with those of other herbaceous studies.

TABLE 2 Model-averaged parameters at the 95% confidence level set for species richness. The best model was identified based on the sum of the Akaike weights ($w + [j]$). Analyses were based on the data for the entire elevational gradient (1,300–2,300 m), and the data were separated into below- (1,300–1,800 m) and above-timberline (1,800–2,300 m) groups. NA = variable not included in the model; (.) = non-significant response variable; (.)^{*} = variable excluded from analysis because of collinearity. Actual evapotranspiration (AET); area (log-transformed) of each elevational band (30 m) on Dongling Mountain (Area)

Variables	All plots	Below-timberline	Above-timberline
Total site factor	NA	0.97**	NA
Frost period	1.00**	0.25**	1.00**
AET	(.)	(.)	(.)
Area	(.)	0.22*	(.) [*]

* $p < 0.05$; ** $p < 0.01$.

4.1 | Trait-based evidence of the importance of overstorey cover

Along the investigated elevational gradient, individual functional diversity exhibited strong trends (Figure 4) that were consistent with our initial hypotheses (Figure 1, Table 1), indicating that the community assembly was influenced by different factors at different ranges in elevation (below and above the timberline). At lower elevations, light availability limited herb richness, potentially due to the selection of functional traits related to light use. The conditions under dense woody cover restricted the functional diversity of LMA and LSR (Figure 4a,b). The constraint on functional traits could reflect the requirement for shade tolerance or a high efficiency of available light use in constituent species at low elevations, while ill-adapted species were excluded. At high elevations, the frost period became the most important driver of herb richness, and we suggest that only those species that exhibit high LT and/or HD can persist at high elevations (Schroeder, Kwak, & Allen, 2001).

Individual traits with differing ecological roles provide additional information related to community assembly mechanisms (Violle et al., 2007). However, notably, the variation in functional traits often depends on the site-specific environment (Coble & Cavaleri, 2015). In this study, the functional diversity of LSR and LMA exhibited different elevational patterns below and above the timberline (Figure 4a,b). Therefore, the functional diversity of LMA and LSR may primarily be driven by light at low elevations, whereas other factors become the most important drivers at high elevations. In particular, many studies have indicated that LMA is related to strategies to adapt to temperature (Van, Martine, Meir, Grace, & Atkin, 2009; Wright et al., 2004) and that leaves with high LMA are better protected against low temperature damage; however, we did not find that the functional diversity of LMA increased with elevation above the timberline. A possible explanation for this result is that although high-LMA leaves may increase the likelihood of survival at a high elevation (Read, Moorhead, Swenson, Bailey, & Sanders, 2014), having high LMA leaves may not be the only successful adaptive strategy; for example, some species rely on stiff and hairy leaves for protection from frost (Pérez-Harguindeguy et al., 2013).

In this study, we assumed that a benign environment would permit diverse functional strategies to coexist, which would in turn support more species. This hypothesis has been supported by many studies (Halpern & Floeter, 2008; Kluge & Kessler, 2011; Spasojevic, Grace, Harrison, & Damschen, 2014); however, it does not consider the effect of competition. The competition among herb species should favour species with different characteristics and increase functional diversity while reducing richness (Spasojevic & Suding, 2012). However, positive relationships between functional diversity and species richness would constitute evidence that competition might not be the dominant factor in determining herb richness along the elevational gradient, which does not imply that such competition is unimportant in shaded or cold conditions, as its role may be

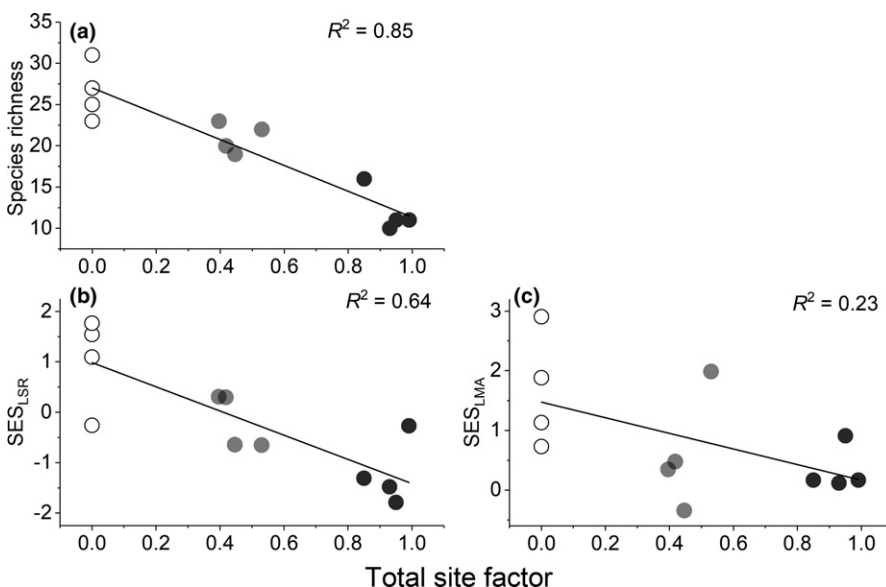


FIGURE 5 Species richness and functional diversity along the horizontal transects. Each horizontal transect includes three cover levels: open area (open circle), sparse cover (grey circle), and dense cover (black circle), with no elevational difference. (a) Species richness; (b) functional diversity of LSR; (c) functional diversity of LMA (based on horizontal transect data). $p < 0.001$ for all regressions



detectable in other functional traits not included in our study. We suggest that competition among herb species is secondary to the effects of light and temperature filters.

One potential source of uncertainty in our analyses is derived from the above-timberline models that exclude area because area covaries with frost period. Larger areas tend to comprise more species; thus, area is usually associated with resource and spatial heterogeneity; analyses based on observations cannot entirely rule out the influence of area. However, the consistency between trait-based observational data and our a priori hypothesis, as well as the influence of frost period, has been supported by other elevational gradient studies (Kluge et al., 2006; McCain, 2007). We are confident that frost period plays a more important role than area in herb richness patterns at high elevations. The mechanistic explanation is most probably directly linked to the control of available liquid water (O'Brien, 2006; Vetaas, 2006)

4.2 | Comparison of elevational patterns of herb richness worldwide

Herb richness often peaks at mid-elevations, similar to the richness trends of both trees and shrubs; however, the mechanisms underlying herb richness are more complex (Tang & Fang, 2004) and vary among climatic regimes. For example, herb richness often peaks at mid-elevations in arid systems (Mahdavi, Akhiani, & Van der Maarel, 2013; Sang, 2009; Whittaker, 1960), which can be explained by water limitation. While studies in trophic systems have found that herb richness declines with elevation (Vázquez & Givnish, 1998) or does not show significant patterns along elevational gradients (Willinghöfer et al., 2012); these patterns have been hypothesized to result from primary productivity or local history. Other recent studies have demonstrated that herb richness is more closely related to local factors (e.g. local topography and tree density; Sproull et al., 2015). However, given that many abiotic and biotic factors covary along elevational gradients, our understanding of the mechanisms shaping elevational herb richness patterns remains limited.

It is instructive that both our vertical and horizontal transect analyses showed that OC was significantly related to herb richness, thus providing additional strong evidence regarding the importance of OC. The effect of OC on herb richness has also been supported by other studies (Camarero, Gutiérrez, & Fortin, 2006; Hodačová & Prach, 2003), suggesting that OC could act as a biotic filter that structures herb communities. In contrast, when Jiang, Ma, Anand, and Zhang (2015) and Shrestha and Vetaas (2009) applied a similar method (based on vertical and horizontal transects), they did not find a negative relationship between OC and herb richness. This disparity might be explained by different environmental conditions; for example, OC may facilitate herb richness in an arid system via increased understory humidity in summer (Ramírez, Rey, Alcántara, & Sánchez-Lafuente, 2006), and therefore, the influence of OC on herb richness might be conditional on multiple limiting factors.

5 | CONCLUSIONS

Many previous studies have demonstrated frequent, strong relationships between species richness and abiotic factors, suggesting that the peak of richness will appear in habitats in which plants are subjected to minimal abiotic stress (Tello & Stevens, 2012). However, our study shows that OC dominates herb richness at low elevations by selecting herb functional traits, suggesting that biotic factors can also be a main driver of elevational richness patterns. This finding highlights the need to broaden our focus beyond climatic and geographical factors. Further work would benefit from additional elevational transect studies that investigate the importance of biotic interactions for elevational richness patterns to draw more general conclusions about the processes underlying elevational richness patterns.

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DATA ACCESSIBILITY

The datasets generated during and/or analysed during this study are available from the corresponding author on reasonable request

REFERENCES

- Barton, K. (2012). MuMIn: multi-model inference. R package ver.1.8.0. Retrieved from <https://cran.r-project.org/web/packages/MuMIn/index.html>
- Boardman, N. K. (1977). Comparative photosynthesis of sun and shade plants. *Annual Review of Plant Biology*, 28, 355–377. <https://doi.org/10.1146/annurev.pp.28.060177.002035>
- Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: A practical information-theoretic approach*. New York, NY: Springer. <https://doi.org/10.1007/b97636>
- Camarero, J. J., Gutiérrez, E., & Fortin, M. J. (2006). Spatial patterns of plant richness across treeline ecotones in the Pyrenees reveal different locations for richness and tree cover boundaries. *Global Ecology and Biogeography*, 15, 182–191. <https://doi.org/10.1111/j.1466-822X.2006.00211.x>
- Clarke, K. R., & Warwick, R. M. (1998). A taxonomic distinctness index and its statistical properties. *Journal of Applied Ecology*, 35, 523–531. <https://doi.org/10.1046/j.1365-2664.1998.3540523.x>
- Coble, A. P., & Cavaleri, M. A. (2015). Light acclimation optimizes leaf functional traits despite height-related constraints in a canopy shading experiment. *Oecologia*, 177, 1131–1143 <https://doi.org/10.1007/s00442-015-3219-4>
- Collins, B., & Pickett, S. (1988). Response of herb layer cover to experimental canopy gaps. *American Midland Naturalist*, 119, 282–290. <https://doi.org/10.2307/2425811>
- Coyle, J. R., Halliday, F. W., Lopez, B. E., Palmquist, K. A., Wilfahrt, P. A., & Hurlbert, A. H. (2014). Using trait and phylogenetic diversity to

- evaluate the generality of the stress-dominance hypothesis in eastern North American tree communities. *Ecography*, 37, 814–826. <https://doi.org/10.1111/ecog.00473>
- Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., ... Lautenbach, S. (2013). Collinearity: A review of methods to deal with it and a simulation study evaluating their performance. *Ecography*, 36, 27–46. <https://doi.org/10.1111/j.1600-0587.2012.07348.x>
- Ehleringer, J. R., & Mooney, H. A. (1978). Leaf hairs: Effects on physiological activity and adaptive value to a desert shrub. *Oecologia*, 37, 183. <https://doi.org/10.1007/BF00344990>
- Fraser, L. H., Jentsch, A., & Sternberg, M. (2014). What drives plant species diversity? A global distributed test of the unimodal relationship between herbaceous species richness and plant biomass. *Journal of Vegetation Science*, 25, 1160–1166. <https://doi.org/10.1111/jvs.12167>
- Gibb, H., Sanders, N. J., Dunn, R. R., Watson, S., Photakis, M., Abril, S., ... Parr, C. L. (2015). Climate mediates the effects of disturbance on ant assemblage structure. *Proceedings of the Royal Society B-Biological Sciences*, 282, 1–6. <https://doi.org/doi:10.1098/rspb.2015.0418>
- Gilliam, F. S. (2007). The ecological significance of the herbaceous layer in temperate forest ecosystems. *BioScience*, 57, 845–858. <https://doi.org/10.1641/B571007>
- Vázquez, G. J. A., & Givnish, T. J. (1998). Altitudinal gradients in tropical forest composition, structure, and diversity in the Sierra de Manantlán. *Journal of Ecology*, 86, 999–1020. <https://doi.org/10.1046/j.1365-2745.1998.00325.x>
- Graham, C. H., Carnaval, A. C., Cadena, C. D., Zamudio, K. R., Roberts, T. E., Parra, J. L., & Sanders, N. J. (2014). The origin and maintenance of montane diversity: Integrating evolutionary and ecological processes. *Ecography*, 37, 711–719. <https://doi.org/10.1111/ecog.00578>
- Grime, J. P. (1973). Competitive exclusion in herbaceous vegetation. *Nature*, 242, 344–347. <https://doi.org/10.1038/242344a0>
- Halpern, B. S., & Floeter, S. R. (2008). Functional diversity responses to changing species richness in reef fish communities. *Marine Ecology Progress Series*, 364, 147–156. <https://doi.org/10.3354/meps07553>
- Helm, A., Kalamees, R., & Zobel, M. (2014). Vegetation patterns and their underlying processes: Where are we now? *Journal of Vegetation Science*, 25, 1113–1116. <https://doi.org/10.1111/jvs.12206>
- Hodačová, D., & Prach, K. (2003). Spoil heaps from brown coal mining: Technical reclamation versus spontaneous revegetation. *Restoration Ecology*, 11, 385–391. <https://doi.org/10.1046/j.1526-100X.2003.00202.x>
- Jiang, Z., Ma, K., Anand, M., & Zhang, Y. (2015). Interplay of temperature and woody cover shapes herb communities along an elevational gradient in a temperate forest in Beijing, China. *Community Ecology*, 16, 215–222. <https://doi.org/10.1556/168.2015.16.2.9>
- Kembel, S. W., Cowan, P. D., Helmus, M. R., Cornwell, W. K., Morlon, H., Ackerly, D. D., ... Webb, C. O. (2010). Picante: R tools for integrating phylogenies and ecology. *Bioinformatics*, 26, 1463–1464. <https://doi.org/10.1093/bioinformatics/btq166>
- Klanderud, K., Vandvik, V., & Goldberg, D. (2015). The importance of biotic vs. abiotic drivers of local plant community composition along regional bioclimatic gradients. *PLoS ONE*, 10, 1–14. <https://doi.org/doi:10.1371/journal.pone.0130205>
- Kluge, J., & Kessler, M. (2011). Phylogenetic diversity, trait diversity and niches: Species assembly of ferns along a tropical elevational gradient. *Journal of Biogeography*, 38, 394–405. <https://doi.org/10.1111/j.1365-2699.2010.02433.x>
- Kluge, J., Kessler, M., & Dunn, R. R. (2006). What drives elevational patterns of diversity? A test of geometric constraints, climate and species pool effects for pteridophytes on an elevational gradient in Costa Rica. *Global Ecology and Biogeography*, 15, 358–371. <https://doi.org/10.1111/j.1466-822X.2006.00223.x>
- Körner, C. (2000). Why are there global gradients in species richness? Mountains might hold the answer. *Trends in Ecology & Evolution*, 15, 513–514. [https://doi.org/10.1016/S0169-5347\(00\)02004-8](https://doi.org/10.1016/S0169-5347(00)02004-8)
- Letten, A. D., Ashcroft, M. B., Keith, D. A., Gollan, J. R., & Ramp, D. (2013). The importance of temporal climate variability for spatial patterns in plant diversity. *Ecography*, 36, 1341–1349. <https://doi.org/10.1111/j.1600-0587.2013.00346.x>
- MacArthur, R. H. (1972). *Geographical ecology: Patterns in the distribution of species*. Princeton, NJ: Princeton University Press.
- Mahdavi, P., Akhiani, H., & Van der Maarel, E. (2013). Species diversity and life-form patterns in steppe vegetation along a 3000 m altitudinal gradient in the Alborz Mountains, Iran. *Folia Geobotanica*, 48, 7–22. <https://doi.org/10.1007/s12224-012-9133-1>
- McCain, C. M. (2007). Could temperature and water availability drive elevational species richness patterns? A global case study for bats. *Global Ecology and Biogeography*, 16, 1–13. <https://doi.org/10.1111/j.1466-8238.2006.00263.x>
- McGill, B. J., Enquist, B. J., Weiher, E., & Westoby, M. (2006). Rebuilding community ecology from functional traits. *Trends in Ecology & Evolution*, 21, 178–185. <https://doi.org/10.1016/j.tree.2006.02.002>
- Mölder, A., Bernhardt-Römermann, M., & Schmidt, W. (2008). Herb-layer diversity in deciduous forests: Raised by tree richness or beaten by beech? *Forest Ecology and Management*, 256, 272–281. <https://doi.org/10.1016/j.foreco.2008.04.012>
- Nogues-Bravo, D., Araújo, M. B., Romdal, T., & Rahbek, C. (2008). Scale effects and human impact on the elevational species richness gradients. *Nature*, 453, U216–U218. <https://doi.org/10.1038/nature06812>
- O'Brien, E. (2006). Biological relativity to water-energy dynamics. *Journal of Biogeography*, 33, 1868–1888. <https://doi.org/10.1111/j.1365-2699.2006.01534.x>
- Oksanen, J., Blanchet, F. G., Kindt, R., Oksanen, M. J., & Suggests, M. (2013). Package 'vegan'. Community ecology package Version 2.0-0. Retrieved from <https://cran.r-project.org/web/packages/vegan/>.
- Pérez-Harguindeguy, N., Díaz, S., Garnier, E., Lavorel, S., Poorter, H., Jau-reguiberry, P., ... Cornelissen, J. H. C. (2013). New handbook for standardised measurement of plant functional traits worldwide. *Australian Journal of Botany*, 61, 167–234. <https://doi.org/10.1071/BT12225>
- Rahbek, C. (2005). The role of spatial scale and the perception of large scale species richness patterns. *Ecology Letters*, 8, 224–239. <https://doi.org/10.1111/j.1461-0248.2004.00701.x>
- Ramírez, J. M., Rey, P. J., Alcántara, J. M., & Sánchez-Lafuente, A. M. (2006). Altitude and woody cover control recruitment of *Helleborus foetidus* in a Mediterranean mountain area. *Ecography*, 29, 375–384. <https://doi.org/10.1111/j.2006.0906-7590.04544.x>
- R Core Team (2014). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from <http://www.R-project.org/>.
- Read, Q. D., Moorhead, L. C., Swenson, N. G., Bailey, J. K., & Sanders, N. J. (2014). Convergent effects of elevation on functional leaf traits within and among species. *Functional Ecology*, 28, 37–45. <https://doi.org/10.1111/1365-2435.12162>
- Reich, P., Tjoelker, M., Walters, M., Vanderklein, D., & Buschena, C. (1998). Close association of RGR, leaf and root morphology, seed mass and shade tolerance in seedlings of nine boreal tree species grown in high and low light. *Functional Ecology*, 12, 327–338. <https://doi.org/10.1046/j.1365-2435.1998.00208.x>
- Ricotta, C., & Moretti, M. (2011). CWM and Rao's quadratic diversity: A unified framework for functional ecology. *Oecologia*, 167, 181–188. <https://doi.org/10.1007/s00442-011-1965-5>
- Sang, W. (2009). Plant diversity patterns and their relationships with soil and climatic factors along an altitudinal gradient in the middle Tianshan Mountain area, Xinjiang, China. *Ecological Research*, 24, 303–314. <https://doi.org/10.1007/s11284-008-0507-z>
- Schroeder, J. I., Kwak, J. M., & Allen, G. J. (2001). Guard cell abscisic acid signalling and engineering drought hardness in plants. *Nature*, 410, 327–330. <https://doi.org/10.1038/35066500>



- Schweiger, O., Klotz, S., Durka, W., & Kuehn, I. (2008). A comparative test of phylogenetic diversity indices. *Oecologia*, 157, 485–495. <https://doi.org/10.1007/s00442-008-1082-2>
- Shrestha, K. B., & Vetaas, O. R. (2009). The forest Ecotone effect on species richness in an arid trans-Himalayan landscape of Nepal. *Folia Geobotanica*, 44, 247–262. <https://doi.org/10.1007/s12224-009-9046-9>
- Spasojevic, M. J., Grace, J. B., Harrison, S., & Damschen, E. I. (2014). Functional diversity supports the physiological tolerance hypothesis for plant species richness along climatic gradients. *Journal of Ecology*, 102, 447–455. <https://doi.org/10.1111/1365-2745.12204>
- Spasojevic, M. J., & Suding, K. N. (2012). Inferring community assembly mechanisms from functional diversity patterns: The importance of multiple assembly processes. *Journal of Ecology*, 100, 652–661. <https://doi.org/10.1111/j.1365-2745.2011.01945.x>
- Sproull, G. J., Quigley, M. F., Sher, A., & González, E. (2015). Long-term changes in composition, diversity and distribution patterns in four herbaceous plant communities along an elevational gradient. *Journal of Vegetation Science*, 26, 552–563. <https://doi.org/10.1111/jvs.12264>
- Sundqvist, M. K., Sanders, N. J., & Wardle, D. A. (2013). Community and ecosystem responses to elevational gradients: Processes, mechanisms, and insights for global change. *Annual Review of Ecology, Evolution, and Systematics*, 44, 261–280. <https://doi.org/10.1146/annurev-ecolsys-110512-135750>
- Tang, Z., & Fang, J. (2004). A review on the elevational patterns of plant species diversity. *Biodiversity Science*, 12, 20–28.
- Tello, J. S., & Stevens, R. D. (2012). Can stochastic geographical evolution re-create macroecological richness–environment correlations? *Global Ecology Biogeography*, 21, 212–223. <https://doi.org/10.1111/j.1466-8238.2011.00661.x>
- Ter Steege, H. (1996). *Winphot 5: A programme to analyze vegetation indices, light and light quality from hemispherical photographs*. Georgetown: Tropenbos-Guyana Programme.
- Van, W., Martine, J., Meir, P., Grace, J., & Atkin, O. K. (2009). Altitudinal variation in leaf mass per unit area, leaf tissue density and foliar nitrogen and phosphorus content along an Amazon-Andes gradient in Peru. *Plant Ecology & Diversity*, 2(3), 243–254.
- Vetaas, O. R. (2006). Biological relativity to water–energy dynamics: A potential unifying theory? *Journal of Biogeography*, 33, 1866–1867. <https://doi.org/10.1111/j.1365-2699.2006.01618.x>
- Violle, C., Navas, M. L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., & Garnier, E. (2007). Let the concept of trait be functional!. *Oikos*, 116, 882–892. <https://doi.org/10.1111/j.0030-1299.2007.15559.x>
- Whittaker, R. H. (1960). Vegetation of the Siskiyou mountains, Oregon and California. *Ecological Monographs*, 30, 279–338. <https://doi.org/10.2307/1943563>
- Willinghöfer, S., Cicuzza, D., & Kessler, M. (2012). Elevational diversity of terrestrial rainforest herbs: When the whole is less than the sum of its parts. *Plant Ecology*, 213, 407–418. <https://doi.org/10.1007/s11258-011-9986-z>
- Wright, I. J., Reich, P. B., Westoby, M., Ackerly, D. D., Baruch, Z., Bongers, F., ... Villar, R. (2004). The worldwide leaf economics spectrum. *Nature*, 428(6985), 821. <https://doi.org/10.1038/nature02403>
- Wu, Y., Colwell, R. K., Rahbek, C., Zhang, C., Quan, Q., Wang, C., & Lei, F. (2013). Explaining the species richness of birds along a subtropical elevational gradient in the Hengduan Mountains. *Journal of Biogeography*, 40, 2310–2323. <https://doi.org/10.1111/jbi.12177>

BIOSKETCH

Zihan jiang is a postdoctoral scientist interested in the effects of biotic interactions on elevational richness patterns. He is also interested in how climate change influences extinction and speciation rates along an elevational gradient.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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