



Can the physiological tolerance hypothesis explain herb richness patterns along an elevational gradient? A trait-based analysis

Zihan Jiang¹, Keming Ma^{1,3} and M. Anand²

¹State Key Lab of Systems Ecology, Research Center for Eco-Environmental Sciences, Chinese Academy of Sciences, CN-100085 Beijing, PR China

²School of Environmental Sciences, University of Guelph, Guelph, Ontario, Canada, N1G 2W1

³Correspondence and reprint requests. Tel/Fax: 86-10-62849104, Email: mkm@rcees.ac.cn

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Abstract: Many taxa show their highest species richness at intermediate elevations, but the underlying reasons for this remain unclear. Here, we suggest that the physiological tolerance hypothesis can explain species richness patterns along elevational gradients, and we used functional diversity to test this hypothesis. We analyzed herb species richness, functional diversity, and environmental conditions along a 1300 m elevational gradient in a temperate forest, Beijing, China. We found that herb richness exhibited a “hump-shaped” relationship with elevation, with peak richness at approximately 1800 m. Functional diversity showed a significant unimodal relationship with elevation. The duration of high temperatures ($\geq 30^{\circ}\text{C}$: DHT) was the best predictor for herb richness and functional diversity along the gradient from 1020 to 1800 m, which suggest richness is limited by high temperature at low elevations. While along the gradient from 1800 to 2300 m, the duration of low temperatures ($\leq 0^{\circ}\text{C}$: DLT) was the most powerful explanatory variable, which indicated at high elevations, richness reduced due to low temperature. Our analyses showed that the functional diversity of traits related to drought-tolerance (leaf mass per area, leaf area, and leaf hardness) exhibited negative relationships with DHT, while functional diversity of traits related to freezing-tolerance (leaf thickness and hair density) exhibited negative relationships with DLT. Taken together, our results demonstrated that the richness-elevation relationship is consistent with the physiological tolerance hypothesis: at low elevations, richness is limited by high temperatures, and at high elevations, richness is reduced due to low temperatures. We concluded that our results provide trait-based support for the physiological tolerance hypothesis, suggesting that mid-elevations offer the most suitable environmental conditions, thus higher numbers of species are able to persist.

Abbreviations: CC–Canopy Cover, DET–Duration of Extreme Temperatures, DHT–Duration of High Temperatures, DLT–Duration of Low Temperatures, HD–Hair Density, LH–Leaf Hardness, LMA–Leaf Mass per Area, LT–Leaf Thickness, MAT–Mean Annual Temperature, SM–Soil Moisture.

Introduction

One of the central issues in community ecology is how to explain the spatial variance in species richness (Grytnes and Vetaas 2002, Nogues-Bravo et al. 2008, Ohlemuller and Wilson 2000). Many biologists have been fascinated by changes in species richness along elevational gradients, as these have proven to be useful platforms to research the effects of environmental change on mechanisms of species coexistence (Grytnes 2003, Shepherd and Kelt 1999). It was long believed that richness patterns along elevational gradients reflected latitudinal patterns (Stevens 1992), because the environmental variation across elevations is similar to that of a latitudinal gradient. However, many studies have shown that taxa reach their greatest richness at mid-elevations (Kessler et al. 2011, Odland and Birks 1999, Romdal and Grytnes 2007, Sanders 2002). This has been referred to as a hump-shaped pattern of richness, and has been found to be the most common pattern along the elevational gradient (Rahbek 1995).

Many hypotheses have been developed to explain this phenomenon, for example, the mid-domain effect (Colwell and Lees 2000), human influences (Nogues-Bravo et al. 2008), productivity gradients (MacArthur 1965), Rapoport's rule (Stevens 1992), and variations in the sample area (Rahbek 1995). However, few empirical studies have addressed the physiological tolerance hypothesis as an explanation of elevational patterns of richness, despite the fact that it is considered to be one of the leading hypotheses (along with the energy-richness and speciation rate hypotheses) to explain the spatial variance in richness (Currie et al. 2004). According to the physiological tolerance hypothesis, environments with suitable temperatures and water availability should have greater richness, because more species can tolerate these benign conditions, whereby only smaller subsets of species can overcome the challenges of more demanding environmental conditions (Roy et al. 1999).

By assuming that functional traits are associated with ecological strategies, functional diversity sheds light on

mechanisms of community assembly (Atkinson et al. 2010, Lebrija-Trejos et al. 2010, Marteinsdóttir and Eriksson 2014, McGill et al. 2006), which in turn, offers a new tool to test whether the richness-elevation relationships are consistent with the physiological tolerance hypothesis (Petchey and Gaston 2002, Spasojevic et al. 2014). We know that under stressful environmental conditions, abiotic filtering is more prevalent (Weiher et al. 2011), and will reduce the range of successful ecological strategies of co-occurring species. For example, in xeric environments, only species with traits that convey drought tolerance can persist, while species without those traits are excluded. As a result, the diversity of functional traits is limited. Conversely, benign environmental conditions permit a wider range of ecological strategies, and in turn, promote a higher level of functional diversity than that under demanding conditions.

In this study, we suggest that the physiological tolerance hypothesis can explain elevational patterns in richness. We assume that the peak of richness shown at mid-elevations is due to the fact that environmental conditions at high and low elevations are more stressful: at low elevations, high temperatures can lead to high evapotranspiration, and therefore increased water stress, such environmental filters might exclude drought intolerant species, while at high elevations, species richness would be limited by low temperatures, especially frost events (Bhattarai et al. 2004), such that species that cannot tolerate freezing would have difficulty surviving. In contrast, mid-elevations offer more favourable conditions (less extreme temperatures), in which more species can live. We addressed two main issues in particular: 1) Can the physiological tolerance hypothesis explain elevational patterns in herb richness? 2) Which environmental variables are the most important in determining elevational patterns of richness and functional diversity?

Methods

Study area

We collected data on Donglingshan Mountain, an extension of the Xiaowutaishan Mountains, 100 km northwest of Beijing, China. The location of the study area is 40°00'–40°03'N and 115°26'–115°30'E. The mean annual precipitation here in the region is 500–650 mm., mean annual temperature is 5–10°C. The area spans an elevational gradient from 1000 m to 2303 m. Its natural vegetation is highly heterogeneous, warm temperate zone deciduous broad-leaved forest (Yun et al. 2008), including primarily oaks (*Quercus* spp.), birches (*Betula* spp.), poplar (*Populus davidiana* Dode) and other mixed deciduous species (e.g., *Tilia* spp., *Ulmus* spp., *Acer* spp., *Juglans mandshurica* Maxim. and *Fraxinus rhynchophylla* Hance, etc.). There are also some conifers (*Pinus tabulaeformis* Carrière, *Platycladus orientalis* (L.) Franco), shrubs (e.g., *Prunus* spp., *Vitex negundo* var. *heterophylla* (Franch.) Rehd., etc.) and herbs (e.g., *Dendranthema chanelii* (Lévl.) Shih, *Saussurea nivea* Turcz., and *Thalictrum minus* L., etc.)

Sampling methods

We studied an elevational gradient on the western slope ranging from 1020 to 2300 m. The width of each transect was 10 m, and the length ranged from 80–200 m. We divided the 15 transects into 219 plots, each 10×10 m². Within each plot, overstory species (only including individuals with height ≥ 3 m) were identified and measured for crown diameter (largest and smallest diameter), and height (measured with Velmex digital hypsometer). Within each plot, three subplots (1 m × 1 m) were selected randomly for the herbaceous inventory.

The leaf functional traits we selected corresponded to those measured in past studies (Cornelissen et al. 2003, Spasojevic and Suding 2012, Westoby et al. 2002) because they have shown significant responses to particular environmental changes and easy to collect. Trait data measurements were taken between July and August, 2013, when herb species had finished their leaf expansion. Within vegetation plots, we selected 26 plots (10 m × 10 m) in an elevational step of 50 m. Within each plot, three subplots (1 m × 1 m) were selected randomly for the inventory of the herb species' leaf traits. For each herb species, leaves were collected from one individual representative; expanded and hardened leaves were sampled when possible. We quantified leaf mass per area (LMA) and leaf carbon-nitrogen ratio (C/N) five times per individual (we cut 5 equal area circular section from one leaf) (YARIO-ELIII Elementar, Germany). We measured leaf area (LA) at least once per individual (WinFOLIA Basic 2004a, REGENT Instruments Inc., Australia), and leaf hardness (LH) three times per individual (Shore Durometer, China). Leaf thickness (LT) was measured three times per individual from the leaf base to tip (Microcalliper, China). We used a class division (5 classes) to quantify leaf hair density (HD: Kluge and Kessler 2011) because this trait is rather subjective. The number of replicate measurements varied among species ranging from 1 to 78, depending on the frequency of presence.

Environmental data

From May 2012 to May 2013, temperature variables were collected from 26 Microdaq data-loggers HoboPro RH/Temp. These were deployed in the center of plot selected for the collection of functional traits data. In each plot, we established one data-logger 10 cm below ground and soil temperature data were collected every 30 min. Canopy cover (CC) was measured in plot-level, calculated as the sum of cover areas of overstory layer species. Soil moisture (SM) was measured six times in each plot by a Moisture Meter HH2 (Delta-T Devices Ltd., UK) and then averaged.

We focused specifically on extreme temperatures in this study, because they are more likely to affect individual fitness than is mean annual temperature (MAT: Reyer et al. 2013, Stenseth et al. 2002). However, we note that simply comparing extreme temperatures may be problematic. For example, two sites might have the same minimum temperature, but the abiotic stress should be stronger on the species that experiences the minimum temperature longer. As such, we focused on the duration of extreme temperature events (Table 1).

Table 1. Factors available for selection as correlates of species richness and functional diversity in single variable models.

Variables	Abbreviation	Range	Unit
Duration of high temperature ($\geq 30^{\circ}\text{C}$)	DHT	0-556	hour
Duration of low temperature ($\leq 0^{\circ}\text{C}$)	DLT	108-714	hour
Duration of high temperature plus duration of low temperature	DET	75-844	hour
Maximum temperature	MaxT	27.1-37.25	$^{\circ}\text{C}$
Minimum temperature	MinT	-4.31-(-13.41)	$^{\circ}\text{C}$
Mean annual temperature	MAT	2.1-6.8	$^{\circ}\text{C}$
Soil nitrogen availability	Soil N	102.11-721.83	mg/kg
Soil phosphorus availability	Soil P	430.21-1272.25	mg/kg
Soil pH	Soil pH	5.2-7.25	
Soil moisture	SM	23.62-83.39	%
Canopy cover	CC	0-299.25	m^2

Different herb species have different thermal requirements and tolerances, and thus the optimal temperature range for most plants is from 0 to 30°C (Abrami 1972, Went 1953). We suggest that temperatures higher than 30°C or lower than 0°C impose stress on herb species. We defined the length of time with temperature $\geq 30^{\circ}\text{C}$ (hour) as the duration of high temperatures (DHT), the length of time with temperature $\leq 0^{\circ}\text{C}$ (hour) as the duration of low temperatures (DLT), and the sum of DHT and DLT as the duration of extreme temperatures (DET). In addition to these variables, we also considered soil N, soil P, soil pH, SM, and CC, because these have been shown to be determining factors in elevational patterns of herb richness (Acharya and Basu 2014, Kooijman and Cammeraat 2010, Loranger-Merciris et al. 2008, Siciliano et al. 2014).

We used a hammer-driven soil core sampler 5 cm in diameter to obtain three soil profiles in each plot at a depth of 0-30 cm (219 plots in sum). Three replicate samples were homogenized by hand after plant material (roots/shoots) and pebbles in each sample were separated by soil sieve (mesh size = 2 mm) and discarded. The samples were then air-dried and soil properties were measured. The measured soil properties included soil nitrogen availability (soil N), soil phosphorus availability (soil P), soil pH, and soil moisture (SM). Soil N was measured using the semimicro Kjeldahl method, and soil P was measured by V-Mo colorimetry (Bao 2000). Soil pH was measured in a 1:2.5 (v/v) soil: water suspension with a digital pH meter (PHS-3C, Shanghai Lida Instrument Company, China).

Analyses

To evaluate the variation in functional diversity along the elevational gradient, we calculated three complementary indices, each of which corresponding to one aspect of functional diversity (Cornwell et al. 2006): functional richness (FRic), functional evenness (FEve), and functional dispersion (FDis). FRic describes how much trait space is filled, which corresponds to the ranges of trait values present in the community, FEve represents how regularly species are distributed in the trait space, and FDis represents the degree of trait dissimilarity among species, they measure how the trait space is filled (Petchey and Gaston 2002). The three measures are. For

each index, we calculated all traits combined (Laliberté and Legendre 2010), as well as each trait individually, and used the mean value of traits per species to calculate the indices.

To identify which environmental factors are most important for species richness and functional diversity, we related environmental factors to herb richness and functional diversity metrics by generalized linear models (GLM). In the model, environmental factors acted as explanatory variables, while species richness and functional diversity were response variables. We fitted single-predictor GLMs for response variables as quadratic and linear functions of each of the explanatory variables. For all significant quadratic and linear terms, we compared these models via the Akaike Information Criterion (AIC). Collinearity of explanatory variables can influence GLM analyses. To mitigate this problem, we evaluated correlations among all significant explanatory variables, and wherever two variables were correlated strongly (Pearson's $|r| > 0.70$) (Letten et al. 2013), we excluded the variable exhibiting the weakest (greater AIC) independent relationship with species richness or functional diversity.

To investigate whether or not the increase in species richness in the lower half of the gradient and the decline in the upper half are determined by different environmental factors, we divided the plot data into two groups: lower half of gradient (range from 1020 to 1800 m, 119 plots) and upper half of gradient (range from 1800 to 2300 m, 100 plots), we chose 1800 m to split data because the peak of herb richness show in here. Then, we conducted separate overall analyses for each of these groups (similar as above), each explanatory variable was included in a separate model. The analyses above were performed using R (R Development Core Team, 2010), while the calculations of functional diversity were conducted with package FD (Laliberté and Legendre 2010).

Results

We documented a total of 154 herb species from 13 families. Along the elevational gradient, the peak of herb richness exhibited at approximately 1800 m (Fig. 1). Functional diversity metrics based on all traits showed significant unimodal relationships with elevation (Fig. 1), except for FEve. The peak of FRic occurred at approximately 1800 m and that of FDis at approximately 1500 m. Patterns of species richness

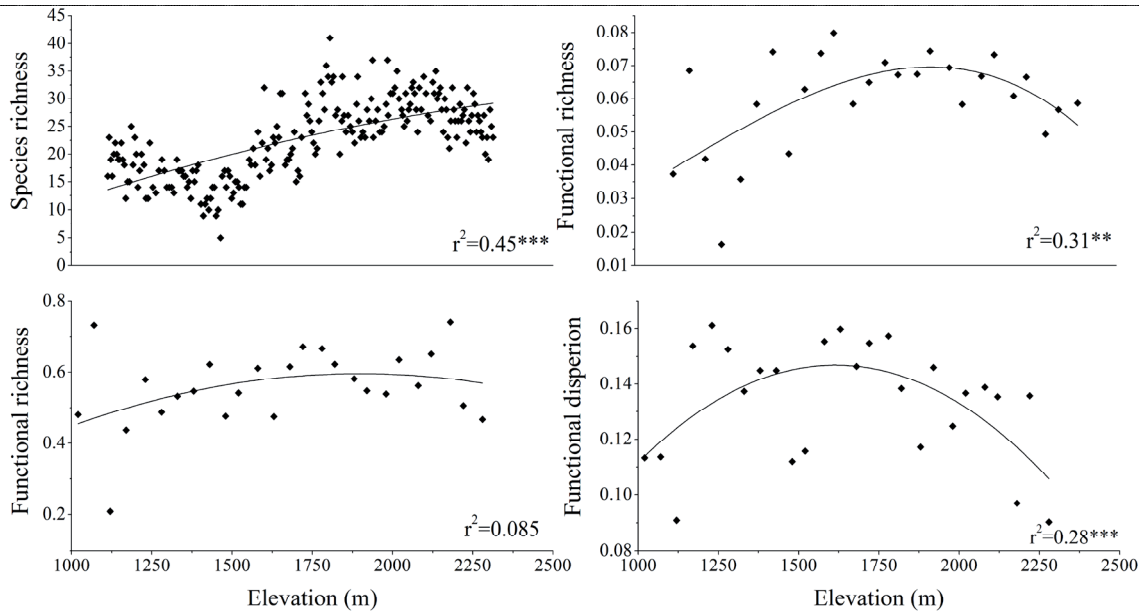


Figure 1. Herb richness and functional diversity patterns along elevational gradient on Donglingshan Mountain, Beijing. Regression lines with quadratic term and r^2 are given. Significance levels are * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

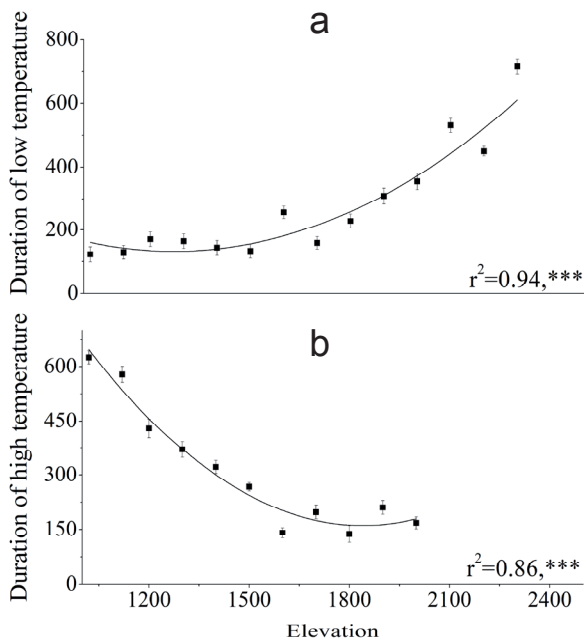


Figure 2. Temperature characteristics measured along an elevational gradient in Donglingshan Mountain, Beijing. Regression lines with quadratic term: (a) Duration of low temperatures ($<0^{\circ}\text{C}$; DLT) along elevational gradient, and (b) Duration of high temperatures ($>30^{\circ}\text{C}$; DHT) along elevational gradient, time expressed in hours. Significance levels are * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

and functional diversity metrics for all traits were correlated significantly ($P < 0.01$), more strongly for the richness-FRic relationship ($r = 0.24$, $P < 0.01$) than for the richness-FDis

($r = 0.14$, $P < 0.01$) and richness-FEve relationship ($r = 0.04$, $P < 0.01$).

Along the elevational gradient, temperature changed significantly with elevation (Fig. 2). Minimum temperatures ranged from -4.08°C at 1020 m to -13.84°C at 2300 m, while maximum temperatures ranged from 33.14°C at 1020 m to 28.33°C at 2300 m. DLT showed a significant positive relationship with elevation (135 h yr^{-1} at 1020 m and 741 h yr^{-1} at 2300 m), whereas DHT showed a significant negative relationship with elevation (556 h yr^{-1} at 1020 m and 0 h yr^{-1} at 2300 m).

The results of the model fitting to environmental factors are presented in Table S1. We considered that low values of the AIC associated with low p values were good fits to the model. As was expected, some environmental variables selected for the GLM analysis were correlated highly, which necessitated exclusion of the weaker (higher AIC) of each collinear pair. In the lower half of the gradient, DET exhibited a strong positive correlation with DHT ($r = 0.95$), MAT was correlated positively with CC ($r = 0.69$), while in the upper half of the gradient, DET was correlated positively with DLT ($r = 0.93$). In those instances, DET and MAT exhibited higher AIC, and thus were excluded. For all plots combined, both species richness and functional diversity showed a significant negative relationship with DET, and it exhibited greater explanatory power than other variables as a predictor of species richness and functional diversity. MAT and SM were correlated poorly with species richness in the linear model, but exhibited significant unimodal relationships with species richness, a result similar to that of Kluge et al. (2006).

When the plot dataset was divided into two groups, our results showed that different groups were influenced by different environmental factors (Table S1). For the lower half of the gradient, DHT emerged as the most important predictor

of richness and functional diversity; in particular, it correlated significantly and uniquely with FRic. In contrast, in the upper half of the gradient, DLT had the strongest explanatory power for both richness and functional diversity, and was the only environmental variable that was correlated significantly with FRic and FDis. No environmental factors showed significant unimodal relationships with richness or functional diversity, either in the lower or upper halves of the gradient.

Individual patterns of functional diversity showed varied relationships with environmental factors (Table S2). Functional diversity metrics based on LMA, LH, and LA were predicted better by DHT, except the FEve of LMA and LH. While for LT and HD, DLT was the most important predictor variable for their FRic and FDis, no environmental factors showed a significant relationship with their FEve. Soil N was the best predictor of FRic of C/N, but FEve and FDis did not have a significant relationship with any environmental factor.

Discussion

Our results supported the hypothesis that the peak of herb richness is shown at mid-elevations and because these represent optimal environmental conditions (less extreme temperatures). We found that the mid-elevation permitted a wider variety of ecological strategies than did the lower or higher elevations, which indicates that the middle elevations have milder conditions in which species can pass the abiotic filters more easily. In contrast, low or high elevations have stronger environmental filters that exclude species unsuited to such soil conditions.

The separate univariate analyses (lower and upper halves of the gradient) indicated that extreme temperatures operate in different ways at different gradients. At lower elevations, high temperatures limit richness, and this process may operate through selection on functional traits related to drought tolerance. Our results showed that the functional diversity of leaf mass per area, leaf hardness, and leaf area was restricted at low elevations (Table S2, Fig. 2) (high leaf mass per area and leaf hardness contributes to protection from drought (Mooney and Dunn 1970), and leaf area is associated with photosynthetic efficiency of water use (Parkhurst and Loucks 1972)). These results demonstrate that species can only persist at low elevations if they possess the functional traits required to overcome challenges from drought. In contrast, at high elevations, herb species are limited by low temperatures, and thus, we suggest that only those species that possess proper leaf hair density and leaf thickness are able to persist in that environment. Soil nutrition is also an important factor in shaping the pattern of elevational richness (Jones et al. 2014, Pausas and Austin 2001, Richardson et al. 2000); however, the lack of a significant relationship between soil nutrition and richness suggests that this did not occur in our data. A probable interpretation of this phenomenon is that soil nutrients should be a less important factor in restricting the range of trait values, for example, many studies have shown that there is no relationship between leaf N content and soil N availability, because high-elevation plants inhibit the dilution

of N and other nutrients in leaf tissue (Körner 1989), which results in high-elevation plants having higher leaf N content.

Although our results indicated that drought limits herb richness at low elevations, soil moisture did not have a significant influence on herb richness (Table S1). One plausible explanation is that an adequate soil water supply may not necessarily guarantee that plant species will be able to avoid drought stress at high temperatures, because as leaf evaporative demand increases exponentially with leaf temperature, plant species are incapable of avoiding water stress under high temperatures, even with adequate availability of soil moisture (Shirke and Pathre 2004). Another possible reason is that we analyzed only the influence of instantaneous data. Perhaps a focus on annual precipitation would be a useful way to test the importance of soil moisture.

One of our important findings was that extreme temperatures provided the best explanation of richness and functional diversity (Table S1, Table S2). These results show that extreme temperatures reflect the abiotic stress along the elevational gradient better than do other environmental factors. In previous studies, Kluge (2006) found a significant unimodal relationship between plant richness and temperature, and suggested that extreme temperatures and humidity limit species richness at lower and higher elevations; however, he provided no direct evidence for that assertion. To our knowledge, our results provide the first empirical evidence of a linkage between extreme temperatures and plant richness along an elevational gradient.

In this study, we suggested that a more benign environment should lead to greater functional diversity. However, this hypothesis does not consider the effects of biotic interactions, such as competition or facilitation. Some researches suggested that competition should favor species with different characteristics, thus increasing functional diversity, while at the same time reducing richness (Spasojevic and Suding 2012). Others indicated that competition could also lead to communities with decreased functional diversity (de Bello et al. 2012, Mayfield and Levine 2010). Therefore, it is important to consider multiple mechanisms of community assembly (Mason et al. 2011). However, resource acquisition traits (Abrams and Chen 2002, Freschet et al. 2013) can only be used to test environmental filter hypotheses. A similar analytic approach to functional traits associated with biotic interaction, such as those related to belowground mutualisms, should be a useful way to test the biotic interaction hypothesis. Moreover, our results showed that species richness and functional diversity had a positive relationship, which provides evidence that biotic interactions are secondary to the effects of environmental filters.

By analyzing the relationships among richness, functional diversity, and environmental factors, we provide novel evidence that the physiological tolerance hypothesis can explain the hump-shaped elevation-richness pattern: at low elevations, species richness is limited by high temperatures and at high elevations, by low temperatures. Because the soil environmental conditions at middle elevations are more benign and support more species, this allows species to engage in

more functional strategies. However, the influence of species interaction on richness is still unknown. In future work, we will focus on functional traits related to species interactions. Those analyses should be a promising avenue for disentangling the mechanisms of environmental filters and competitive exclusion.

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Electronic supplements

Table S1. Results of generalized linear model testing how environmental factors are related to herb richness and functional diversity metrics.

Table S2. Results of generalized linear model testing how environmental factors related to individual trait functional diversity.

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