# Interplay of temperature and woody cover shapes herb communities along an elevational gradient in a temperate forest in Beijing, China

Zihan Jiang[1,2], Keming Ma[1,3], M. Anand[2] and Yuxin Zhang[1]

[1] *State Key Lab of Systems Ecology, Research Center for Eco-Environmental Sciences, Chinese Academy of Sciences, CN-100085 Beijing, PR China*
[2] *School of Environmental Sciences, Univ. of Guelph, Guelph, Ontario, Canada, N1G 2W1*
[3] *Corresponding author. P.O. Box 2871, Beijing 100085, P. R. China, Tel/Fax: 86-10-62849104m, Email: mkm@ rcees.ac.cn*

**Abstract:** Abiotic and biotic factors have the potential to alter herb communities, however, few studies consider feedback between them. This study explores how variation of species interaction and climatic conditions associated with changes in altitude affect herb community composition. We sampled accumulated temperatures of growth duration (June-November) (ATGD), maximum summer temperatures (MST) and herb community composition (herb height, abundance, richness) on non-gaps and forest-gaps site across an elevational gradient. A significant negative relationship was detected between MST and herb richness. The temperature of non-gaps was cooler than that of forest gaps, and overstory cover positively correlated with herb abundance. However, the ATGD exhibited a negative relationship with overstory cover, in that overstory cover decreased with ATGD. We suggested that temperature has a profound effect on height and richness of herb communities, while the overstory cover is moderating the effect of temperature on herb community structure and influence the abundance of herb community. Conversely, decreases in ATGD weakened the relative importance of overstory cover. We concluded that the interaction of temperature and overstory cover shapes the morphology, abundance and richness of herb communities.

**Abbreviations:** ATGD – Accumulated Temperatures of Growth Duration, MST– Maximum Summer Temperatures, OC – Overstory Cover.

## Introduction

Understanding and predicting the responses of communities to the changing environment experienced has been a central issue in ecology for decades (Gomes da Silva et al. 2014, Grytnes and Vetaas 2002, Nogues-Bravo et al. 2008, Ohlemuller and Wilson 2000, Rochow 1970). For any species, distribution and abundance are determined both by tolerance to abiotic conditions and by interactions with other organisms (Hutchinson 1957, Randall 1982). Many studies have emphasized the influence of abiotic factors (Boggs and Murphy 1997, Daubenmire 1943, Kluge et al. 2006, Sundqvist et al. 2013), and have suggested that temperature is one of the environmental challenges that has important consequences for herb community structure along elevational gradients (Hodkinson 1999, Jeremy and Hodkinson 1999 Roff 1980). Temperature had a strong impact on the physiology, which can alter everything from growth rates, metabolism, body size (Parmesan 2006) to life history, geographic ranges (Colwell et al. 2008). Therefore, temperature change across elevation is likely to profoundly effect on the morphology, distribution and abundance of species. For example, elevational range partitioning among herb species is

often due to differences in thermal adaptation (Daubenmire 1943, Lowe 1964.). Moreover, decreased growing season temperatures and durations with elevation limit growth and reproduction (Hill and Hodkinson 1995, Machac et al. 2011). Hence, predicting and understanding of how temperature affects the distribution and abundance of herb species is one of most important challenges in biology.

Biotic interactions are also a determinant of community structure (Hodkinson 2005). In forest, overwhelming evidence exists that overstory-layer species can influence herb communities greatly (Caldeira et al. 2014, Mölder et al. 2008, Price and Morgan 2008), as these species can influence the productivity and recruitment of herb species directly through competition for both competition for light and available nutrients (Ludwig et al. 2004), or indirectly through altering the microhabitat of the herb layer (i.e., temperature, humidity; Crozier and Boerner 1984, Ramírez et al. 2006). The temperature experienced by herb species under overstory cover can differ from the immediate surroundings (De Frenne et al. 2013), the temperature within dense forest usually is cooler than in forest gap, thus overstory cover ameliorates the stress on herb species imposed by the high summer temperature. The spatial variation of overstory cover can increase under-

story light availability heterogeneity (Burton et al. 2014) and control the availability of resources (Bartels and Chen 2013), thus can control richness of herb species (Mölder et al. 2008, Mullah et al. 2014, Vanhellemont et al. 2014).

Herb species comprise the majority of plant species diversity in forest systems and influence the nutrient cycling and energy exchange (Gilliam 2007). Forest systems have recently experienced pronounced climate warming, it is important to evaluate the impact of environmental change. However, it may be more appropriate to consider how the interplay of abiotic and biotic factors influences communities, because biotic interactions also can buffer or alter the role of abiotic factors (Dunson and Travis 1991), whereas, the relative importances of biotic changes as abiotic conditions change. By offering steeping environmental gradient, elevational gradients have proved to be useful platforms to research the response of herb species on environmental change. At low elevations, overstory species are abundant, herb communities should strongly affected by overstory cover. With elevation increasing, decreasing temperature limit productivity of overstory species are rare and absent, the influence of abiotic factor should be increasing. A numbers of studies indicated that temperature and overstory cover can each be an important determinant of the herb community (Burton et al. 2014, Smith et al. 2008). However, how the relative importance of temperature and overstory cover change along elevational gradient is not completely understood.

Here we compiled plant data from 120 vegetation plots in temperate forests, the plots distributed across 3 regions (from 1020 m to 1770 m). In each region, we compared herb communities in forest gaps with in non-gaps; we treated non-gaps as a control test. From these plots, we test for herb community responses to temperature (accumulated temperature of growth duration (June-November) (ATGD), maximum summer temperature (MST)) and assessed the potential role of change in overstory cover in buffering or altering such response. Second, we analyzed the role of the overstory cover as a determinant for herb communities by considering whether overstory cover change the temperature experience of herb species, and third, we assessed how temperature changed the biotic interactions between overstory-layer species and herbs. Here, we hypothesize that: (1) Temperature and overstory cover can each be important determinant of herb community. (2) Overstory cover can buffer or alter the responses of herb community. (3) Variation of temperature change relative importance of overstory cover on herb community.

## Methods

### Study area

We collected data in 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 (see Appendix Fig S1). The mean annual precipitation in the region is 500–650 mm, a typical warm, temperate, continental monsoon climate. The mean annual temperature is 5-10⁰C. The area spans an elevational gradient from 1000 m to 2303 m. Its natural vegetation consists of highly heterogeneous warm temperate zone deciduous broad-leaved forest (Yun et al, 2008), including primarily oaks (*Quercus* spp.), mixed deciduous species (e.g., *Tilia* spp., *Ulmus* spp., *Acer* spp., *Juglans mandshurica* and *Fraxinus rhynchophylla* etc.), birches (*Betula* spp.) and poplar (*Populus davidiana*). There are also some conifers (*Pinus tabuliformis, Platycladus orientalis*) and shrubs (e.g., *Prunus* spp., *Vitex negundo* var. *heterophylla*, etc.).

Because this framework might call into question whether the three elevation sites can be combined for data analysis, we kept the vegetation types as similar as possible when we collected data, and tested the validity of considering the three sites as one by conducting a detrended canonical correspondence analysis of herb species (see Appendix Fig S2). The results showed that herb communities turnover did not change significantly at the transition among elevation sites, which suggests that all elevation sites belong to a single floristic unit.

### Sampling methods

We selected three sites along the elevational range of oak forest in the study area: Gouchaozi (1020 m), Gangou (1400 m) and Xiamawei (1700 m). We chose this range because below 1020 m, the natural forest disappears due to human activity, and the timberline occurs at approximately 1750 m. Sites were selected within single catchment, so other than the elevational variation, the environmental conditions in each site were similar: orientation (west-facing), slope (5-10 degree), soil (eutric cambisol).

To identify overstory cover and temperature associated with herb community composition, we established 10 overstory plots 100 m² (10 m ×10 m) in size at each elevation site. In each plot, all overstory-layer species (only included individual height ≥ 3 m) were identified and measured for breast-height diameter, crown diameter (largest and smallest diameter), and height (measured with Velmex digital hypsometer) for overstory-layer records. Within each overstory plot, three sub-plots (1 m × 1 m) were selected randomly for the inventory of herbaceous vegetation; the height and abundance (number of individuals) was recorded for each herb species. At each elevation, we also placed 30 plots (1 m × 1 m) in the forest gap. We identified gaps according to light condition by using a digital camera Nikon D610 equipped with a fish-eye lens; we took hemispheric photographs in order to explore the light conditions. We calculated the canopy openness (the percentage of total sky area that is found in overlapping gaps in the canopy) by performed Winphot 5 (Ter Steege 1996). In this case, plots can be surveyed if the canopy openness ≥ 90%, then height and abundance were recorded (number of individuals) for each herb species. Plots within site were as close as possible in order to eliminate the influence of environmental heterogeneity. For statistical analysis, mean values of plots or subplots were used.

**Table 1.** Characteristics of understory and forest gaps sampled at three elevation sites. Numbers represent means for each treatment and sharing the same letter indicates a nonsignificant difference (p ≤ 0.05: mixed model ANOVA and Tukey's adjusted least significant difference).

| Characteristics | 1020 m | | 1400 m | | 1700 m | |
|---|---|---|---|---|---|---|
| | Understory | Forest gap | Understory | Forest gap | Understory | Forest gap |
| Woody cover (m$^2$) | 186.15a | | 140.42b | | 64.13c | |
| Stand basal area (m$^2$.ha$^{-1}$) | 5.74a | | 2.43b | | 1.61c | |
| Number of overstory-layer species | 13a | | 7b | | 4c | |
| Accumulated temperature ($^0$C) | 11.99×10$^4$a | 12.63×10$^4$b | 11.53×10$^4$c | 12.15×10$^4$d | 10.76×10$^4$e | 10.92×10$^4$e |
| Maximum temperature ($^0$C) | 23.37a | 26.16b | 20.13c | 23.63d | 20.13e | 21.78f |
| Soil moisture (%) | 51.37a | 32.11b | 70.39c | 62.33d | 59.30a | 55.39a |
| Total nitrogen (g.kg$^{-1}$) | 0.24a | 0.26a | 0.28a | 0.25a | 0.23a | 0.24a |
| Total phosphorus (g.kg$^{-1}$) | 0.024a | 0.028a | 0.028a | 0.030a | 0.027a | 0.023a |
| Soil pH | 6.13a | 6.52a | 6.51a | 6.36a | 6.54a | 6.37a |
| Soil organic matter (%) | 6.32a | 6.14a | 6.88a | 6.60a | 5.99a | 6.12a |

Temperature data were collected at each elevation site from June, 2011 to November, 2012 using Microdaq data-loggers HoboPro RH/Temp. At each elevation site, we established three data-loggers for each plot type (forest gap or non-gap), thus temperature data were not associated to plots. Temperature data were collected every 30 min. We used hammer-driven soil core sampler of 5 cm in diameter to obtain three soil profiles at a depth of 0-30 cm in each plot. Three replicate samples were homogenized by hand mixing after large live plant material (roots and shoots) and pebbles in each sample were separated by hand and discarded. The samples were then air-dried and sieved to measure soil properties. The parameters of soil properties variables included soil organic matter, total nitrogen, total potassium. Soil organic matter was measured by the $K_2Cr_2O_7$ titration method after digestion (Nelson and Sommers 1974). We used the semi-micro Kjeldahl method to measure total nitrogen, with V-Mo colorimetry, and total potassium was resolved by flame photometer (Bao 2000). Soil moisture was measured by Moisture Meter HH2 (Delta-T Devices Ltd, UK) six times at a depth of 10 cm in each plot and then averaged.

*Analysis*

In this study, we mainly analyze the influence of ATGD and MST. It is expected that altitudinal comparisons of ATGD and MST more biologically meaningful than mean annual temperature. Because mean annual temperature is confounded with the length of the dormant season and does not reflect the degree of fluctuation during the growing period (Ramírez et al. 2006, Körner 2007). In this study, MST calculated as the summer (May-August) maximum temperatures ATGD calculated as adding together successive mean daily temperature (May-November). We used a linear mixed model to test whether there were significant environmental differences among cover types (non-gaps and forest gaps) and elevation sites, using biotic and abiotic factors as fixed effects, and plot (nested in elevation) as a random effect. We did not conduct further analysis of the parameters of soil properties, abundance of overstory-layer species (number of individuals)(AOS) and stand basal area (BA)(m$^2$ha$^{-1}$), because pa-

rameters of soil properties and soil moisture do not appear to change significantly among cover types and elevation sites (Table 1), and both AOS and BA were highly correlated with overstory cover (AOS: r = 0.82, $p<0.01$; BA: r=0.74, $p<0.01$).

To assess the role of overstory cover and temperature in herb community, we used a linear mixed model to test whether herb height, abundance and richness were modified by temperature (ATGD and MST) and overstory cover. After log (1+x) transformed abundance and average height data, we treated ATGD, MST and overstory cover as fixed effects and plot (nested in elevation) as a random effect. We used another linear mixed model to explore how the temperature change overstory cover and overstory-layer species richness, we treated ATGD and MST as fixed effects and plot (nested in elevation) as a random effect. We used the Kenward-Roger modification of the F-test (Kenward and Roger 1997) to determine the significance of fixed effects, because this method is more appropriate for small sample sizes than is the asymptotic $\chi^2$ test. To assess height, abundance and richness of herb species differences between forest gaps and non-gaps at each elevation, we used a paired difference *t*-test.

To assess how the overstory cover buffer or alter the responses of herb community to temperature, we estimated the differences of herb community composition between forest gaps and non-gaps across elevations, we log (1+x)-transformed abundance data to meet the assumptions of normality and equal variance. Subsequently, we used analysis of similarities (ANOSIM) to test whether community composition differed significantly among cover types and elevation sites. ANOSIM is uses ranked Bray–Curtis dissimilarities to test whether there is a significant differences in species composition between groups (Legendre and Legendre 1998). The ANOSIM produces an R statistic ranging from 0 to 1 and expresses the similarity between groups. We performed 9999 randomizations of the original data to calculate the significance of the ANOSIM statistic. We also compared rank-abundance plots to explore whether herb relative abundance modified by temperature and overstory cover. For each site, we plotted the relative abundance of each species on a logarithmic scale against the species' rank. All of these analyses

**Table 2.** Results of the linear mixed model testing how the temperature and overstory cover related to herb richness, abundance and average height (only include forest gap plots). Block (nested in elevation) was treated as a random factor.

| Characteristics | | Height | | | Richness | | | Abundance | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | DF | Error DF | F | p | Error DF | F | p | Error DF | F | p |
| ATGD | 5 | 54 | 1.52 | < 0.01 | 54 | 1.40 | 0.35 | 54 | 1.65 | 0.20 |
| MST | 5 | 54 | 1.25 | 0.33 | 54 | 2.33 | < 0.01 | 54 | 2.67 | 0.26 |
| OC | 27 | 54 | 0.17 | 0.61 | 54 | 19.19 | < 0.05 | 54 | 11.91 | < 0.01 |
| ATGD×OC | 27 | 54 | 3.54 | 0.22 | 54 | 4.22 | 0.11 | 54 | 6.25 | 0.15 |
| MST×OC | 27 | 54 | 1.32 | 0.31 | 54 | 5.70 | < 0.05 | 54 | 5.73 | 0.09 |
| Random effects | | | | | | | | | | |
| Block (elevation) | 27 | | 0.00 | 0.95 | | 1.92 | 0.18 | | 2.35 | 0.17 |



**Figure 1.** Herb species characteristics measured in forest gaps (empty bars) and non-gaps (filled bars) across three elevation sites. Response variables include: (A) Height, (B) Richness, (C) Abundance. Bars represent means for each treatment and error bars are 95% confidence intervals of the mean (untransformed). Bars sharing the same letter are not significantly different ($p \leq 0.05$, mixed model ANOVA and Tukey's adjusted least significant difference).
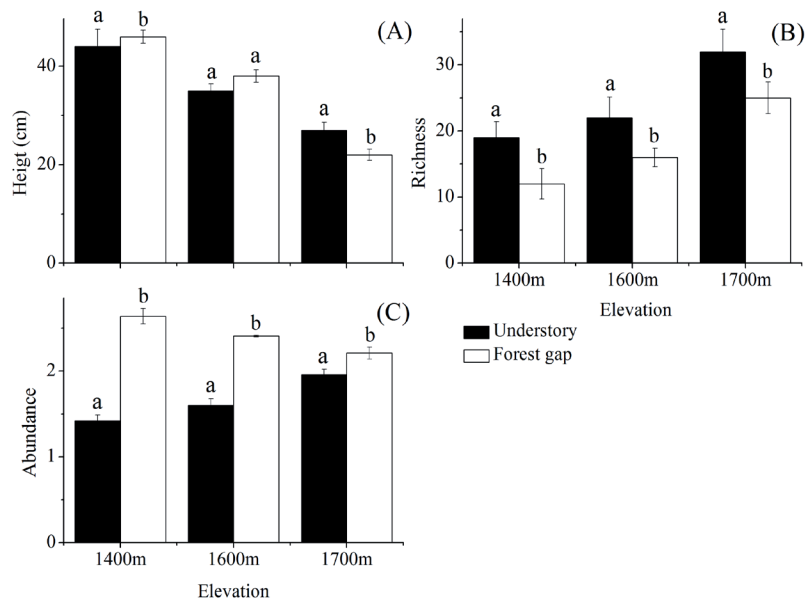
were conducted in R 3.01 (Laliberté et al. 2010, Oksanen et al. 2013).

## Results

A total of 9 overstory-layer species (tree species: 6; shrub species: 3) and 72 herb species were recorded in the three elevation sites. *Quercus liaotungensis* was the only dominant species at all elevations, accounting for 95% of total BA at 1020 m, 98% at 1400 m and 96% at 1700 m. Our results revealed that the ATGD and MST decreased with elevation (Table 1); thus, the species at higher elevations would be expected to experience a shorter growth period. ATGD and MST was significantly higher in forest gaps than in the non-gaps, which was consistent at all elevations.

There was a significant relationship between ATGD and herb height (Table 2). Herb height decreased with elevation in both forest gaps and non-gaps, but the difference of height between forest gaps and non-gaps across the elevation sites were highly variable (Fig. 1A). Herb height in forest gaps was greater than in the non-gaps at 1020 m, but the difference was insignificant at 1400 m, and significantly less than in

non-gaps sites at 1700 m. In contrast, richness and abundance was unrelated to ATGD. The richness significantly related to MST and overstory cover, and there was a significant interaction relationship (Table 2). Herb richness increased with elevation in both forest gaps and non-gaps (Fig. 1B), and it was significantly greater in non-gaps than in forest gaps at all elevations. Finally, abundance of herb was negative significantly related to overstory cover (Table 2). We found ATGD was positive correlated with overstory cover (Table 3). In other word, ATGD indirectly influence herb community. Herb abundance in forest gaps and non-gaps exhibited different elevational patterns (Fig. 1C). The abundance in forest gaps was significantly greater than in non-gaps at all elevations, but the difference in herb abundance between forest gap and non-gaps decreased with elevation.

Herb community composition in non-gaps changed significantly with elevation (Table 4, Fig. 2). Herb richness increased with elevation, while the proportional abundance of dominant species decreased. There are 19 herb species at 1020 m, herb community characterized by *Deyeuxia arundinacea*, *Artemisia sacrorum*, and *Spodiopogon sibiricus*, and these species constituted 42% of the total abundance. At 1400 m, non-gaps sites had 22 herb species and were character-

**Table 3.** Results of the linear mixed model testing how the temperature related to overstory cover and tree richness (only include forest gap plots). Block (nested in elevation) was treated as a random factor.

| Characteristics | DF | Overstory cover | | | Tree richness | | |
|---|---|---|---|---|---|---|---|
| | | Error DF | F | p | Error DF | F | p |
| Accumulated temperature | 5 | 54 | 12.56 | < 0.01 | 54 | 5.63 | < 0.05 |
| Maximum summer temperature | 5 | 54 | 1.56 | 0.52 | 54 | 2.56 | 0.23 |
| Random effects | | | | | | | |
| Block (elevation) | 27 | | 2.33 | 0.12 | | 1.89 | 0.11 |

**Table 4.** Pairwise comparisons of plant community composition between site types using the analysis of similarity (ANOSIM) procedure. Values of R> 0.75 indicate that groups are well separated, values between 0.5 and 0.75 suggest overlapping but distinguishable groups, and values < 0.25 describe the groups that can barely be separated. Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' '.

| | 1020 m | | 1400 m | | 1700 m | |
|---|---|---|---|---|---|---|
| | Understory | Forest gap | Understory | Forest gap | Understory | Forest gap |
| 1020 m | | | | | | |
| Understory | | | | | | |
| Forest gap | 0.45 * | | | | | |
| 1400 m | | | | | | |
| Understory | 0.41 ** | 0.51 * | | | | |
| Forest gap | 0.47 ** | 0.35 * | 0.33 ** | | | |
| 1700 m | | | | | | |
| Understory | 0.81 ** | 0.43 * | 0.48 ** | 0.44 ** | | |
| Forest gap | 0.83 ** | 0.38 * | 0.53 ** | 0.31 * | 0.31 ** | |
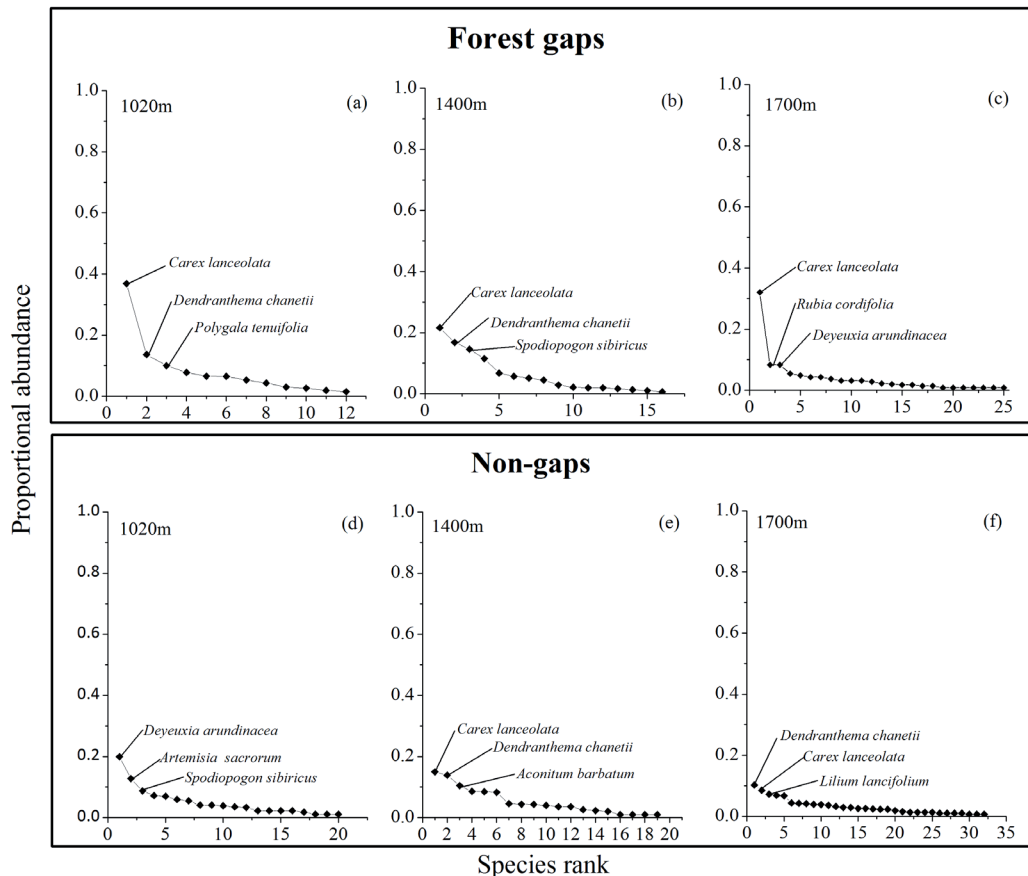


**Figure 2.** Rank/abundance plots for the herb community: (a), (b), (c) the herb communities in forest gaps. (d), (e), (f) the herb communities in non-gaps. For each site, we plotted the relative abundance of each species on a logarithmic scale against the species' rank, from the most abundant to the least abundant species. We signed the top three abundant species..

ized by a different suite of species than at 1020 m: *Carex lanceolata*, *Dendranthema chanetii* and *Aconitum barbatum*, these species constituted 38% of the total abundance. At 1700 m, non-gaps sites had 32 herb species characterized by *Dendranthema chanetii*, *Carex lanceolata* and *Lilium lancifolium*; these top three dominant species constituted 25% of the total abundance.

The herb community composition in forest gaps was similar, as these sites all shared an abundance of *Carex lanceolata* and *Dendranthema chanetii* (Fig. 2). The proportional abundance of the dominant species in forest gaps was greater than in the non-gaps within an elevation site. Pairwise comparisons among forest gaps generated lower $R_{ANOSIM}$ statistics than among non-gaps; forest gaps had significantly different species composition from non-gaps within a given elevation. This difference was driven primarily by the abundance of dominant species, which decreased across elevations, while the number of rare species increased.

## Discussion

Our investigation describes how the interaction of temperature and overstory cover influence herb community composition. Forest gaps are more extreme microhabitats than non-gaps, because overstory cover ameliorate the stress on herb community imposes by MST. Herb communities located at higher elevation undergo milder environmental conditions (lower MST). However, the relative importance of overstory cover decreased with elevation because lower ATGD limit productivity of overstory-layer species.

We found that temperature and overstory cover played a vital role in determining herb community composition and structure across elevations. For any given herb species, growth and reproduction were promoted by temperature and seasonal development, with the growth season being shorter and later across elevations. In our study, herb height decreased with elevation, it is tempting to speculate that accumulated temperature may shift the aboveground/belowground biomass allocation patterns (Ashton 2003, Leuschner et al. 2007), some studies indicated that root biomass and productivity decreased with elevation due to low temperature (Bauhus and Bartsch 1996, Cairns et al. 1997). However, the abundance of herb species in the forest gaps did not decrease with elevation, some studies have indicated that many plant species have more efficient photosynthesis than their lower elevation counterparts (Denno et al. 1996, Körner and Diemer 1994), this mechanism should partly offset the effect of low accumulated temperatures. In contrast, we speculated light availability should be a more important environmental variable for herb abundance because light limits photosynthetic carbon gain, which in turn influences growth and mortality. Our results indicated that the maximum temperature in summer is a good predictor of herb richness, with higher richness at higher elevations where maximum summer temperature is lower. The richness of rare species increased with elevation, while the abundance of drought tolerant and heliophilous species which dominated at low elevations (i.e., *Dendranthema chanetii, Carex lancifolia, Deyeuxia arundinacea*) decreased

with elevation. These results suggested that the maximum temperature in summer acts as a structuring agent, such that only a few drought tolerant species have the ability to persist and dominate at lower elevations with higher MST. With increasing elevation, environmental conditions in both forest gaps and non-gaps become more suitable, and thus more species can survive. Our conclusions are consistent with Kluge et al. (2006), who suggested that the physical environment at higher elevations is more benign for most organisms, because higher elevations offer more moderate temperatures. Another possible reason is that drought tolerant species may be lost competitive ability on colder, high-elevation site; such an inference is weakening by the unavailability data on the herb inter-specific competition. Future work would benefit from targeted investigation of relationships between richness and competitive exclusion across different elevation site.

However, our results revealed that the overstory cover buffer and modified the effect of temperature on herb abundance and richness (Table. 2, Fig. 1). At 1020 m and 1400 m, the difference in abundance between the forest gaps and non-gaps was greater than the difference among forest gaps across elevations, such that overstory cover and herb abundance appeared to closer relationship than herb abundance and accumulated temperature. Some studies suggested that the cover provided by overstory-layer species decreased forest-floor light (Burton et al. 2014), leading to environmental conditions that are more harsh than those in the immediate surroundings (Ramírez et al. 2006), and litter from overstory-layer species can decrease herb productivity (Bowles et al. 2007, Fornara and Du Toit 2008). However, our results indicated that more herb species persisted in the non-gaps. Thus, it would be expected that overstory cover ameliorates the stress of high summer temperatures effectively (Ramírez et al. 2006), so that the non-gaps should offer more suitable conditions for herb species. Some studies indicated that overstory-layer species can influence soil moisture (Burton et al. 2014, Ludwig et al. 2004, Mölder et al. 2008, Vourlitis et al. 2014). But the pattern is not consistent among study sites. Burton (2014) suggested soil moisture increased with gap sizes, in contrast, Bartels (2013) indicted that overstory-layer species improved soil moisture. Our results revealed that soil moisture at non-gap higher than at forest gap, likely caused by effect of gap size (Gray et al. 2002).

The strength of the biotic linkage between overstory-layer species and herbs was altered by the effect of ATGD. Grime (1979) provided a conceptual model of how the interaction between competitive species and stress tolerant species may change along an environmental stress gradient. We suggest that a similar relationship between the importance of biotic and abiotic conditions may exist in forest. At low elevations, the importance of biotic interaction is high because overstory cover restricts the abundance of herbs. As elevation increases, the vigor of overstory-layer species decreases. Thus, lower accumulated temperature limits productivity, leading to a decrease in the importance of overstory-layer species for herb communities. Grime classified plants according to the C-S-R model, and suggested that highly competitive species have higher vigor in conditions of low abiotic stress, while they

are more sensitive to environmental change than are stress-tolerant species. In summary, temperature changes the influence of overstory-layer species.

In summary, our results imply that the interplay between overstory cover and temperature shape herb communities along elevational gradients. We also inferred that overstory cover determines herb abundance and buffers the effect of maximum summer temperature as an environmental filter. However, accumulated temperature weakens the effect of overstory cover as a structure agent and plays a greater role at higher elevations. It is worth noting that the recent decades of global warming not only change species distribution, but the diversity pattern as well. We suggest that more species will overcome the barrier of overwintering at high elevation sites due to temperature increases, but the influence of maximum summer temperature will increase. We recommend an increased consideration of how herb diversity patterns may change with global warming.

## References

Ashton, P.S. 2003. Floristic zonation of tree communities on wet tropical mountains revisited. *Perspect. Plant Ecol.* 6: 87-104.

Bao, S. 2000. *Analysis Method of Soil Agricultural Chemistry.* China Agr. Press, Beijing.

Bartels, S.F. and H.Y.H. Chen. 2013. Interactions between overstory and understory vegetation along an overstory compositional gradient. *J. Veg. Sci.* 24: 543-552.

Bauhus, J. and N. Bartsch. 1996. Fine-root growth in beech (*Fagus sylvatica*) forest gaps. *Can. J. Forest. Res.* 26: 2153-2159.

Boggs, C.L. and D.D. Murphy. 1997. Community composition in mountain ecosystems: climatic determinants of montane butterfly distributions. *Global Ecol. Biogeogr.* 6: 39-48.

Bowles, M.L., K.A. Jacobs and J.L. Mengler. 2007. Long-term changes in an oak forest's woody understory and herb layer with repeated burning. *J. Torrey Bot. Soc.* 134: 223-237.

Burton, J.I., D.J. Mladenoff, J.A. Forrester, and M.K. Clayton. 2014. Experimentally linking disturbance, resources and productivity to diversity in forest ground-layer plant communities. *J. Ecol.* 102: 1634-1648.

Caldeira, M.C., I. Ibanez, C. Nogueira, M.N. Bugalho, X. Lecomte, A. Moreira and J.S. Pereira. 2014. Direct and indirect effects of tree canopy facilitation in the recruitment of Mediterranean oaks. *J. Appl. Ecol.* 51: 349-358.

Cairns, M.A., S. Brown, E.H. Helmer and G.A. Baumgardner. 1997. Root biomass allocation in the world's upland forests. *Oecologia* 111: 1-11.

Colwell, R.K., G. Brehm, C.L. Cardelus, A.C. Gilman and J.T. Longino. 2008. Global warming, elevational range shifts, and lowland biotic attrition in the wet tropics. *Science* 322: 258-261.

Crozier, C.R. and R.E. Boerner. 1984. Correlations of understory herb distribution patterns with microhabitats under different tree species in a mixed mesophytic forest. *Oecologia* 62: 337-343.

Daubenmire, R. 1943. Soil temperature versus drought as a factor determining lower altitudinal limits of trees in the Rocky Mountains. *Bot. Gaz.* 105: 1-13.

De Frenne, P. et al. 2013. Microclimate moderates plant responses to macroclimate warming. *P. Natl. Acad. of Sci. USA.* 110: 18561-18565.

Denno, R.F., G.K. Roderick, M.A. Peterson, A.F. Huberty, H.G. Dobel, M.D. Eubanks, J.E. Losey and G.A. Langellotto. 1996. Habitat persistence underlies intraspecific variation in the dispersal strategies of planthoppers. *Ecol. Monogr.* 66: 389-408.

Dunson, W.A. and J. Travis. 1991. The role of abiotic factors in community organization. *Am. Nat.* 138: 1067-1091.

Fornara, D.A. and J.T. Du Toit. 2008. Browsing-induced effects on leaf litter quality and decomposition in a southern African savanna. *Ecosystems* 11: 238-249.

Gilliam, F.S. 2007. The ecological significance of the herbaceous layer in temperate forest ecosystems. *Bioscience* 57: 845-858.

Gomes da Silva, F.K., F. Lopes Sd, L.C. Serramo Lopez, J.I. Miranda de Melo and D.M. de Brito Melo Trovao. 2014. Patterns of species richness and conservation in the Caatinga along elevational gradients in a semiarid ecosystem. *J. Arid. Environ.* 110: 47-52.

Gray, A.N., T.A. Spies and M.J. Easter. 2002. Microclimatic and soil moisture responses to gap formation in coastal Douglas-fir forests. *Can. J. Forest Res.* 32: 332-343.

Grime, J.P. 1979. *Plant Strategies and Vegetation Processes.* John Wiley & Sons, Toronto.

Grytnes, J.A. and O.R. Vetaas. 2002. Species richness and altitude: A comparison between null models and interpolated plant species richness along the Himalayan altitudinal gradient. Nepal. *Am. Nat.* 159: 294-304.

Hill, J.K. and I.D. Hodkinson. 1995. Effects of temperature on phenological synchrony and altitudinal distribution of jumping plant lice (Hemiptera: Psylloidea) on dwarf willow (*Salix lapponum*) in Norway. *Ecol. Entomol.* 20: 237-244.

Hodkinson, I.D. 1999. Species response to global environmental change or why ecophysiological models are important: a reply to Davis et al. *J. Anim. Ecol.* 68: 1259-1262.

Hodkinson, I.D. 2005. Terrestrial insects along elevation gradients: species and community responses to altitude. *Biol. Rev.* 80: 489-513.

Hutchinson, G.E. 1957. Concluding remarks. Population studies: animal ecology and demography. In: *Cold Spring Harbor Symposia on Quantitative Biology.* Cold Spring Harbor Lab Press. pp. 415-427.

Jeremy, M. and I.D. Hodkinson. 1999. Species at the edge of their range: the significance of the thermal environment for the distribution of congeneric *Craspedolepta* species (Sternorrhyncha: Psylloidea) living on *Chamerion angustifolium* (Onagraceae). *Eur. J. Entomol.* 96: 103-109.

Kenward, M.G. and J.H. Roger. 1997. Small sample inference for fixed effects from restricted maximum likelihood. *Biometrics* 53: 983-997.

Kluge, J., M. Kessler and R.R. Dunn. 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 Ecol. Biogeogr.* 15: 358-371.

Körner, C. and M. Diemer. 1994. Evidence that Plants from High Altitudes Retain their Greater Photosyntheti Efficiency Under Elevated $CO_2$. *Funct. Ecol.* 8: 58-68.

Körner, C. 2007. The use of 'altitude' in ecological research. *Trends Ecol. Evol.* 22: 569-574.

Laliberté, E.B. Shipley and M.E. Laliberté. 2010. Package 'FD' Measuring functional diversity (FD) from multiple traits, and other tools for functional ecology. https://cran.r-project.org/web/packages/fd

Legendre, P. and L. Legendre. 1998. *Numerical Ecology.* 2nd English edn. Elsevier, Amsterdam.

Leuschner, C., G. Moser, C. Bertsch, M. Roederstein and D. Hertel. 2007. Large altitudinal increase in tree root/shoot ratio in tropical mountain forests of Ecuador. *Basic Appl. Ecol.* 8: 219-230.

Lowe, C.H. 1964. *Arizona's Natural Environment: Landscapes and Habitats.* University of Arizona Press, Tucson, Arizona, USA.

Ludwig, F., H. de Kroon, F. Berendse and H.H. Prins. 2004. The influence of savanna trees on nutrient, water and light availability and the understory vegetation. *Plant Ecol.* 170: 93-105.

Machac, A., M. Janda, R.R. Dunn and N.J. Sanders. 2011. Elevational gradients in phylogenetic structure of ant communities reveal the interplay of biotic and abiotic constraints on diversity. *Ecography* 34: 364-371.

Mölder, A., M. Bernhardt-Römermann and W. Schmidt. 2008. Herb-layer diversity in deciduous forests: raised by tree richness or beaten by beech? *Forest. Ecol. Manag.* 256: 272-281.

Mullah, C.J.A., K. Klanderud, O. Totland and B. Kigomo. 2014. Relationships between the density of two potential restoration tree species and plant species abundance and richness in a degraded Afromontane forest of Kenya. *Afr. J. Ecol.* 52:77-87.

Nelson, D.W. and L.A. Sommers. 1974. A rapid and accurate procedure for estimating organic carbon in soil. *Proceedings of the Indiana Academy of Science* pp. 456-462.

Nogues-Bravo, D., M.B. Araujo, T. Lasanta and J.I. Lopez-Moreno. 2008. Climate change in Mediterranean mountains during the 21st century. *Ambio* 37: 280-285.

Ohlemuller, R. and J.B. Wilson. 2000. Vascular plant species richness along latitudinal and altitudinal gradients: a contribution from New Zealand temperate rainforests. *Ecol. Lett.* 3: 262-266.

Oksanen, J.F.G. Blanchet, R. Kindt, M. J. Oksanen and M. Suggests. 2013. Package 'vegan' Community ecology package Version 2.3. https://cran.r-project.org/web/packages/vegan

Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. *Annu. Rev. Ecol. Evol. S.* 37: 637-669.

Price, J.N. and J.W. Morgan. 2008. Woody plant encroachment reduces species richness of herb-rich woodlands in southern Australia. *Austral. Ecol.* 33: 278-289.

Ramírez, J.M., P.J. Rey, J.M. Alcántara and A.M. Sánchez-Lafuente. 2006. Altitude and woody cover control recruitment of *Helleborus foetidus* in a Mediterranean mountain area. *Ecography* 29: 375-384.

Randall, M.G. 1982. The dynamics of an insect population throughout its altitudinal distribution: *Coleophora alticolella* (Lepidoptera) in northern England. *J. Anim. Ecol.* 51: 1: 993-1016.

Rochow, T.F. 1970. Ecological investigations of *Thlaspi alpestre* L. along an elevational gradient in Central Rocky Mountains. *Ecology* 51:649-&.

Roff, D. 1980. Optimizing development time in a seasonal environment: the 'ups and downs' of clinal variation. *Oecologia* 45: 202-208.

Smith, K.J., W.S. Keeton, M.J. Twery and D.R. Tobi. 2008. Understory plant responses to uneven-aged forestry alternatives in northern hardwood-conifer forests. *Can. J. Forest Res.* 38: 1303-1318.

Sundqvist, M.K., N.J. Sanders and D.A. Wardle. 2013. Community and ecosystem responses to elevational gradients: processes, mechanisms, and insights for global change. *Annu. Rev. Ecol. Evol. S.* 44: 261-280.

Ter Steege, H. 1996. Winphot 5: a programme to analyze vegetation indices, light and light quality from hemispherical photographs. Tropenbos-Guyana Programme Tropenbos. Guyana.

Vanhellemont, M., L. Baeten and K. Verheyen. 2014. Relating changes in understory diversity to environmental drivers in an ancient forest in northern Belgium. *Plant Ecol. Evol.* 147: 22-32.

Vourlitis, G.L., F.A. Lobo, S. Lawrence, K. Holt, A. Zappia, O.B. Pinto and J.D.S. Nogueira. 2014. Nutrient resorption in tropical savanna forests and woodlands of central Brazil. *Plant Ecol.* 215: 963-975.

Yun, F., M. Keming and Z. Yunxin. 2008. DCCA analysis of plant species distributions in different strata of oak (*Quercus liaotungensis*) forest along an altitudinal gradient in Dongling Mountain, China. *J. Plant Ecol. (China Version).* 32: 568-573.

**Electronic supplements**

**Figures S1-S2.**

The file may be downloaded from www.akademiai.com.