How forest gaps shaped plant diversity along an elevational gradient in Wolong National Nature Reserve?

CHEN Li[1,2], HAN Wangya[1,2], LIU Dan[1,2], *LIU Guohua[1,2]

1. State Key Laboratory of Urban and Regional Ecology, Research Center for Eco-environmental Sciences, CAS, Beijing 100085, China;
2. School of Resources and Environment, University of Chinese Academy of Sciences, Beijing 100049, China

Abstract: Understanding the underlying ecological processes that control plant diversity within (α-diversity) and among (β-diversity) forest gaps is important for managing natural forest ecosystems, and it is also a prerequisite for identifying the formation and maintenance mechanisms of forest plant communities. In this study, we focused on the interrelationships among habitat type (gap/non-gap plots), gap size, elevation and environmental factors, and we explored their effects on plant diversity (α-diversity and β-diversity). To do this, a total of 21 non-gap (i.e., closed canopy) plots (100 m^2) and 63 gap plots, including 21 with large gaps (200–410 m^2), 21 with medium gaps (100–200 m^2) and 21 with small gaps (38.5–100 m^2),were selected along an elevational gradient in a subalpine coniferous forest of southwestern China. Using structural equation models (SEMs), we analyzed how forest gaps affected plant diversity (α-diversity and β-diversity) along an elevational gradient. The results showed that (1) as elevation increased, unimodal patterns of α-diversity were found in different-sized gaps, and β-diversity showed a consistent sinusoidal function pattern in different-sized gaps. The gap size was positively related to α-diversity, but this effect disappeared above 3500 masl. Moreover, the patterns of α-diversity and β-diversity in non-gap plots were irregular along the elevational gradient. (2) SEMs demonstrated that many environmental factors, such as the annual mean air temperature (AMAT), ultraviolet-A radiation (365 nm, UV-A365), ultraviolet-B1 radiation (297 nm, UV-B297), moss thickness (MT), soil carbon/nitrogen ratio (C/N ratio), NH$_4$-N and NO$_3$-N, were significantly affected by elevation, which then affected α-diversity and β-diversity. The photosynthetic photon flux density (PPFD), UV-A365 and UV-B297 were significantly higher in plots with forest gaps than in the non-gap plots. Moreover, the PPFD and UV-A365 were positively and directly affected by gap size. Surprisingly, except for the NH$_4$-N and the C/N ratios, the below-ground environmental factors showed little or no relationships with forest gaps. All of these effects contributed to plant diversity. Overall, the above-ground environmental factors were more sensitive to gap-forming disturbances than the below-ground environmental factors, which affected α-diversity and β-diversity. The predicted pathway in the SEMs of the elevational effects on α-diversity and

Author: Chen Li (1989–), PhD, specialized in landscape ecology. E-mail: lichen_st@rcees.ac.cn
*Corresponding author: Liu Guohua (1965–), Professor, E-mail: ghliu@rcees.ac.cn

β-diversity was relatively complicated compared with the effects of forest gaps. These results can provide valuable insights into the underlying mechanisms driving the diversity-habitat relationship in the subalpine coniferous forests of southwestern China.

Keywords: forest gap; elevation; environmental factors; plant diversity; subalpine coniferous forest

1   Introduction

Quantifying the heterogeneity of biodiversity within (α-diversity) and among (β-diversity) samples at multiple scales along environmental gradients has been a central theme in ecology (Crist and Veech 2006; Kraft *et al*., 2011). Currently, biodiversity in mountain forests is a major research topic because of the sensitive responses of these forests to disturbance, such as climate change and human activities. With increasing elevation, many environmental factors show distinct gradients, especially temperature and light radiation availability, and five patterns of diversity have been reported for mountainous landscapes (Rahbek, 1995; McCain, 2007). Though many striking issues related to the effects of plant diversity variation on local communities have been widely documented over the past decade (Korner, 1992; Hardtle *et al*., 2003; Bongers *et al*., 2009; Molina-Venegas *et al*., 2016; Woch *et al*., 2017), the mechanisms underlying environmental gradients remain an important challenge because multiple processes may concurrently govern variation in diversity (Ricklefs, 2004; Tang and Fang 2004; Kraft *et al*., 2011). More importantly, an appropriate method of analysis is still a key limitation for establishing connections between α-diversity/β-diversity and ecological factors (Crist and Veech, 2006). Further, several indices and a mathematical framework for α-diversity and β-diversity have been proposed; however, the availability of several potential methods inevitably produces some uncertainties regarding the use of these methods (Bello *et al*., 2010). Among the existing indices and mathematical frameworks, species richness is one of the simplest and most effective strategies for describing the α-diversity of local communities (Hardtle *et al*., 2003; Tang and Fang, 2004); furthermore, γ-diversity is widely accepted as the total diversity of a region, and β-diversity is calculated by α-diversity and γ-diversity, depending on the research purposes (Bello *et al*., 2010; Molina-Venegas *et al*., 2016).

It is widely accepted that species richness displays monotonic decreases or unimodal patterns as elevation increases (Rahbek, 1995; Beck and Chey, 2008). A large number of studies have proposed that the diversity is mainly dominated by the availability of resources and the metabolic theory of ecology (MTE) (Raymond *et al*., 2006; Beck and Chey, 2008), where higher species diversity is expected to occur at relatively low or medium elevations because of resource (i.e., temperature, water, light and soil) availability (Galhidy *et al*., 2006; Toledo *et al*., 2011). Moreover, in addition to elevation, gap-forming disturbances also alter environmental conditions and resource availability (Galhidy *et al*., 2006; Raymond *et al*., 2006; Molina-Venegas *et al*., 2016). These alterations, in turn, affect the regeneration and distribution of plants (Korner, 1992; Muscolo *et al*., 2014). In a Sierran conifer forest, the variation in species richness was higher in forest gaps than it was in non-gap plots; additionally, the variation in species richness was positively related to the gap size (Battles *et al*., 2001). However, a key current question exists regarding the effects of forest gaps and elevation on plant diversity; this uncertainty persists because both factors have an important but dissimi-

lar influence on the distribution of resources (Vetaas and Grytnes, 2002; Kraft *et al*., 2011). Studies comparing gap/non-gap plots or different-sized gaps have demonstrated variations in air temperature as well as variations in solar radiation and soil parameters (Naaf and Wulf, 2007; Muscolo *et al*., 2011; Molina-Venegas *et al*., 2016). These environmental factors clearly changed from non-gap plots to gap plots and increased with gap size (Vajari *et al*., 2012; Muscolo *et al*., 2014). However, at higher elevations, though the large gaps receive more light and photosynthetic photon flux density (PPFD), there is not necessarily a reduction in plant competition for soil nutrients, and temperature can still have negative effects on plant distribution (Raymond *et al*., 2006).

   This study was conducted in a primeval coniferous forest in southwestern China. This coniferous forest is one of the most important natural forests in China and plays an irreplaceable role in the provision of regional ecological services in this area (Liu *et al*., 2016; Chen *et al*., 2018). Moreover, gap-based silvicultural research and applications play an important role in maintaining and promoting diversity in the closed understory (Vajari *et al*., 2012). Importantly, this subalpine coniferous forest provides a unique opportunity for studying the effects of forest gaps and elevation on α-diversity and β-diversity because of the terrain of the alpine valleys. Therefore, to tease apart the influences of forest gaps and elevation on plant diversity, our study focused on the underlying ecological mechanisms and examined how forest gaps and elevation shaped the plant diversity (i.e., α-diversity and β-diversity) in this subalpine montane ecosystem. In addition, we also assessed which environmental factors (excluding forest gap and elevation) were affected by forest gaps or/and elevation and how these factors, in turn, affected α-diversity and β-diversity. The objectives of our study were to answer the following questions: (1) How do α-diversity and β-diversity vary in non-gap plots and in different-sized gaps along the elevational gradient? (2) How do forest gaps shape plant diversity within (α-diversity) and among (β-diversity) samples along the elevational gradient?

2   Material and methods

2.1   Study area

The study area is located in the Wolong National Nature Reserve in southwestern China. The climate in this region is a subtropical inland mountain climate. The average annual rainfall fluctuates in the range of 1200–1800 mm, and the monthly precipitation is the highest in August (approximately 340 mm). The annual mean air temperate (AMAT) is between 4.1 and 5.1℃, and the mean monthly air temperature is the lowest in December (–4℃). The soil is classified as subalpine meadow soil and brown coniferous forest soil (Liu *et al*., 2016). The area is characterized by its primeval forest and alpine valley physical features, and it also provides important habitat for the giant panda. The climatic and plant types vary distinctly along the increasing elevation gradient from 1218 to 4900 m above sea level (masl). The plant community gradually shifts from shrubland at low elevation and progresses as elevation increases to deciduous broad-leaved forest, mountain coniferous forest, subalpine coniferous forest, alpine scrub, and finally, mesophorbium at high elevation.

   Our experimental sites were established in a subalpine coniferous forest in the southern

part of the Wolong National Nature Reserve (30°49′N, 102°56′E, from 3000 to 3700 masl) (Figure 1). This subalpine coniferous forest is a mature forest that receives little disturbance from human beings; rather, snowstorms and other natural incidents are the main types of disturbance. The canopy is dominated by *Abies faxoniana*; however, *Acer maxi mowiczii* and *Betula utilis* are found below 3500 masl. The shrub layer composition consists of Rhodo-dendroideae and *Fargesianitida* and varies with elevation. Under the closed *Abies faxoniana* canopy, the herb layer is rather sparse and poor, and the moss layer is thicker. In our study area, the timberline occurs at approximately 3700 masl, and the tree line occurs at 3820 masl. Above 3800 masl, subalpine coniferous forest has been replaced by alpine scrub and meso-phorbium vegetation, such as *Rhododendron*, *Lonicera*, *Rhodiola* and *Rosa*.

2.2   Experimental design and data collection

In August–September 2015 and June–August 2017, 84 plots (area range: 38.5–410 m^2) were randomly selected roughly along a belt transect (width × length: 30 m × 1600 m) along the elevation gradient that was identified in this mature forest in 2014, and these plots were di-vided into four categories according to their disturbance intensity, i.e., plots with large gaps (N = 21; area ranged from 200 to 410 m^2), medium gaps (N = 21; area ranged from 100 to 200 m^2), small gaps (N = 21; area ranged from 38.5 to 100 m^2), and non-gap plots (N = 21; 10 m × 10 m). Three plots from each category were selected within each 100-m elevation interval between 3000 and 3700 m (seven elevation intervals in total). Gap size was calcu-lated using the formula for the area of a circle or ellipse (Runkle, 1981). The non-gap plots were located at least 10 m from the plots with gaps.

In each plot (gap/non-gap plots), two belt transects were established, and each crossed through the center of the gap or non-gap plot, radiated outward from east to west and from north to south and extended to the edges of gap (Figure 1c). Nine subplots (1 m^2) were used for within-plot sampling and were located on the two transects, with one subplot located at the center of the gap or non-gap plot; the remaining subplots were evenly distributed along the two transects (Anderson and Leopold, 2002). In total, we sampled 756 subplots.

Except for forest gap and elevation, the above-ground environmental factors (e.g., PPFD) (LI-190, Li-Cor Inc.), ultraviolet-A radiation (365 nm, UV-A365) (UV radiometer, UV-A, Photoelectric Instrument Factory of Beijing Normal University (PIFBNU), China), ultravio-let-B$_1$ radiation (297 nm, UV-B297) (UV radiometer, UV-B, Photoelectric Instrument Fac-tory of Beijing Normal University, China), and ultraviolet-B$_2$ radiation (254 nm, UV-B 254) (UV radiometer, UV-B, PIFBNU, China) were measured 1 m above ground level at the cen-ter of each plot. Any low-growing vegetation (height ≈ 1 m) that shaded the sensor was moved before the reading was recorded. The PPFD was measured under completely overcast sky conditions because these conditions provided a stable value and were well correlated with the growing season PPFD (Parent and Messier, 1996; Gendron *et al*., 1998). Because of the potentially high physiological effects of solar radiation on plant regeneration caused by strong solar ultraviolet radiation (UV), the values for solar radiation were recorded under cloudless conditions (Piazena and Hader, 2009; Barnes *et al*., 2017). These light measure-ments were taken between June 7th and September 20th and between 9 a.m. and 4 p.m. based on the corresponding weather conditions. The thick layers of bryophytes are known to play a significant role in soil waterholding, soil temperature maintenance, soil C cycling and

soil N cycling (Lindo and Gonzalez, 2010). The plant diversity was directly and/or indirectly influenced by these bryophytes. In our study, the moss thickness (MT) of each plot was also measured in three randomly selected subplots. Two button thermometers (iButton, DS1923-F5#, USA) were fixed at 1 m above the ground in each forest gap; one thermometer was fixed in the center of forest gap, and the other thermometer was fixed at the edge of forest gap. Furthermore, only one button thermometer was fixed in the center of each non-gap plot. We assessed the AMAT within each plot by using field monitoring and combining the data from the regression equations of elevation and temperature (slope = –0.003, $R^2 = 0.93$).
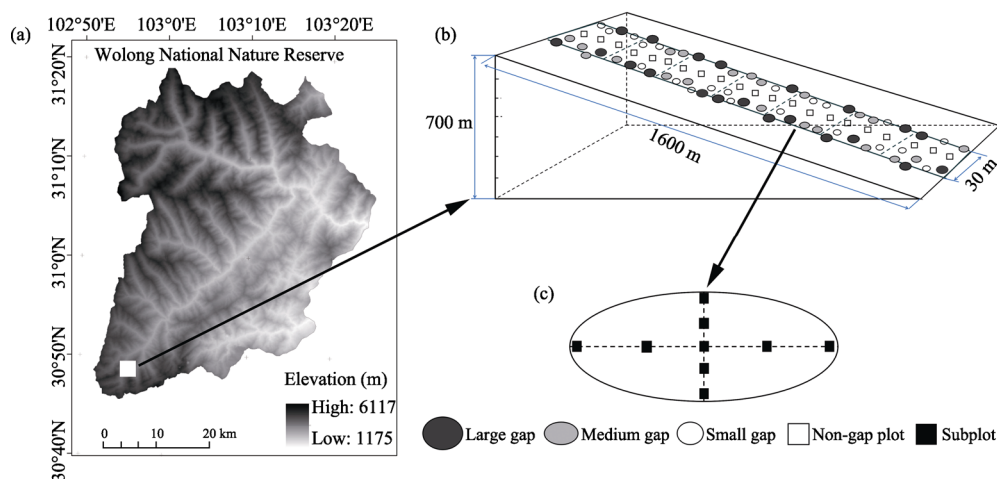

Figure 1 Diagram showing the information about location and topography (a), sampling pots (b) and subplots (c) in the Wolong National Nature Reserve in southwest China. In panel b, each elevation interval contains three plots of each category. Panel c illustrates how the nine subplots were distributed within a plot.

Below-ground environmental factors included soil physical and chemical properties, and together they form an important component of the habitat because of their influence on plant distribution (Hardtle *et al*., 2003; Molina-Venegas *et al*., 2016).The annual mean soil temperature (AMST) was monitored at a depth of 0–10 cm in the soil layer using button thermometers fixed in the center of each plot (iButton, DS1923-F5#, USA). All soil samples (0–10 cm) were collected randomly from three points in each plot. The soil samples were air dried and then sieved through a 2-mm mesh screen to remove debris and roots. The following eight edaphic variables were analyzed: soil water content (SWC, %), soil pH (pH-meter, Hach HQ40d), soil total carbon (STC, %), soil total nitrogen (STN, %), carbon/nitrogen ratio (C/N ratio), soil total sulfur (STS, %), NH_4-N (mg kg^{-1}), and NO_3-N (mg kg^{-1}).

Vegetation data were recorded during the growing seasons (i.e., in Aug–Sep 2015 and Jun–Aug 2017). In addition to the tall trees and shrubs within each plot, the species richness of the low-growing vegetation (i.e., tree seedlings and smaller plants) was calculated in each subplot. The α-diversity was defined as the species richness, which was determined by the total species richness of the nine subplots within each plot. The γ-diversity was defined as the total richness of the 12 plots at each 100-m elevation interval, and the β-diversity was defined as the heterogeneity in the species composition among the 12 plots at each elevation

interval. Here, β-diversity was measured using multiplicative β partitioning ($\beta = 1 - \alpha/\gamma$) (Kraft *et al*., 2011). In our study, the spatial scale of β-diversity was smaller than those in many other studies; however, our study still captured the responses to fine-grained environmental heterogeneity (Kraft *et al*., 2007).

2.3   Data analysis

To test for differences among treatments (i.e., between different habitat types (gap/non-gaps), among different-sized gaps or elevation gradients), the above- and below-ground environmental factors and the α-diversity and β-diversity were compared using one-way ANOVA, and two-way ANOVA was used to test interactions between factors. Pearson's correlation was used to identify significant correlations between gap size and plant diversity. These data were analyzed using SPSS 20.0 (IBMCo, Armonk, NY, USA). Unless otherwise indicated, statistical analyses were conducted at the significance level of $\alpha = 0.05$.

Structural equation models (SEMs) were used to analyze the effects and correlations (direct and indirect) among forest gaps (different habitat types and different-sized gaps), elevation, α-diversity and β-diversity and above- and below-ground environmental variables of the plots. The SEM analyses were performed in Amos 22.0 (SPSS Inc., USA). Initially, we considered that there was a directional dependence among the parameters based on the correlation explanation proposed in previous research (Vetaas and Grytnes, 2002; Hardtle *et al*., 2003; Kubota *et al*., 2004; Vajari *et al*., 2012), and we assumed an a *priori* hypothetical model (Figure 2). In our case, the above- and below-ground environmental factors and the α-diversity and β-diversity were closely associated with forest gap and elevation, either directly or indirectly; however, these variables di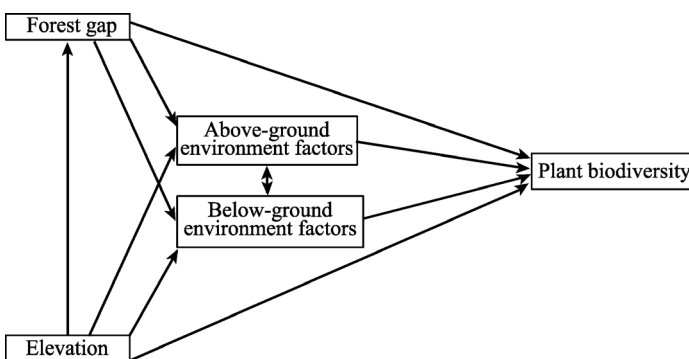d not affect forest gap and elevation. Next, we compared all hypothesized candidate models with significant pathways, and we searched for a model that displayed a better fit to the observed data using the smallest AIC (Akaike's information criterion) (Kubota *et al*., 2004; Chen *et al*., 2018). Finally, the direct effects, indirect effects, and total effects of forest gaps and elevation on the diversity of the subalpine coniferous forest were evaluated.

Figure 2   Conceptual model used to test the link among forest gaps (gap/non-gap plots and gap sizes), elevation, environmental factors (above- and below-ground environmental factors) and plant diversity (α-diversity and β-diversity)

3   Results

3.1   Effects of forest gaps or/and elevation on diversity

A total of 83 species and 49 families were found in our study area. Unimodal patterns were found between α-diversity/γ-diversity and elevation (Figures 3a and 3b). The results showed

that the relationship between β-diversity and elevation applied to the hyperbolic sine equation (Figures 3c and 3d). One-way ANOVA (Table 1) showed that the α-diversity and β-diversity differed significantly (α-diversity: N = 84, F = 51.59, $p<0.001$; β-diversity: N = 84, F = 2.28, p = 0.049) among the seven elevation intervals. The plant diversity also varied markedly in the different habitat types (i.e., plots with forest gaps and non-gap plots) (α-diversity: N = 84, F = 555.76, $p < 0.001$; β-diversity: N = 84, F = 125.80, $p< 0.001$). Moreover, α-diversity was positively related to gap size (N = 63, R^2 = 0.28, p = 0.025), but the opposite relationship was observed between β-diversity and gap size (N = 63, R^2 = –0.662, $p< 0.001$) (Table 2). However, α-diversity was similar (N = 63, F = 0.12, p = 0.888) (Table 1) among the different-sized gaps at the high elevations (≥3500 m).
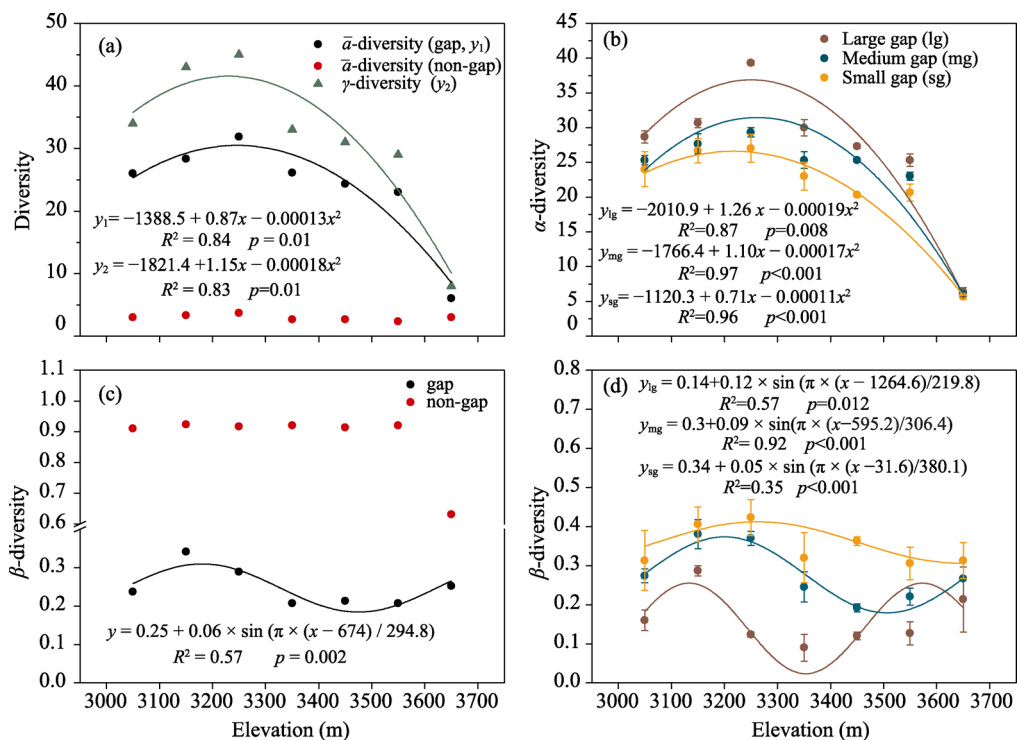

Figure 3 Nonlinear fitting results of α (a, b), β (c, d), and γ (a) diversity in non-gap plots or different-sized gaps along the elevation gradient with the mean α in different-sized gaps at the same elevation interval

3.2 Effects of forest gaps or/and elevation on environmental factors

Almost all of the environmental factors were significantly affected by elevation, except for the PPFD (N = 84, F = 0.02, p = 1.00; N = 63, F = 0.576, p = 0.75), NH_4-N (N = 84, F = 1.71, p = 0.13) and the C/N ratio (N = 63, F = 1.64, p = 0.15) (Table 1). However, both the interaction between elevation and habitat types and the interaction between elevation and gap size significantly affected the soil NH_4-N (N = 84, F = 10.62, $p < 0.001$; N = 63, F = 2.71, $p<0.001$) (Table 1). The AMAT was similar (N = 84, F = 1.34, p = 0.25) between the plots with forest gaps and the non-gap plots, but the AMAT was significantly influenced by the interaction between habitat types and elevation (N = 84, F = 2.94, p = 0.013) (Table 1).

Table 1 One-way ANOVA results comparing the effects of habitat type, gap size and elevation. F and P values are derived from ANOVA.

Variables	Habitat types N=84	Elevation (all plots), N=84	Gap size N=63	Elevation (gaps), N=63
Above-ground environmental factors				
Annual mean air temperature (°C)	1.34	47.07***	0.115	36.42***
PPFD (μ mol m^{-2} s^{-1})	3771.46***	0.02	37.41***	0.576
UV-A365 (μ W cm^{-2})	91.30***	5.52***	20.43***	12.73***
UV-B297 (μ W cm^{-2})	30.50***	15.78***	1.00	144.94***
UV-B254 (μ W cm^{-2})	78.16***	6.78***	12.044***	21.503***
Moss thickness (cm)	4.2*	6.81***	0.876	4.74***
Below-ground environmental factors				
Annual mean soil temperature (°C)	1.02	285.51***	0.03	314.76***
Soil water content (%)	0.17	10.80***	0.03	13.96***
Soil pH	1.83	3.45**	0.93	3.65**
Soil total carbon (%)	3.18	17.33***	2.83	9.87***
Soil total nitrogen (%)	7.84**	38.77***	2.63	37.38***
Soil total sulfur (%)	5.83***	2.64*	5.60***	3.56***
Carbon/nitrogen ratio	1.94	2.40*	0.35	1.64
NH$_4$-N (mg kg^{-1})	8.20***	1.71	2.47	11.82***
NO$_3$- N (mg kg^{-1})	3.64*	5.71*	0.33	18.06***

***$p<0.001$, **$p<0.01$, *$p<0.05$

3.3 Relationships between environmental factors and diversity

As seen in Table 2, the above-ground environmental factors dramatically improved from the non-gap plots to the plots with forest gaps; therefore, they were positively related to the α-diversity. In forest gaps, many above-ground environmental factors were positively and significantly related to α-diversity, with the exception of ultraviolet radiation (i.e., UV-A365, UV-B297 and UV-B254). The β-diversity was significantly negatively correlated with the PPFD (N = 84, r = –0.944, p < 0.001, N = 63, r = –0.54, p < 0.001) and the ultraviolet radiation (UV-A365, UV-B297 and UV-B254). The correlation analysis results based on all plots indicated that there was a negative and significant correlation between MT and β-diversity (N = 84, r = –0.35, p < 0.001).

For the below-ground environmental factors (Table 2), the AMST (N = 84, r = 0.44, p < 0.001; N = 63, r = 0.653, p < 0.001), STC (N = 84, r = 0.38, p < 0.001; N = 63, r = 0.38, p < 0.01) and STN (N = 84, r = 0.55, p < 0.001; N = 63, r = 0.59, p < 0.001) were significantly positively correlated with the α-diversity in all plots and in different-sized gaps. NH$_4$-N (N = 84, r = –0.51, p < 0.001) had a significantly negative relationship with α-diversity in all plots, and NO$_3$-N (N = 63, r = –0.29, p < 0.01) was negatively and significantly related to α-diversity in different-sized gaps. In all plots, the STN (N = 84, r = –0.23, p < 0.01), C/N ratio (N = 84, r = –0.25, p < 0.01), NH$_4$-N (N = 84, r = 0.74, p < 0.01) and NO$_3$-N (N = 84, r = –0.25, p < 0.01) were significantly related to β-diversity. However, there were nonsignificant correlations between β-diversity and below-ground environmental factors in different-sized gaps, with the exception of NO$_3$-N (N = 63, r = –0.25, p < 0.01).

Table 2 Pearson correlation results between environmental factors (above- and below-ground environmental factors) and diversity (α-diversity and β-diversity)

	Above-ground environment factors							
	PPFD	UV-A365	UV-B297	UV-B254	MT			
All plots (N=84)								
α-diversity	0.81***	0.43***	0.02	0.39***	0.03			
β-diversity	−0.944***	−0.83***	−0.57***	−0.79***	−0.35**			
Gaps (N=63)								
α-diversity	0.44***	−0.34***	−0.72***	−0.36***	0.28**			
β-diversity	−0.54***	−0.61***	−0.3**	−0.54***	0.14			

	Below-ground environment factors								
	AMST	pH	SWC	STC	STN	C/N ratio	NH$_4$-N	NO$_3$-N	STS
All plots (N=84)									
α-diversity	0.44***	0.14	−0.1	0.38***	0.55***	0.04	−0.51***	−0.003	−0.09
β-diversity	0.01	−0.1	0.07	−0.2	−0.23**	−0.25**	0.74***	−0.25**	0.17
Gaps (N=63)									
α-diversity	0.653***	0.03	−0.13	0.38**	0.59***	−0.14	0.21	−0.29**	0.21
β-diversity	0.224	0.12	0.15	−0.13	0.02	−0.13	0.05	−0.25**	−0.22

***$p<0.001$, **$p<0.01$, *$p<0.05$

3.4 The influencing mechanism of forest gaps and elevation on diversity

The a *priori* model (Figure 2) did not significantly represent the genuine relationships among the variables in our study area; thus, the best fit models exhibited variations, which indicated a good adjustment was applied to our observed data. The best-fit models were selected using the χ^2 test, GFI, CFI, RMESA and AIC (Table 3). Despite the significant or nonsignificant differentiation and correlation in the ANOVA and Pearson correlation analyses (Tables 1 and 2), several pathways contributed to the different results of the SEMs; thesepathways included the forest gaps (habitat types and gap area) and elevation, the above- and below-ground environmental factors and the α-diversity and β-diversity.

Table 3 Values of the fit indices of the four structural equation models for α-diversity and β-diversity in a subalpine coniferous forest (For the information associated with models a, b, c, and d, see Figure 3)

Models	Model fit indices						
	χ^2	DF	p	RMSEA	GFI	CFI	AIC
a	3.869	8	0.869	<0.001	0.988	1	59.869
b	9.609	13	0.726	<0.001	0.974	1	73.609
c	0.216	3	0.975	<0.001	0.99	1	36.216
d	10.119	14	0.753	<0.001	0.959	1	54.119
Criterion	–	–	>0.05	<0.05	>0.9	>0.9	Lowest

For the α-diversity indicators (Figures 4a and 4c), the selected variables (i.e., PPFD, UV-B297, AMAT, MT, C/N ratio and UV-A365) explained a moderate amount of the variance (habitat types and elevation: 0.73; gap area and elevation: 0.55) in the final models (Table 4). Our SEMs also indicated that elevation had both direct and indirect effects on α-diversity through its impacts on the above-ground environmental factors (UV-A365, UV-B297, AMAT, and MT) and the below-ground environmental factors (C/N ratio);
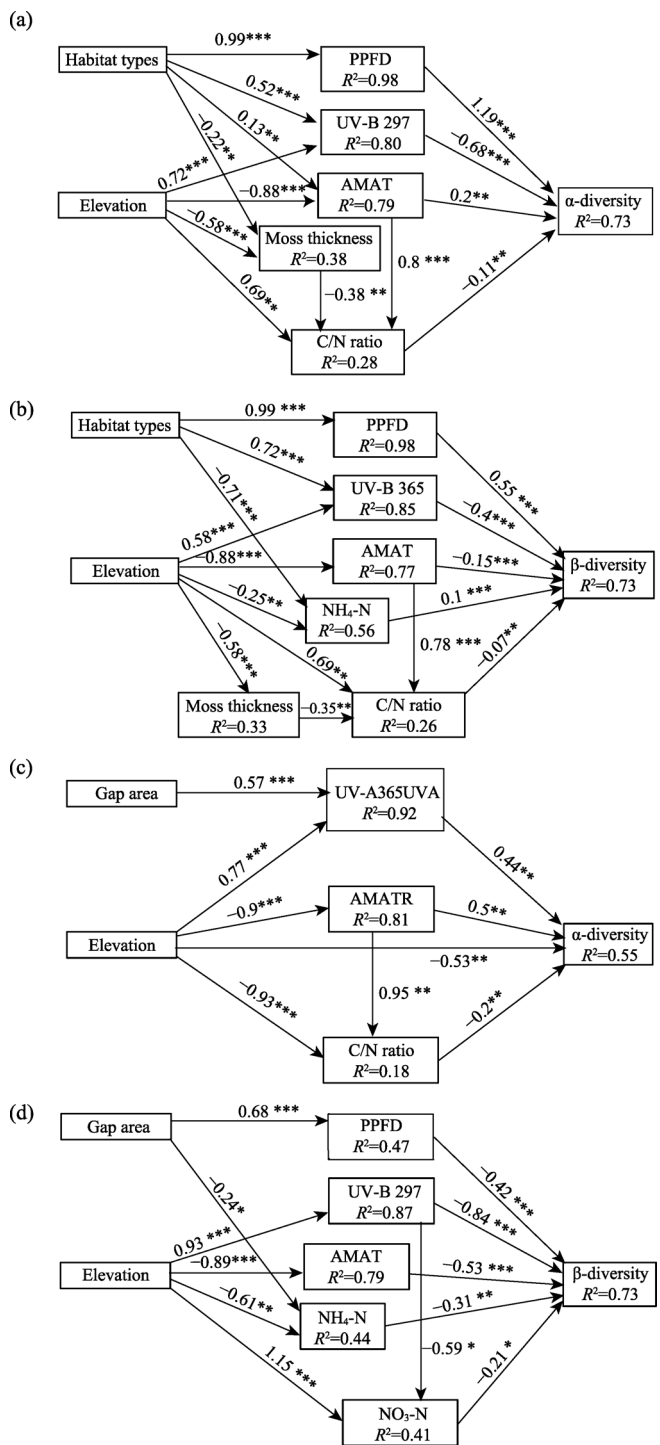
Figure 4 Best-fitting structural equation models. Four models are presented in relation to the four aspects of forest gaps (gap/non-gap and gap area) and elevational effects on diversity (α-diversity and β-diversity). Positive and negative pathways are indicated by black and gray lines, respectively. Arrow thickness is scaled to illustrate the relative strength of effects, and significant coefficients are indicated with asterisks (* $p<0.05$; ** $p<0.01$; *** $p<0.001$). The coefficient of determination (R^2) is shown in the black box for all response variables. The independent variable, as a predictor, is the habitat type coded as plots with gaps = 2 and non-gap plots = 1; thus, in the SEMs, the habitat type is an ordered categorical variable.

Table 4 Standardized total effect, indirect effect and direct effect of predictor variables on α-diversity and β-diversity for the best SEMs, as shown in Figure 3

	All plots (N=84)								
	Elevation	Habitat types	AMAT	PPFD	UV-B297	UV-A365	C/N ratio	MT	NH$_4$-N
Total effect									
α-diversity	–0.7	0.77	0.13	1.13	–0.68	—	–0.11	0.04	—
β-diversity	–0.14	–0.9	–0.21	–0.55	—	–0.4	–0.07	0.03	0.1
Direct effect									
α-diversity	0	0	0.21	1.13	–0.68	—	–0.11	0	—
β-diversity	0	0	–0.15	–0.55	—	–0.4	–0.07	0	0.1
Indirect effect									
α-diversity	–0.7	0.77	–0.09	0	0	—	0	0.04	—
β-diversity	–0.14	–0.9	–0.06	0	—	0	–0.07	0.03	0

	Gaps (N=63)								
	Elevation	Gap area	AMAT	PPFD	UV-A365	UV-B297	C/N ratio	NH$_4$-N	NO$_3$-N
Total effect									
α-diversity	–0.66	0.25	0.31	—	0.44	—	–0.2	—	—
β-diversity	–0.26	–0.21	–0.53	–0.42	—	–0.72	—	–0.31	–0.21
Direct effect									
α-diversity	–0.53	0	0.5	—	0.44	—	–0.2	—	—
β-diversity	0	0	–0.53	–0.42	—	–0.84	—	–0.31	–0.21
Indirect effect									
α-diversity	–0.13	0.25	–0.19	—	0	—	0	—	—
β-diversity	–0.26	–0.21	0	0	—	0.12	—	0	0

moreover, the SEMs predicted that forest gaps (including different habitat types and gap areas) affected the α-diversity mainly by influencing the above-ground environmental factors (PPFD, UV-A365, UV-B297, AMAT, and MT). The total effect of the environmental factors on the α-diversity in all plots varied in the following order: PPFD (1.128), UV-B297 (-0.678), AMAT (0.126), C/N ratio (–0.106) and MT (0.04). In different-sized gaps, the rank of the AMAT (0.308) total effect on the α-diversity was greater than the effects of the C/N ratio (–0.203) but less than the effects of the ultraviolet radiation (UV-A365, 0.436).

In the best-fit models of β-diversity indicators (Figures 4b and 4d), the β-diversity consisted of the differences in species richness among the large, medium, and small gaps and the non-gap plots in each elevation interval; thus, more environmental factors had opposite positive/negative correlations with β-diversity than was observed with α-diversity. Based on the final model shown in Figure 3, we compared the total effect of the relative importance of forest gaps (including habitat type and gap area) and elevation. Habitat type (–0.9) had a larger total effect on β-diversity than did elevation (–0.14) (Table 4). The total effect of environmental factors on β-diversity in all plots varied in the following order: PPFD (–0.548), UV-A365 (–0.399), AMAT (–0.207), NH$_4$-N (0.1), C/N ratio (–0.071) and MT (0.025). Moreover, in different-sized gaps, the rank varied in the following order: UV-B297 (–0.715), AMAT (–0.525), PPFD (–0.417), NH$_4$-N (–0.309) and NO$_3$-N (–0.213).

4   Discussion

4.1   Environmental factors and plant diversity

Above ground, the size of forest gap had a direct effect on the solar radiation, which in turn, affected plant diversity (Diaci *et al*., 2012). Raymond and Munson (2006) and Caquet *et al*. (2012) reported that during the growing season, plant regeneration was positively correlated with light availability. Moreover, numerous studies have reported that temperature and solar ultraviolet radiation were affected by elevation; thus, these variables affected plant diversity. (Piazena and Hader, 2009; Cienciala *et al*., 2016; Barnes *et al*., 2017). Our results support the idea that, in forest gaps, the temperature and solar radiation (i.e., PPFD and ultraviolet radiation) were the most important variables that influenced the α-diversity and β-diversity as elevation increased. Moreover, our results also suggest that α-diversity and β-diversity were indirectly affected by MT in different habitat types along the elevational gradient. Furthermore, more than 26% of the variation in the C/N ratio was explained by the combined effects of elevation, AMAT and MT (Figures 3A and 3B); however, we did not find any evidence supporting the effect and correlation from below-ground environmental factors to above-ground environmental factors (i.e., the effects of soil properties on MT).

The below-ground environmental factors of soil temperature, water content and nutrient cycling were strongly related to plant regeneration and diversity in forest gaps (Scharenbroch and Bockheim, 2007; Scharenbroch and Bockheim, 2008; Muscolo *et al*., 2014; Santibáñez-Andrade *et al*., 2015). Surprisingly, the relationships between several soil properties (e.g., temperature, water content, pH, total carbon, total nitrogen and total sulfur) and α-diversity/β-diversity were discarded in our resulting models. Finally, the plant diversity was mainly affected by the C/N ratio, NH_4-N and NO_3-N in the SEMs. These results were consistent with the conclusions of Denslow *et al*. (1998), who stated that forest gaps had a slight effect on the soil NH_4-N and NO_3-N pools, which then affected vegetation regeneration in a tropical wet forest. These results were probably partly related to both the litter decomposition rates and the quantity of nutrients demanded in the research area (Ping *et al*., 2015; Barbier *et al*., 2008; Cienciala *et al*., 2016). Our findings demonstrated that the increase in the α-diversity was related to the low soil C/N ratio (Figures 3a and 3c). A similar relationship was also found between soil NH_4-N and β-diversity among different-sized gaps (Figure 3d) and between soil NO_3-N and β-diversity (Figure 3d). However, soil NH_4-N exhibited opposing effects on β-diversity between the plots with gaps and the non-gap plots along the elevational gradient (Figure 3b). This result indicated that the positive/negative effects of the below-ground environmental factors on the β-diversity did not have to be unidirectional from the non-gap plots to the plots with small gaps, medium gaps, and large gaps.

4.2   Forest gap effects on α- and β-diversity

Several studies on plant regeneration have focused on the relationships between forest gap size, environmental factors and α-diversity (Hardtle *et al*., 2003; Muscolo *et al*., 2011; Kern *et al*., 2013; Muscolo *et al*., 2014). The AMAT, light levels, soil nutrients, and plant diversity are generally higher in forest gaps than in closed canopies (Denslow *et al*., 1998; Sariyildiz, 2008). Our study supports that forest gaps significantly improved α-diversity compared with

the non-gap plots, and α-diversity was positively and indirectly affected by gap size (Wang and Liu, 2011; Gray *et al*., 2012). Muscolo *et al*. (2014) showed that gap size often determines species composition. Garbarino *et al*. (2012) reported that there was higher plant diversity in large gaps because shade-intolerant and early successional species were found only in large gaps in an old-growth forest. However, our results also suggest that at high elevations ($\geq$ 3500 m), this difference in α-diversity was not significant among different-sized gaps (38.5–410 m^2). Different from the α-diversity among different-sized gaps at low elevations, both the subtle difference in species diversity and the low species richness contributed to the similar α-diversity values found among the different sized-gaps at high elevations. One of the most likely explanations is that most species find it difficult to adapt to the extreme environment at high elevations. Thus, a low-intensity logging disturbance should be considered as a viable method used to maintain the abundance of canopy trees, which can protect the regeneration of tree seedlings and smaller plants from the harsh weather more than large canopy openings can (Chen *et al*., 2018).

It is widely recognized that β-diversity is not independent from variation in either α-diversity or γ-diversity (Kraft *et al*., 2011). The major focus of our study was on α-diversity and β-diversity because γ-diversity represents regional diversity, which differs in scope from our objectives (Loreau, 2000). Our results showed that the effects of forest gap on α-diversity and β-diversity were related in terms of ecological mechanisms. In our study region, among these below-ground environmental factors, the soil NH_4-N was negatively influenced by the habitat types and gap area, thus affecting β-diversity. Like the α-diversity, the PPFD and ultraviolet radiation still played important roles in the forest gap processes that affect β-diversity (Figures 4b and 4d). These results indicated that it may be possible to effectively narrow the differences in species richness among non-gap plots and different-sized gaps by changing the light condition or soil NH_4-N (Condit *et al*., 2002; Duivenvoorden *et al*., 2002).

4.3 Elevation effects on α- and β-diversity

Descriptions and examinations of α-diversity across elevation gradients have received great attention because they reveal the general mechanisms affecting the distribution of biodiversity (Vetaas and Grytnes, 2002; Molina-Venegas *et al*., 2016). Our study supports the idea that, in mountainous landscapes, the α-diversity in forest gaps exhibits a hump-shaped pattern along the elevational gradient (Wang *et al*., 2007). Brown *et al*. (2004) found that low temperatures have emerged as a limiting factor affecting species diversity at high elevations. According to McCain (2007) and Kreft and Jetz (2007), α-diversity was limited by the availability of water (measured by potential evapotranspiration) and energy (measured by temperature) at high elevations along latitudinal gradients. Our findings here partially support the previously reported correlations between the α-diversity and the elevation of gaps. The results of the SEMs indicated that, along the elevational gradient, the α-diversity was positively related with the AMAT, while the ultraviolet radiation (UV-A365 and UV-B297) and soil properties (C/N ratio) can also directly limit the α-diversity, especially in high-elevation gaps (Tang and Fang, 2004). These differences may be associated with research scales, which may rely too strongly on latitude-related decreases in temperature and

water availability at large scales instead of considering alternatives such as decreasing ambient environmental factors like soil and light radiation (Korner, 1992).

A previous study reported a nonsignificant pattern of β-diversity along an elevational gradient (Dolezal and Srutek, 2002). According to Fernandezpalacios and Denicolas (1995), there was a weak negative relationship between β-diversity and elevation on the windward slope, while no rule for β-diversity variation was observed for the leeward slope. Our study showed that with increasing elevation, the sinusoidal function of the β-diversity variation trend in forest gaps was selected based the lowest AIC value among several different functions; however, no significant pattern of β-diversity existed in the closed-canopy plots (i.e., the non-gap plots) along the elevational gradient. The patterns of β-diversity may be associated with the degree of variation in habitats along the elevational gradient (Tang and Fang, 2004), and when the canopy cannot provide protection from harsh weather conditions, the microenvironments in forest gaps changed more than those in the closed-canopy plots as elevation increased (Denslow, 1987; Jin *et al*., 2015).

4.4 Implications for forest management

One of the main goals for forest managers at the level of the forest landscape is to find a balance between utilization and preservation. Therefore, management strategies should adopt realistic and pragmatic approaches. In this regard, and as a more straightforward driver of plant diversity than elevation, logging gaps will have higher α-diversity than will closed-canopy plots. Additionally, community dissimilarity (β-diversity) in large gaps $(200–402 \text{ m}^2)$ was lower than that in smaller gaps $(38.5–100 \text{ m}^2)$ in this study. In addition, at high elevations ($\geqslant 3500$ m), lower-intensity practices better conserved the abundance of tall trees; however, the plant species were the same because the positive relationships between gap size and α-diversity disappeared. Moreover, in our SEMs, the relevance of the relationship between indicators afforded a new perspective on the ecological mechanisms of forest gaps and elevation effects on plant diversity. Furthermore, in environments with different-sized gaps, NH_4-N and NO_3-N were negatively and directly related with β-diversity. Thus, improving soil qualities after silvicultural practices may enhance the plan to develop the diversity of subalpine coniferous forests.

5   Conclusions

Our study proposed an accurate and simple quantitative method for assessing the effects of forest gaps and elevation on plant diversity based on changes in above- and below-ground environmental factors under a "direct and indirect" analytical framework. The double-index evaluation (i.e., α-diversity and β-diversity) was introduced to explain the underlying mechanisms of variation in vegetation at the landscape scale. Using SEMs, our study indicated that the AMAT, PPFD and MT, which were dominated by the habitat type and gap size along the elevational gradient, could positively contribute to improving α-diversity. The influence of environmental factors varied with elevation, which offers dual perspectives regarding the understanding of variations in plant diversity. (1) The diversity-elevation patterns were more evident in plots with forest gaps than in non-gap plots, and the large gaps

supported high localized plant diversity in the subalpine coniferous forest of southeastern China. (2) The above-ground environmental factors should be responsible for more complex and major effects on α-diversity and β-diversity than are the below-ground environmental factors in forest gaps because of the indirect effects and more predicted pathways. (3) The large gap-based management policies are advocated at low elevations. In terms of both species richness and favorable habitat for tree seedlings and smaller plants, less management may be more suitable to maintain plant diversity at high elevations. Our research highlighted the underlying mechanisms of the effects of forest gaps and elevation on α-diversity and β-diversity as well as their overall relationships with above- and below-ground environmental factors; furthermore, our research strongly suggested that, as the important drivers of plant diversity, the above-ground environmental factors were more easily affected by forest gaps and elevation than were the below-ground environmental factors.

References

Anderson K L, Leopold D J, 2002. The role of canopy gaps in maintaining vascular plant diversity at a forested wetland in New York State. *Journal of the Torrey Botanical Society*, 129(3): 238–250.

Barbier S, Gosselin F, Balandier P, 2008. Influence of tree species on understory vegetation diversity and mechanisms involved: A critical review for temperate and boreal forests. *Forest Ecology and Management*, 254(3): 1–15.

Barnes P W, Ryel R J, Flint S D, 2017. UV screening in native and non-native plant species in the tropical alpine: Implications for climate change-driven migration of species to higher elevations. *Frontiers in Plant Science*, 8(1): 1451.

Battles J J, Shlisky A J, Barrett R H, 2001. The effects of forest management on plant species diversity in a Sierranconifer forest. *Forest Ecology and Management*, 146(1–3): 211–222.

Beck J, Chey V K, 2008. Explaining the elevational diversity pattern of geometrid moths from Borneo: A test of five hypotheses. *Journal of Biogeography*, 35(8): 1452–1464.

Bello F D, Lavergne S, Meynard C N *et al*., 2010. The partitioning of diversity: Showing Theseus a way out of the labyrinth. *Journal of Vegetation Science*, 21(5): 992–1000.

Bongers F, Poorter F, Hawthorne W *et al*., 2009. The intermediate disturbance hypothesis applies to tropical forest, but disturbance contributes little to tree diversity. *Ecology Letters*, 12(8): 798–805.

Brown J H, Gillooly J F, Allen A P *et al.*, 2004. Toward a metabolic theory of ecology. *Ecology*, 85(7): 1771–1789.

Caquet B, Montpied P, Dreyer E *et al*., 2010. Response to canopy opening does not act as a filter to Fagus sylvatica and Acer sp advance regeneration in a mixed temperate forest. *Annals of Forest Science*, 67(1): 105p1–105p11.

Chen L, Liu, G H, Liu D, 2018. How forest gap and elevation shaped *Abiesfaxoniana* Rehd. et Wils. Regeneration in a subalpine coniferous forest, Southwestern China. *Forests*, 9(5). doi: 10.3390/f9050271

Cienciala E, Russ R, Santruckova H *et al*., 2016. Discerning environmental factors affecting current tree growth in Central Europe. *Science of the Total Environment*, 573: 541–554.

Condit R, Pitman N, Leigh E G *et al*., 2002. Beta-diversity in tropical forest trees. *Science*, 295(5555): 666–669.

Crist T O, Veech J A, 2006. Additive partitioning of rarefaction curves and species-area relationships: Unifying alpha-, beta- and gamma-diversity with sample size and habitat area. *Ecology Letters*, 9(8): 923–932.

Denslow J S, 1987. Tropical rainforest gaps and tree species diversity. A*nnual Review of Ecology and Systematics*,18: 431–451.

Denslow J S, Ellison A M, Sanford R E, 1998. Treefall gap size effects on above- and below-ground processes in a tropical wet forest. *Journal of Ecology*, 86(4): 597–609.

Diaci J, Adamic T, Rozman A, 2012. Gap recruitment and partitioning in an old-growth beech forest of the Dinaric Mountains: Influences of light regime, herb competition and browsing. *Forest Ecology and Management*, 285: 20–28.

Dolezal J, Srutek M, 2002. Altitudinal changes in composition and structure of mountain-temperate vegetation: A case study from the Western Carpathians. *Plant Ecology*, 158(2): 201–221.

Duivenvoorden J F, Svenning J C, Wright S J, 2002. Beta diversity in tropical forests. *Science*, 295(5555): 636–637.

Fernandezpalacios F M, Denicolas J P, 1995. Attitudinal pattern of vegetation variation on Tenerife. *Journal of Vegetation Science*, 6(2): 183–190.

Galhidy L, Mihok B, Hagyo A *et al*., 2006. Effects of gap size and associated changes in light and soil moisture on the understorey vegetation of a Hungarian beech forest. *Plant Ecology*, 183(1): 133–145.

Garbarino M, Mondino E B, Lingua E *et al*., 2012. Gap disturbances and regeneration patterns in a Bosnian old-growth forest: A multispectral remote sensing and ground-based approach. *Annals of Forest Science*, 69(5): 617–625.

Gendron F, Messier C, Comeau P G, 1998. Comparison of various methods for estimating the mean growing season percent photosynthetic photon flux density in forests. *Agricultural and Forest Meteorology*, 92(1): 55–70.

Gray A N, Spies T A, Pabst R J, 2012. Canopy gaps affect long-term patterns of tree growth and mortality in mature and old-growth forests in the Pacific Northwest. *Forest Ecology and Management*, 281: 111–120.

Hardtle W, Oheimb G V, Westphal C, 2003. The effects of light and soil conditions on the species richness of the ground vegetation of deciduous forests in northern Germany (Schleswig-Holstein). *Forest Ecology and Management*, 182(1–3): 327–338.

Jin Y, Qian H, Yu M, 2015. Phylogenetic structure of tree species across different life stages from seedlings to canopy trees in a subtropical evergreen broad-leaved forest. *Plos One*, 10(6): e0131162.

Kern C C, Montgomery R A, Reich P B *et al*., 2013. Canopy gap size influences niche partitioning of the ground-layer plant community in a northern temperate forest. *Journal of Plant Ecology*, 6(1): 101–112.

Korner C, 1992. Why are there global gradients in species richness? Mountains might hold the answer. *Trends in Ecology & Evolution*, 45(8): 618–619.

Kraft N J B, Comita L S, Chase J M *et al*., 2011. Disentangling the drivers of beta diversity along latitudinal and elevational gradients. *Science*, 333(6050): 1755–1758.

Kraft N J B, Cornwell W K, Webb C O *et al*., 2007. Trait evolution, community assembly, and the phylogenetic structure of ecological communities. *American Naturalist*, 170(2): 271–283.

Kreft H, Jetz W, 2007. Global patterns and determinants of vascular plant diversity. *Proceedings of the National Academy of Sciences of the United States of America*, 104(14): 5925–5930.

Kubota Y, Murata H, Kikuzawa K, 2004. Effects of topographic heterogeneity on tree species richness and stand dynamics in a subtropical forest in Okinawa Island, southern Japan. *Journal of Ecology*, 92(2): 230–240.

Lindo Z G A, 2010. The bryosphere: An integral and influential component of the Earth's biosphere. Ecosystems, 13(4): 612–627.

Liu D, Wu X, Shi S L *et al*., 2016. A hollow bacterial diversity pattern with elevation in Wolong Nature Reserve, Western Sichuan Plateau. *Journal of Soils and Sediments*, 16(10): 2365–2374.

Loreau M, 2000. Are communities saturated on the relationship between α, β and γ diversity. *Ecology Letters*, 3(2): 73–76.

McCain C, 2007. Area and mammalian elevational diversity. *Ecology*, 88(1): 76–86.

Molina-Venegas R, Aparicio A, Lavergne S *et al*., 2016. How soil and elevation shape local plant biodiversity in a Mediterranean hotspot. *Biodiversity and Conservation*, 25(6): 1133–1149.

Muscolo A, Bagnato S, Sidari M *et al*., 2014. A review of the roles of forest canopy gaps. *Journal of Forestry Research*, 25(4): 725–736.

Muscolo A, Mallamaci C, Sidari M *et al*., 2011. Effect of gap size and soil chemical properties on the natural regeneration in black pine (*Pinusnigra*. Arn.) stands. *Tree Forest Science Biotechnology*, 5: 65–71.

Naaf T, Wulf M, 2007. Effects of gap size, light and herbivory on the herb layer vegetation in European beech

forest gaps. *Forest Ecology and Management*, 244(1–3): 141–149.

Parent S, Messier C, 1996. A simple and efficient method to estimate microsite light availability under a forest canopy. *Canadian Journal of Forest Research*, 26(1): 151–154.

Piazena H, Hader D P, 2009. Solar UV-B and UV-A irradiance in arid high-mountain regions: Measurements on the island of Tenerife as compared to previous tropical Andes data. *Journal of Geophysical Research-Biogeosciences*, 114: 1–15.

Ping A, Li X J, Zheng Y R *et al*., 2015. Distribution of plant species and species-soil relationship in the east central Gurbantunggut Desert, China. *Journal of Geographical Sciences,* 25(1): 101–112.

Rahbek C, 1995. The elevational gradient of species richness: A uniform pattern. *Ecography*, 18(2): 200–205.

Raymond P, Munson A D, Ruel J C *et al*., 2006. Spatial patterns of soil microclimate, light, regeneration, and growth within silvicultural gaps of mixed tolerant hardwood – white pine stands. *Canadian Journal of Forest Research*, 36(3): 639–651.

Ricklefs R E, 2004. A comprehensive framework for global patterns in biodiversity. *Ecology Letters*, 7(1): 1–15.

Runkle J R, 1981. Gap regeneration in some old-growth forests of the eastern United-States. *Ecology*, 62(4): 1041–1051.

Santibáñez-Andrade G, Castillo-Argüero S, Vega-Peña E V *et al*., 2015. Structural equation modeling as a tool to develop conservation strategies using environmental indicators: The case of the forests of the Magdalena river basin in Mexico City. *Ecological Indicators*, 54: 124–136.

Sariyildiz T, 2008. Effects of gap-size classes on long-term litter decomposition rates of beech, oak and chestnut species at high elevations in northeast Turkey. *Ecosystems*, 11(6): 841–853.

Scharenbroch B C, Bockheim J G, 2007. Impacts of forest gaps on soil properties and processes in old growth northern hardwood-hemlock forests. *Plant and Soil*, 294(1/2): 219–233.

Scharenbroch B C, Bockheim J G, 2008. Gaps and soil C dynamics in old growth northern hardwood-hemlock forests. *Ecosystems*, 11(3): 426–441.

Tang Z Y, Fang J Y, 2004. A review on the elevational patterns of plant species diversity. *Biodiversity Science*, 12: 20–28. (in Chinese)

Toledo M, Poorter L, Peña-Claros M *et al*., 2011. Climate is a stronger driver of tree and forest growth rates than soil and disturbance. *Journal of Ecology*, 99(1): 254–264.

Vajari K A, Jalilvand H, Pourmajidian M R *et al*., 2012. Effect of canopy gap size and ecological factors on species diversity and beech seedlings in managed beech stands in Hyrcanian forests. *Journal of Forestry Research*, 23(2): 217–222.

Vetaas O R, Grytnes J A, 2002. Distribution of vascular plant species richness and endemic richness along the Himalayan elevation gradient in Nepal. *Global Ecology and Biogeography*, 11(4): 291–301.

Wang G L, Liu F, 2011. The influence of gap creation on the regeneration of Pinus tabuliformis planted forest and its role in the near-natural cultivation strategy for planted forest management. *Forest Ecology and Management*, 262(3): 413–423.

Wang Z, Tang Z Y, Fang J Y, 2007. Altitudinal patterns of seed plant richness in the Gaoligong Mountains, south-east Tibet, China. *Diversity and Distributions*, 13(6): 845–854.

Woch M W, Stefanowicz A M, Stanek M, 2017. Waste heaps left by historical Zn-Pb ore mining are hotspots of species diversity of beech forest understory vegetation. *Science of Total Environment*, 599: 32–41.