

Effects of Topography and Land use on Woody Plant Species Composition and Beta Diversity in an Arid Trans-Himalayan Landscape, Nepal

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Abstract: Distribution patterns of plant species are believed to be impacted by small-scale habitat heterogeneity. However, there have been few comparative studies examining how woody vegetation composition and diversity varies with aspects of different orientations in the Trans-Himalayan region at a local scale. Here, we examined the effects of incoming solar radiation on variation in woody species composition and compared the diversity between the northeast- and southwest-facing slopes in a Trans-Himalayan valley of Nepal. We also examined the implicit interactions between slope orientation and land use in determining the compositional variations between the slopes. We selected two pairs of northeast- and southwest-facing slopes where the first pair has a similar land use and differs in exposure only (Pisang site) while the other pair has clear differences in land use in addition to slope exposure (Braka site). In each site, we sampled 72 plots (36 on each slope) in which the presence and absence of woody species, environmental variables, and disturbance were recorded. Correspondence Analysis (CA) results suggested that the woody species composition significantly varied between northeast- and southwest-facing slopes at both sites, and was significantly correlated with measured environmental variables such as radiation index, altitude, and canopy openness. In the Braka site,

mean alpha diversity was significantly higher on southwest-facing slopes. In contrast, beta diversity and gamma diversity were greater on northeast-facing slopes at both sites. Our results suggest that topographic variables (e.g., radiation index) affect species composition between the slopes, likely due to their influence on small scale abiotic environmental variables. However, the effects of land use, such as livestock browsing/grazing may interact with the effects of slope exposure, effectively reducing differences in species composition within slopes but enhancing the differences in beta diversity between contrasting slopes in the Braka. We conclude that slope orientation and land use are important factors in structuring the woody species composition and diversity in the arid Trans-Himalayan region. We suggest that both environmental and land use variables should be taken into consideration in future studies on plant community structure along the cultural landscapes.

Keywords: Correspondence analysis; Diversity; Environmental gradients; Himalaya; Land use; Topographic aspect; Woody vegetation

Introduction

At a regional scale, climate (e.g., temperature

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and precipitation) is an important determinant of woody species richness (Currie and Paquin 1987; Hawkins et al. 2003). However, at small spatial scales, biotic interactions (Currie 1991; Whittaker et al. 2001), local environmental factors such as light availability (Svenning 2000), moisture, topography (Pausas 1994; Moeslund et al. 2013), and land use patterns may have a strong influence on plant species composition and diversity (Sherman et al. 2007).

In mountainous regions, topographic features such as slope orientation and elevation play a major role in structuring vegetation composition due to variations in incoming solar radiation (Holland and Steyne 1975; Gallardo-Cruz et al. 2009). Scherrer and Körner (2010) have shown that the mountain topography can influence temperature differences over very short horizontal distances. Therefore, the differential distribution of solar radiation between north- and south-facing slopes may produce differences in micro-climate (e.g., temperature) and water balance (moisture) between the slopes, which result in different plant community composition and richness (Vetaas 2000; Gallardo-Cruz et al. 2009; Zhuang et al. 2012; Moeslund et al. 2013). In arid conditions where rainfall does not exceed 400 mm per year, higher species richness on relatively moist north-facing slopes may generally be expected compared to sun-exposed south-facing slopes (Vetaas 1992; Sternberg and Shoshany 2001). However, at higher elevations, energy inputs may be an important limiting factor; therefore, south-facing slopes may support higher species richness due to higher energy input (Hawkins et al. 2003). Thus, how slopes impact plant community structure and diversity at high elevations remains an open question.

In addition to the above noted factors, geomorphological variations within slopes and differences in land use patterns between contrasting slopes can influence community structure and diversity (Burnett et al. 1998). In some mountainous regions (e.g., Trans-Himalayan), the warmer, southwest-facing slopes were historically used for agriculture (Aase and Vetaas 2007; Aase et al. 2010). Because of this, southwest-facing slopes are impacted more by anthropogenic activities (e.g., active agriculture, grazing, and frequent movement of domestic

animals) compared to northeast-facing slopes (Aase et al. 2010). These moderate disturbances may influence plant species diversity positively (Hobbs and Huenneke 1992). When the interactions between land-use patterns and microclimatic conditions become dominant (Byers 2005; Schickhoff 2005), such interactions may sometimes hinder an otherwise potentially clear relationship between vegetation structure and abiotic factors (Shrestha and Vetaas 2009). Therefore, the underlying causes of variation in plant species composition and diversity with slope orientation should be sought not only from environmental factors, but also from differences in land use and land cover (Kreutzmann 2012). We aim to investigate the effects of slope orientation and land use differences on woody species composition and diversity. For the purpose of this study, we included trees, shrubs, saplings, seedlings, and woody climbers that have hard stems as woody plant species. We selected two study sites in the Trans-Himalayan region of north-central Nepal, one with similar and very low impact from human land use between opposing slopes (Pisang), and the other with contrasting land use between opposing slopes (Braka).

We hypothesized that differences in species composition and diversity between contrasting slope orientation would be larger in sites which also differed in historical land use. Specifically, we asked the following questions: (1) Do woody species composition and diversity differ between northeast- and southwest-facing slopes with similar and limited land use? (2) Do woody species composition and diversity differ between northeast- and southwest-facing slopes with strong and different land use patterns? (3) What explains the potential differences, if any, in woody species composition and diversity between the slopes?

1 Materials and Methods

1.1 Study sites

Two study sites, Pisang and Braka, are located in the Trans-Himalayan region between the Annapurna mountain range and the Tibetan Plateau above 3000 m above sea level (a.s.l.). These sites are located nearly 10 km apart along an

east-west oriented U-shaped valley in the upper part of Manang District, north-central Nepal (28°45'N, 84°15'E) (Figure 1). The geomorphological conditions of both sites are comparable (see Weidinger 2006), being influenced by glacial erosion, glacial and interglacial deposits, and frequent landslides. In addition, the differences in topographical structure between northeast- and southwest-facing slopes of the Braka (authors' pers. obs.) are noteworthy: northeast-facing slopes have relatively complex terrains, which are more broken and incised compared to southwest-facing slopes. However, we did not see such contrast in topographical structure between opposing slopes in Pisang.

The study area lies in the rain shadow of the Annapurna mountain range where high mountains act as climatic barriers and block the monsoon clouds. As a result, the area receives less than 400 mm yr⁻¹ precipitation (ICIMOD 1995), occurring mostly during the monsoon season (June-September). Hence, the climate in the area is cold-temperate and relatively dry. Snow is common in

winter and melting of snow and glaciers are important sources of fresh water. Mean maximum/minimum temperatures (recorded at a station approximately 15 km west of the field site) are 20°/10°C in summer and 11°/-3°C in winter (DHM 2008) with an average growing period of about 120 days. The southwest-facing slopes are exposed to the sun throughout the day and are much warmer and drier than north-east facing slopes (Aase and Vetaas 2007).

The vegetation of the area comprises predominantly conifer and birch forests mixed with steppe plant communities. The northern belt of the valley supports a temperate montane forest with large coniferous trees. *Pinus wallichiana* A. B. Jacks. is the predominant species in northeast- and southwest-facing slopes (Mong and Vetaas 2006), except around the tree-line of northeast-facing slopes, where *Abies spectabilis* (D. Don) Mirb. and *Betula utilis* D. Don are also common. Other woody species found in the area include *Juniperus indica* Bertol., *Berberis* spp. L., *Rosa sericea* Lindl., and *Cotoneaster* spp. Medik. Shrubby vegetation is

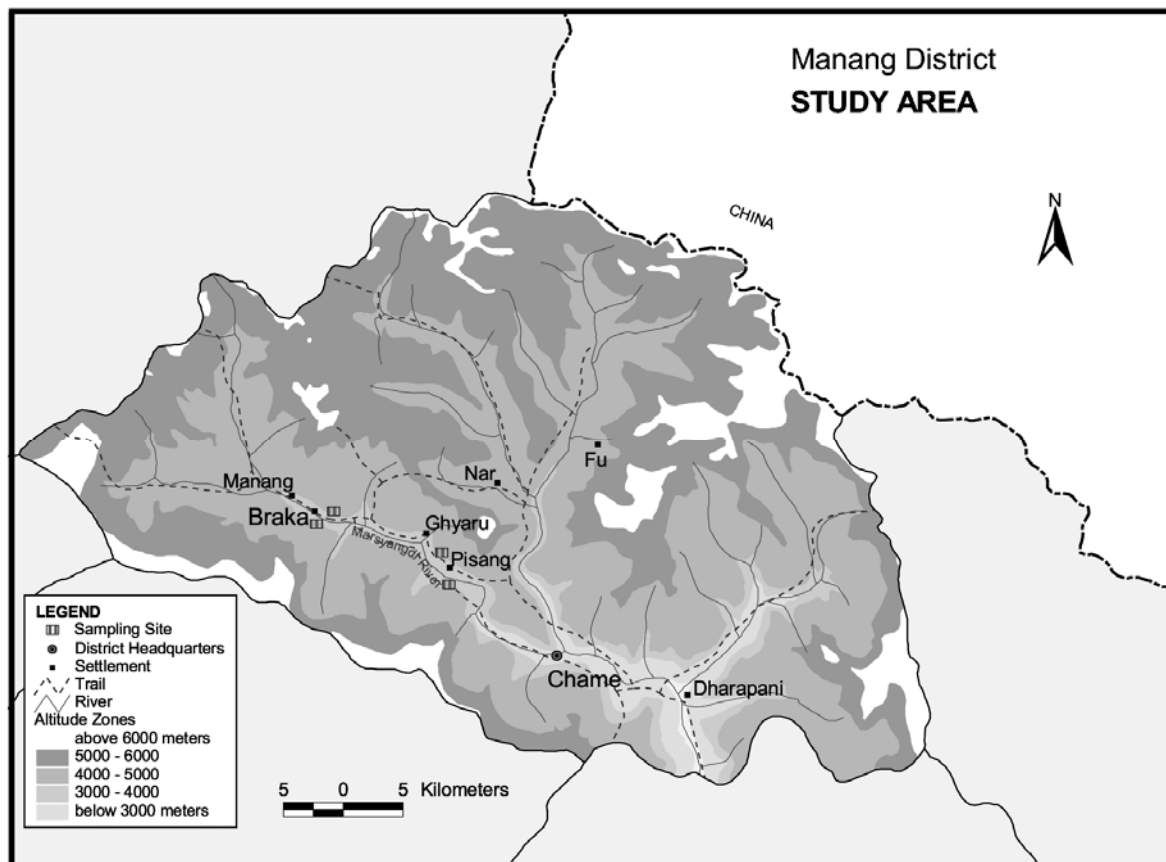


Figure 1 Location map of Manang district and study area.

more common on southwest-facing slopes. In Braka, however, there is a clear difference in tree canopy structure between northeast- and southwest-facing slopes. Southwest-facing slopes are dominated by a single canopy tree, *Pinus wallichiana*, but northeast-facing slopes have three canopy tree species (*Abies spectabilis* and *Betula utilis* at higher elevations, and *Pinus wallichiana* at lower elevations).

1.2 Land use

The current predominant land use within the study area is pastoral agriculture and domestic animal husbandry (Aase et al. 2010). Major anthropogenic impacts on the forests include wood cutting for timber, harvesting of non-timber products, and grazing, although the Annapurna Conservation Area Project initiated conservation in the region by promoting land use practices that aim to reduce anthropogenic pressure on forest ecosystems. In recent years, historical natural disturbance regimes have become disrupted as wildfires, common until the late 1960's, have been suppressed (Authors' *pers. comm.* with manager at the Annapurna Conservation Area Project). According to local people, occasional small scale forest fires are common in these forests, and we also observed fire scars on big fallen trees and surface soil.

The land use histories of the northeast- and southwest-facing slopes differ. Agricultural activity in the valley, including terrace cultivation, began on southwest-facing slopes around 500 years ago, whereas no agriculture existed historically on the northeast-facing slopes (van Spengen 1987; Aase et al. 2010). Although Pisang and Braka are broadly comparable in geomorphology and local climate, they are strikingly different in actual land use patterns between opposing slopes. In Pisang, in modern times, land use patterns between northeast- and southwest-facing slopes have become more similar. Both slopes are equidistant from human settlements, close to agricultural fields, and have similar grazing pressure (Authors' *pers. obs.* and *comm.* with local farmers). In contrast, for Braka, the southwest-facing slopes are located close to cultivated lands, human settlements and often grazed by domestic animals (e.g., goat, sheep, and cattle). Thus, southwest-facing slopes of Braka

may receive greater anthropogenic pressure than northeast-facing slopes, which are less heavily grazed by domestic animals during the late summer and early fall.

1.3 Vegetation sampling

At each study site, one northeast- and one southwest-facing slope were sampled in order to comparatively assess their woody plant composition and diversity. Physical distance between northeast- and southwest-facing slopes in Pisang and Braka is approximately 750 m and 1200 m, respectively. Each slope contained six transects spaced approximately 100 m apart, running parallel to the slope from 3500 to 3700 m a.s.l.. Often, elevation is used as a surrogate for temperature, moisture, and insolation. Decrease in temperature as one moves into higher elevations is steeper in the treeline ecotone, which drives abrupt changes in plant species growth and development (Paulsen et al. 2000). Therefore, we expected that small changes in elevation could result in significant differences in environmental variables such as temperature and moisture. On each transect, six plots (10 m × 10 m) were established at vertical intervals of 40 m a.s.l., and a total of 36 plots in each of the four slopes (n=144 plots altogether). Each plot was divided into four sub-plots (5 m × 5 m) and the presence of all woody plant species within the sub-plot was recorded. All woody species were identified in the field using Polunin and Stainton (1984). Species not identified in the field were taken to the National Herbarium and Tribhuvan University Central Herbarium (TUCH), Kathmandu Nepal and identified to the species level. Species nomenclature follows Press et al. (2000) and The Plant List (2010). An estimate of abundance (0 - 4 scale) was also assigned to each species based on its presence in sub-plots (e.g., a species that was present in all 4 sub-plots had abundance 4 and absent from all had abundance 0) and abundance data were used in the ordination analyses.

For each plot (10 m × 10 m), we recorded altitude using altimeter and slope inclination and slope aspect using clinometer compass. A relative radiation index (RRI), which is a relative measure of the slope exposure to radiation at noon at specific location (Oke 1987; Vetaas 1992), was

calculated for each plot as a function of aspect, latitude, and slope. It has been suggested that RRI values may be biologically more relevant than a simple nominal variable north-east/south-west (Austin et al. 1984). RRI was calculated using the following algorithm: $RRI = \cos(180^\circ - \Omega) \times \sin(\beta) \times \sin(\Phi) + \cos(\beta) \times \cos(\Phi)$, where Ω = aspect (slope azimuth), Φ = latitude, and β = slope inclination. Three climate loggers that recorded temperature every third hour were located at both north-facing slope (between 3450-3900 m a.s.l.) and south-facing slope (3200-4200 m a.s.l.). The loggers were running from April 2003 to October 2005, and the mean annual temperatures were 4.75°C in north-facing slope and 6.0°C in south, i.e. a difference of 1.25°C. We made a visual estimate of percentage tree canopy cover in each plot. We also recorded the degree of disturbance subjectively by recording the number of cut trees (stumps) and signs of fire, including fire scars on trees and charcoal in the surface soil for each plot. General characteristics of the study sites are presented in Table 1.

1.4 Data analyses

Correspondence Analysis (CA) (ter Braak and Šmilauer 2002), a type of indirect gradient analysis, was performed using the categorical estimate (0 - 4 scale) of species abundance in order to visualize the variation in woody species composition between two opposing slopes of each site. Correspondence Analysis extracts the main floristic gradients in the species abundance data based on reciprocal averaging. The extracted gradients are transformed into axes of a multidimensional ordination space; the first and second axes represent the two most important floristic gradients that account for the largest part of variation in species composition. To

test the overall community compositional differences between northeast and southwest-facing slopes, we performed analysis of similarities (ANOSIM, Clarke 1993) tests. ANOSIM is a non-parametric (randomization-based) multivariate analysis used to measure variation in species composition based on a given dissimilarity matrix (herein, Bray-Curtis dissimilarity). ANOSIM provides a test statistic *R* (between 0 and 1) that measures the extent to which between group dissimilarity values are greater than within group values. Ordinations were performed with CANOCO, version 4.5 (ter Braak and Šmilauer 2002) and ANOSIM tests were performed using the program R version 2.8.1 (R Development Core Team 2008).

We described the woody species diversity of northeast- and southwest-facing slopes of both sites using alpha, beta, and gamma diversity (Whittaker 1972); as these indices are ecologically meaningful, easily interpretable, and provide a common basis for describing community diversity (Jost 2007). Alpha diversity (α) is the number of species within a plot. Beta diversity (β), defined as the rate of compositional change between sampling plots, was calculated as $(S/\bar{\alpha})$ (McCune and Grace 2002), where *S* is the total number of species recorded in a study system (overall diversity in each slope, i.e. gamma diversity) and $\bar{\alpha}$ is the mean alpha diversity within each slope.

2 Results

2.1 Woody species composition and environmental relationships

Thirty-six species of woody plants from 23 genera and 17 families and 29 species of woody plants from 20 genera and 14 families were

Table 1 General characteristics of the northeast- and the southwest-facing slopes of Pisang and Braka sites. († = Standard Deviation, ¶ = presence/absence data)

Variables	Pisang				Braka			
	NW-facing		SW-facing		NE-facing		SW-facing	
	Mean	SD†	Mean	SD†	Mean	SD†	Mean	SD†
Slope angle	35.47°	±6.16°	33.77°	±8.27°	25.30°	±6.67°	26.80°	±11.86
Radiation index (RRI)	0.56	±0.14	0.86	±0.06	0.62	±0.09	0.91	± 0.029
Fire¶	+		-		+			
Cut trees (stumps)	0.47	±0.88	1.44	±1.1	1.11	± 1.48	0.83	± 1.48
% Tree canopy cover	48.33	±34.96	48.8	±23.43	46.94	± 22.23	40.55	± 40.77
Dead trees (dead)	1	±1.30	0.52	±0.87	0.05	0	-	-

recorded from Pisang and Braka, respectively (Appendix 1). Nineteen species were common to both northeast- and southwest-facing slopes in Pisang while 12 species were common to both slopes in Braka. Overall, the number of woody species ranged from 7 to 15 per plot in Pisang and 2 to 17 per plot in Braka. In Pisang and Braka, some higher altitude plots had recently been burned on the northeast-facing slopes. Because the results were broadly similar whether these plots were omitted or included, we report results with burned plots included.

CA ordination indicated woody species composition of northeast-facing and southwest-facing plots of both the sites were strongly separated in ordination space with no overlaps (Pisang Figure 2a and Braka Figure 2b). In both sites, plots from northeast-facing slopes were spread in the ordination space (compositionally different) whereas plots from southwest-facing slopes were clustered (compositionally similar) (Figure 2a and Figure 2b). The overall ANOSIM test (based on 999 permutations) revealed significant differences in community composition between northeast- and southwest-facing slopes for Pisang ($R=0.7006, P<0.0001$) and Braka ($R=0.765, P<0.0001$).

The first and second CA-axes (eigenvalue 0.42 and 0.23, respectively) together explained 42.1% of the total compositional variations, and measured environmental variables well explained the

extracted variation in community composition (species-environmental correlation, $r=0.92$ and $r=0.84$, first and second axes, respectively) for Pisang (Table 2). RRI was significantly negatively correlated with the first CA-axis ($r=-0.78$), fire and canopy showed significantly positive ($r=0.54$) and negative ($r=-0.61$) correlation with the second axis. For Braka, the first two CA-axes (eigenvalue 0.40 and 0.23, respectively) explained 40.6% of compositional variations. RRI was significantly negatively correlated with the first CA-axis ($r=-0.80$). Altitude showed a significant positive correlation with the second axis ($r=0.49$) and fire showed a significant positive correlation with the first axis ($r=0.38$) (Table 2).

2.2 Species diversity

In Pisang, mean alpha diversity did not differ between northeast- and southwest-facing slopes. In contrast, southwest-facing slope had much higher mean alpha diversity than northeast-facing slope in Braka (Table 3). Northeast-facing slopes had higher beta diversity in both sites. However, the difference was greater at Braka compared to Pisang (Table 3). Beta diversity in northeast-facing slopes of Braka was almost twice as much relative to southwest-facing slopes. Landscape scale species richness (gamma diversity) was higher for northeast-facing slopes in both Pisang and Braka (Table 3).

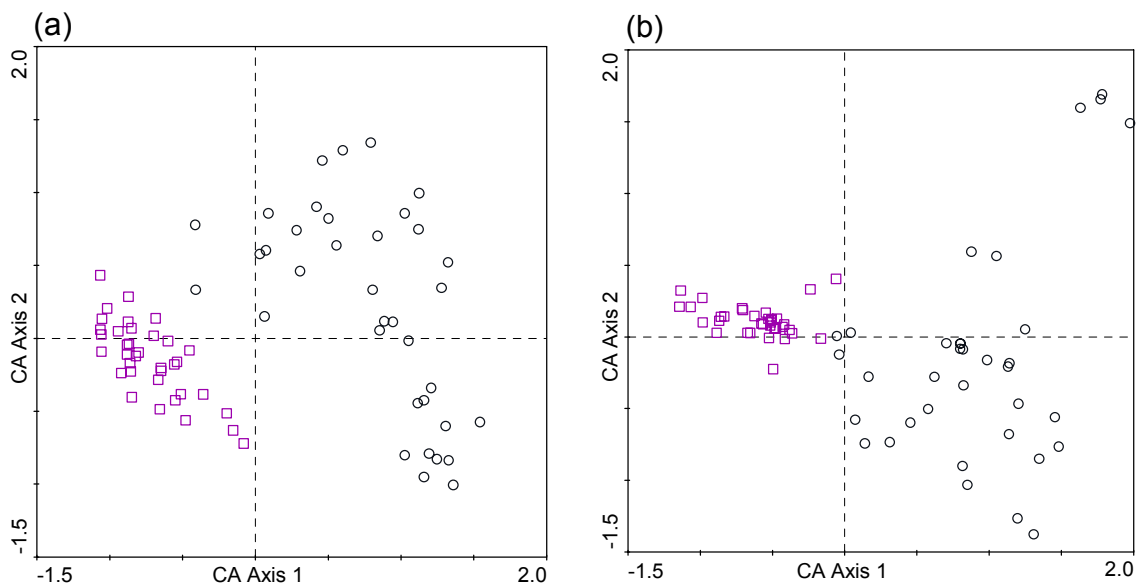


Figure 2 Diagram of Correspondence Analysis for the (a) Pisang and (b) Braka, North-east aspect = ○ (black); South-west aspect = □ (purple)

Table 2 Summary statistics of Correspondence Analysis at the two first ordination axes at the two sites (Pisang and Braka)

	Pisang		Braka	
	Axis 1	Axis 2	Axis 1	Axis 2
Eigenvalues	0.42	0.23	0.40	0.231
Cumulative % sp. var.†	27.3	14.8	25.8	14.8
Sp-env. cor.††	0.924	0.841	0.89	0.64
Inter-set correlations				
Altitude	0.04	-0.15	0.03	0.49**
RRI	-0.78**	0.11	-0.80**	0.28*
Stumps	-0.36*	-0.28*	0.09	0.17
Canopy	0.25*	-0.61**	0.23	0.24
Fire	0.12	0.54**	0.38*	0.18

Notes: Significant intersite correlation coefficients (*R*) between environmental variables and Correspondence Analysis axes (Axis 1 and Axis 2) for Pisang and Braka areas are shown (**P* < 0.05, ***P* < 0.01, NS = not significant). Abbreviations: † % sp. var. = Percentage variance explained; ††Sp-env. cor. = Species environment correlations

Table 3 Species diversity measures for woody species composition of northeast- and southwest-facing slopes from Pisang and Braka sites.

Site	Slope	Diversity		
		Gamma	Mean alpha	Beta
Pisang	NE-facing	30	10.84	2.76
	SW-facing	22	10.94	2.01
Braka	NE-facing	26	7.25	3.58
	SW-facing	18	9.25	1.94

3 Discussion

3.1 Species composition and environmental influence

The overall ordination results indicated that multiple environmental factors explained the majority of woody species composition for both sites as suggested for other mountain ranges (Zhuang et al. 2012; Zhang et al. 2013). However, relative radiation index was by far the most important environmental variable, accounting for the most compositional variation as described by CA axes. This is consistent with Ferrer-Castan and Vetaas (2003) findings for some of the mountain ranges in south-eastern Spain. Their results suggested that local-scale variations in woody species composition between north-facing and south-facing slopes were primarily governed by

radiation index.

Often, slope exposure and incoming radiation is considered a surrogate for moisture availability (Stohlgren and Bachand 1997). In the northern hemisphere, southwest-facing slopes receive a greater intensity and duration of solar radiation compared to northeast-facing slopes, and are therefore likely to be drier. Differences in duration and intensity of incoming solar radiation likely support different forest structures between north-east and south-west-facing slopes (Aase and Vetaas 2007). A recent study in the Trans-Himalayan region recorded higher soil moisture on north-facing slopes and the same factor explained the greater variations in plant species composition between the slopes (Panthi et al. 2007). The amount of incident solar radiation may also influence the soil and air temperature near the surface of the ground (Shreve 1924). Soil temperatures have important effects on plants' growth and initial establishment (such as seed germination and root growth) (Shreve 1924). In general, south-facing slopes are snow-free earlier in the year than north-facing slopes (Keller et al. 2005), and increases in soil temperature following snowmelt likely triggers seedling recruitment. However, growth of seedlings on north-facing slopes may be limited by soil temperature in the presence of longer snow period (Danby and Hik 2007). In this study, in contrast to northeast-facing slopes, southwest-facing slopes supported well developed light-demanding shrubby vegetation (authors' *per. obs*) and we can anticipate that these differences likely produced compositional variations between slopes that we observed here. However, northeast-facing slopes which are exposed to radiation for shorter periods of time may have a positive water balance and likely support well-developed moisture loving canopy trees (Harrison et al. 2011). Relative to other areas within the Trans-Himalayan region, our study site is drier (average annual rainfall less than 400 mm) due to rain shadow effects of the Annapurna massif (ICIMOD 1995). We assume that the rain shadow may have a significant effect on the moisture gradient at much smaller scale and hence between the slopes. Because of this mesic northeast-facing slopes may be conducive for tree growth and support well developed three different canopy trees including moisture thriving *Abies spectabilis* and

Betula utilis. Although southwest-facing slopes in the Pisang harbour some individual trees of *Abies spectabilis* and *Betula utilis*, at elevations beyond 3000 m a.s.l. forests of *Pinus wallichiana*, *Abies spectabilis*, and *Betula utilis* are common on the north-facing slopes (Aase and Vetaas 2007). We therefore assumed that the differences in incoming solar radiation that influence temperature and moisture between the slopes likely produced the woody species compositional variations between opposing slopes (Moeslund et al. 2013).

The larger compositional differences within the northeast-facing slopes compared to southwest-facing slopes of Braka (Figure 2b) suggest that compositional differences may not simply be produced by environmental differences between the slopes, but some other underlying factor (e.g., anthropogenic activities) may also influence compositional dissimilarities between the slopes. Shrestha and Vetaas (2009) suggested that grazing and browsing by domestic animals could potentially override some of the environmental effects in vegetation composition in the cultural landscapes of Trans-Himalaya. This was also demonstrated by Roche et al. (1998) in Europe and Bellemare et al. (2002) in eastern North America. Very recently, it is demonstrated that the climate variables become less important compared to fire, livestock grazing, and logging in explaining variations in woody species composition across the elevation gradient at eastern Cascades, Washington, USA (Haugo et al. 2010). Although we did not explicitly quantify the grazing differences between northeast- and southwest-facing slopes, it should be noted that the southwest-facing slopes at Braka site experienced higher grazing pressure because the slopes are closer to the settlements, have easily accessible topography, close to the agriculture fields, and are driveways to higher elevation pastures (Authors' pers. comm. with local farmers). We assume that anthropogenic movements associated with animal herding may increase propagule dispersal and increase the homogeneity and decrease compositional differences within southwest-facing slope of Braka site.

3.2 Species diversity

Species diversity results suggest that southwest-facing slopes had higher mean alpha

diversity compared to northeast-facing slopes, but the difference was much higher at Braka. In contrast, beta and gamma diversity were relatively higher for northeast-facing slopes. This is consistent with a classic positive relation between beta diversity and gamma diversity across broad geographical scale (Kraft et al. 2011). However, the difference in beta diversity between the slopes was greater at Braka compared to Pisang. If this was caused by difference in land use only, the difference should be close to zero in Pisang, but this is not the case. Greater difference in mean alpha and beta diversity between slopes of Braka may have several probable explanations: a) topographical differences between the slopes, b) presence of different canopy trees, and c) the different history of land use between the slopes. Because north-facing slopes of Braka are located at relatively complex, broken, and incised terrains compared to southwest-facing slopes, topographical variations likely generate diverse plant assemblages on northeast-facing slopes. It was suggested that complex topographic relief may produce variation in incoming solar radiation (Fu and Rich 2002), and we hypothesize that differences in solar radiation may generate small scale environmental heterogeneity in the landscape, ultimately resulting in species segregation (Segura et al. 2002) and thereby increasing beta diversity (Poulos et al. 2007). Furthermore, Poulos and Camp (2010) suggested that mountains with more uneven and broken topography may provide diverse habitats potentially colonized by different plant species and, thus, increase species diversity within the site.

In addition, in Braka, southwest-facing slopes are dominated by single canopy trees, *Pinus wallichiana* while northeast-facing slopes are dominated by three different types of canopy trees (*Abies spectabilis* and *Betula utilis* at higher elevations, and *Pinus wallichiana* at lower elevations). We expected that different canopy trees likely produce different degrees of shade and greater litter load or cover on the forest floor. These variations may generate highly localized, yet significant, differences on availability of resources (nutrients and light), which eventually drive inter-specific competition (Aerts 1999) that may produce many small local populations contributing in higher beta diversity (Jankowski et al. 2009). An

important but rare finding came from a study by Harrison et al. (2006) who found that beta diversity between the slopes in the Californian serpentine flora was positively related to the differences in percentage ground cover by leaf litter. Sporadic fire (prevalent in some plots at higher elevation on north-east facing slope of Braka) may have created habitat heterogeneity and thus, increased beta diversity (Cowling et al. 1996).

Land use such as grazing greatly influences the vegetation structure and plant species diversity (Hofgaard 1997). Higher differences in alpha and beta diversity between the slopes of Braka may be related to different land use history, including extensive use of southwest-facing slopes for grazing and browsing. We suggest that greater degree of browsing on the southwest-facing slopes (Authors' per. comm. with local farmers) likely results in similar composition and decreases beta diversity (Hobbs and Huenneke 1992). Here, we suggest that browsing may open up the areas that were previously under shade, providing opportunities for regeneration of shade intolerant species (cf. Bhattarai et al. 2004). Furthermore, browsing pressure may become a selective force towards dominance of some browsing tolerant species subsequently reducing beta diversity (Mouquet and Loreau 2003). Thus, under these circumstances, effects of environmental variables could be overridden by anthropogenic activities. This is consistent with the findings of Vellend and colleagues (Vellend et al. 2007). They highlighted that biotic homogenization, which reduces beta diversity, is influenced by human land use patterns and overshadows the relation between species diversity and environmental gradients. Thus, to reconsider the classic slope aspect effects on vegetation composition and diversity, one should incorporate historical land use changes (Gallardo-Cruz et al. 2009; Kreutzmann 2012).

4 Conclusions

In conclusion, our results suggest that topography and contemporary and historical differences in land uses associated with slope orientation drive overall woody species composition and diversity between opposite slopes

in arid Trans-Himalayan landscape. Since land use systems that have been practiced in high mountainous regions for centuries seem to influence species community structure, species richness, and diversity in the landscape (Sherman et al. 2007), land use patterns are becoming a significant factor in changing species distribution and diversity. Thus, incorporating previous land use patterns is essential to better understand woody species distribution in topographically distinct cultural landscapes (Kreutzmann 2012), and may be applied to other functional groups of plants (e.g. herbs, forbs, and grasses). Future studies that integrate multiple spatial scales and other functional groups of plants, including their structure in relation to abiotic factors, land use, site history will lead to a more profound and comprehensive understanding of the structure and diversity of plant species between northeast- and southwest-facing slopes.

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