



# Facilitation by a dwarf shrub enhances plant diversity of human-valued species at high elevations in the Himalayas of Nepal

Rabindra Parajuli<sup>a,b,\*</sup>, Michael J. O'Brien<sup>c</sup>, Bishnu Timilsina<sup>a</sup>,  
Francisco I. Pugnaire<sup>d</sup>, Christian Schöb<sup>e</sup>, Suresh K. Ghimire<sup>a</sup>

<sup>a</sup>Central Department of Botany, Tribhuvan University, Kirtipur, Kathmandu, Nepal

<sup>b</sup>Department of Geosciences, Florida Atlantic University, 777 Glades Rd, Boca Raton, FL 33431, USA

<sup>c</sup>Área de Biodiversidad y Conservación, Universidad Rey Juan Carlos, c/Tulipán s/n., E-28933 Móstoles, Spain

<sup>d</sup>Spain Estación Experimental de Zonas Áridas, Consejo Superior de Investigaciones Científicas (EEZA-CSIC), Carretera de Sacramento s/n, 04120 La Cañada de San Urbano, Almería, Spain

<sup>e</sup>Institute of Agricultural Sciences, ETH Zurich, Universitätsstrasse 2, 8092 Zurich, Switzerland

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## Abstract

Facilitation is a global phenomenon that occurs when one species promotes the growth, survival, or reproduction of another species, mostly in stressful environments. However, the importance of facilitation by shrubs in maintaining plant community diversity is not well evaluated in the Himalayas, especially for the richness and conservation of medicinal and human-valued species. Therefore, we aimed to explore the facilitative role of a dwarf shrub species, *Berberis angulosa*, in maintaining plant composition and richness of human-valued species in the Langtang valley of Nepal's Himalayas. We censused plant species in open patches and beneath *Berberis* during monsoon and post-monsoon (dry) seasons at three elevations.

Total species richness and richness of human-valued species were significantly higher inside the *Berberis* canopy than in gaps; the former being 39% and the latter 46% greater under shrubs than in open sites. Facilitation by *Berberis* shrubs promoted plant community diversity irrespective of season and elevation; however, higher differences in mean species richness for both total plant species and human-valued species during the dry season and at high elevation indicated increased facilitation intensity under more stressful conditions. The facilitative effect of *Berberis* shrubs increased, combining both seasons, overall plant diversity by 19% (total=105), and human-valued species by 16% (total=56). Our results show the importance of facilitation by nurse shrubs in structuring plant communities and protecting medicinal and socio-ecologically important plants, thus enriching ecosystem services in the Himalayas. These results suggest nurse plant species should be incorporated into conservation policies and management strategies for effective biodiversity conservation and sustainability, especially in the face of climate change.

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**Keywords:** Alpine grasslands; Biodiversity conservation; Ecosystem services; Medicinal herbs; Positive interaction; Species richness; Stressful environments

\*Corresponding author at: Department of Geosciences, Florida Atlantic University, 777 Glades Rd, Boca Raton, FL 33431, USA.  
E-mail address: [rparajuli2019@fau.edu](mailto:rparajuli2019@fau.edu) (R. Parajuli).

## Introduction

Plant interactions play a crucial role in structuring plant communities and maintaining species diversity (Armas & Pugnaire, 2005). Pure positive or negative interactions are uncommon in plant communities, as interactions are rather complex and dynamic relationships largely determined by resource availability and abiotic conditions (Callaway, 2007; O'Brien et al., 2017; Pugnaire & Luque, 2001; Pugnaire et al., 2015). Competition usually prevails in benign conditions, whereas facilitation is more evident in stressful and low-productivity environments (Bertness & Callaway, 1994). Although competition was historically considered to be the main element structuring plant communities (e.g., Connell, 1983; Grime, 1973), facilitation is now fully integrated into plant community theory (Brooker et al., 2008; Bruno et al., 2003; Callaway, 2007), and its importance for community structure and diversity are widely recognized (Butterfield et al., 2013; Kikvidze et al., 2015; Schöb, Armas & Pugnaire, 2013).

Facilitation occurs when one species alters its surrounding micro-environment to decrease the intensity of physical and/or biotic disturbance or stress, thus making suitable micro-habitat for other, less stress-tolerant species (Callaway, 2007; Hacker & Gaines, 1997); such benefactor species are commonly termed nurses (Flores & Jurado, 2003). Most commonly, nurse species ameliorate environmental conditions within or under their canopies by improving soil nutrients and moisture content, buffering soil temperatures, protecting from herbivores, drought, intense wind, and solar radiation (Brooker et al., 2008; Callaway, 2007). Facilitation largely depends on environmental conditions, and may vary across spatial and temporal scales (reviewed in Callaway, 2007). Studies from different environments suggest that facilitation is more evident at higher elevations (for e.g., Arroyo et al., 2003; Callaway et al., 2002; but see, Dvorsky et al., 2013), and during dry seasons (Kikvidze et al., 2006; Veblen, 2008).

Generally, cushions and small (dwarf and low stature) shrubs are documented as facilitators in high-elevation environments such as the Himalayas (e.g., Ale et al., 2018; Cavieres et al., 2014; Chen et al., 2015; Iyengar et al., 2017; Pugnaire et al., 2015). Cushion plants' role in structuring plant communities is well explored at the local, regional and global scales (e.g., Cavieres & Badano, 2009; Cavieres et al., 2014; Chen et al., 2015; Kikvidze et al., 2015), however, their role for plant community richness and diversity, especially in high-elevation environments, has recently gained attention (e.g., Ballantyne & Pickering, 2015; Iyengar et al., 2017; Liancourt, Bagousse-Pinguet, Rixen, & Dolezal, 2017; Pistón et al., 2016). Interestingly, findings are inconsistent regarding the facilitative role of shrubs and its implication to plant community diversity in alpine mountains. For example, Ballantyne and Pickering (2015) reported enhanced plant diversity at the community level in the Australian Alps; Pistón et al. (2016) recorded overall

positive effects on community richness and phylogenetic diversity in the Sierra Nevada Mountains of Spain whereas Iyengar et al. (2017) did not find evidence of shrubs increasing plant diversity at the landscape level, even though they reported improved richness at plot level in the semi-arid, high-elevation rangelands of Trans-Himalayas in India.

High-elevation environments, especially the Himalayas, are well known for their severe life conditions. In those areas, plants face low temperatures, excessive radiation, short growing seasons, drought, and unstable substrates (Körner, 2003). Biotic disturbance due to widespread overgrazing and trampling is also one of the limiting factors for plant growth and survival in the Himalayas (Aryal et al., 2015; Körner, 2003). Dwarf shrubs represent one of the life forms which are best adapted to those extreme environments (Billings & Mooney, 1968; Körner, 2003), and favor the development of distinctive micro-environments beneath them due to their low stature, and thick and compact canopy structure (Körner, 2003; Schöb, Armas, Guler, Prieto & Pugnaire, 2013). Furthermore, thorny and strong sclerophyllous shrubs play a pivotal role in reducing the impact of grazing on plant communities by protecting less-tolerant species (Bakker et al., 2004; Howard et al., 2012; Tirado et al., 2015).

The Himalayas, also called the 'third pole' for their physical and environmental extremes, are among the least explored regions of the world. They are important areas for ecological, environmental, and biogeographical studies due to their steep elevation gradients, their high sensitivity to natural and anthropogenic drivers of change, and their diverse landscape with unique habitats and biodiversity (Chaudhary, 1998; Xu et al., 2009). The Langtang valley, lying in the Eastern Himalayas, is a part of the Indo-Burma biodiversity hotspot – one of the eight 'hottest biodiversity hotspots' in the globe (Myers et al., 2000). The Eastern Himalayas supports one of the world's richest alpine flora having nearly one third of endemism (Dhar, 2002), and is among the regions having the most severe impacts of climate change on biodiversity (Shrestha et al., 2012). Additionally, the livelihood of people in these regions largely depends on plants for transhumance, traditional medicine, food and are linked to socio-cultural rituals and values (Aryal et al., 2014; Chaudhary, 1998; Ghimire et al., 2006; Ghimire et al., 2008). Due to environmental stress, exacerbated by anthropogenic activities, plant biodiversity in the Himalayas is experiencing cascading impacts of climate change (Xu et al., 2009). Therefore, understanding interaction patterns is crucial to precisely predict and quantify the consequences of climatic changes on plant communities (Tylianakis et al., 2008), and consequently for biodiversity conservation and people's livelihood in the Himalayas.

While facilitation is a well-studied area of community ecology, knowledge about the facilitative interactions in the Himalayas are still very limited regardless of their high ecological and conservation significance. Moreover, despite being the dominant life forms in the Himalayan high-

elevation regions (Körner, 2003; Polunin & Stainton, 1984), the facilitative effects of shrubs on community richness and diversity are poorly understood (but see Iyengar et al., 2017; Liancourt et al., 2017). Corollary to this, research evaluating the role of shrubs, and nurse species in general, for the richness of medicinal and useful plant species, and protection of important alpine flora having high conservation value is largely lacking.

Here, we investigated the nurse effect of a dwarf shrub, *Berberis angulosa* (*Berberis*), on plant community diversity and human services in the Langtang valley, one of the high-elevation alpine landscapes in Nepal's Himalaya. We compared species richness, floristic composition, and richness of human-valued species in plots beneath *Berberis* shrubs and in adjacent open areas, and explored spatial associations and preferences of species to these habitats during both monsoon and post monsoon (dry) seasons. We predicted that facilitation by *Berberis* shrubs promotes plant diversity and richness of human-valued species irrespective of the growing season.

## Materials and methods

### Study area

The field work was conducted in the Langtang valley in Langtang National Park, Central Nepal (28° 12.57'–28° 12.828' N; 85° 31.732'–85° 34.146' E; Fig. 1) from 3595 m to 3860 m above sea level (asl). Langtang valley is one of the inner Himalayan valleys of Nepal fed by big glaciers (Stainton, 1972) and characterized by rugged topography. Vegetation on the valley floor is shrubby-steppe type (scrub) above the tree line with a mosaic that includes grasslands, shrublands, and a few stands of trees (Miehe et al., 2015; Stainton, 1972). Patches of the dominant dwarf shrub species, *Rhododendron lepidotum*, *Juniperus recurva* and *Berberis angulosa*, create shrub-grassland mosaics in the upper region (3600–4000 m asl) of the valley (Aryal, 2009; Bhatta et al., 2018; Miehe et al., 2015).

The study area is a high-elevation pasture in the eastern Himalaya, with cold climate and mean annual precipitation of ~650 mm (Bhatta et al., 2018). Average climatic variables, recorded at Kyanjing station (3920 m asl, <0.5 km from the nearest sampling transect; Government of Nepal, Department of Hydrology and Meteorology, 1989–2009), are higher in July (relative humidity = 99%, temperature = 10.3°C and total precipitation = 156 mm) in the valley and lower in October (relative humidity = 73%, temperature = 5.5°C and total precipitation = 43 mm). We conducted this research in three different altitudinal belts (~3600, ~3725 and ~3850 m asl) laying three different longitudinal transects (Appendix A: Fig. S3). The altitudinal belts were selected by considering the upper and lower altitudinal limits of the distribution of *Berberis* shrubs in the valley.

### Focal nurse species

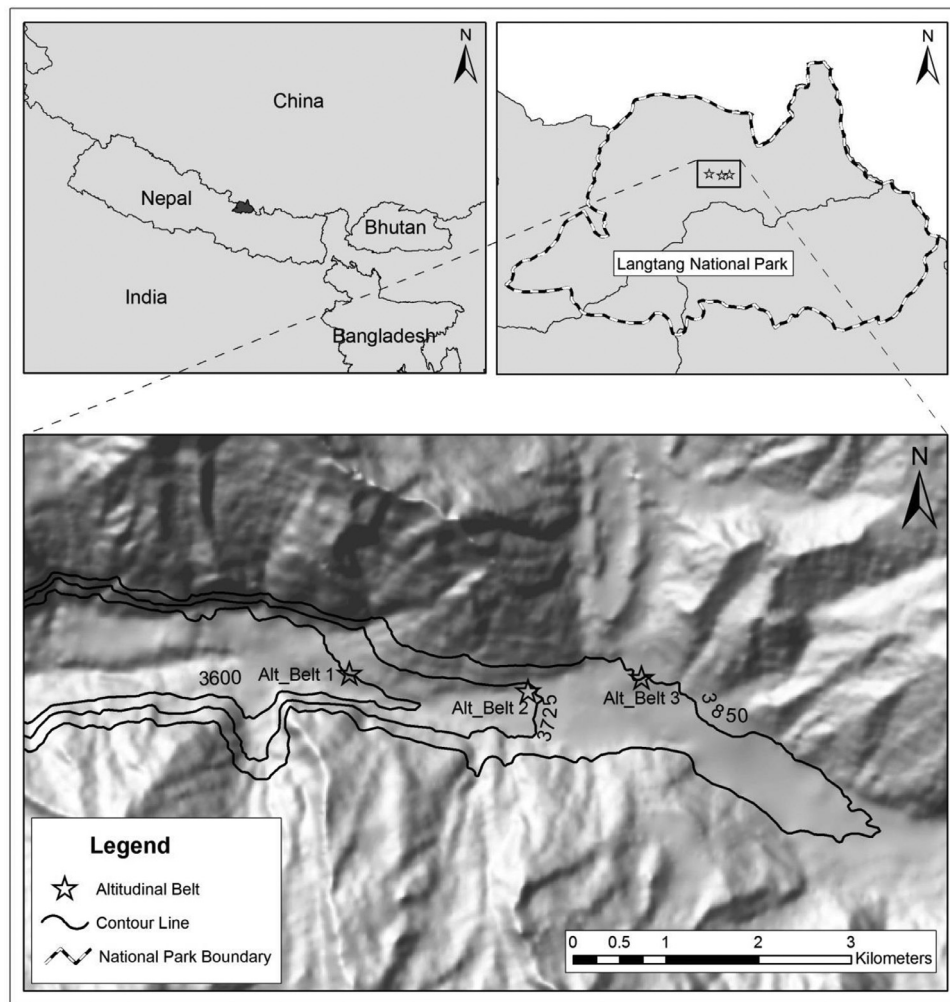
The focal nurse species, *Berberis angulosa* (hereinafter *Berberis*) is a deciduous, profusely branched, erect dwarf shrub endemic to the Himalayas (Nepal, Bhutan, Sikkim and Tibetan Plateau) (Adhikari et al., 2012). Occurring between 3000 and 4500 m asl, it is one of the dominant dwarf shrubs in the high elevation pastures in Nepal (Adhikari et al., 2012; Miehe et al., 2015). It is a spiny shrub with 1–3 cm long spines and small, slightly coriaceous, obovate to lanceolate and mucronate leaves, 0.5–1.5 × 1.5–4.5 cm in size, with 1–3 spinulose teeth on each side (Adhikari et al., 2012; Fig. S2) thus making it difficult for livestock browsing and hence protecting communities beneath their canopies. Though it reaches up to two meters in height, in our study site they were, on average, 0.61 ± 0.2 m tall (Table 1) with an estimated 15% cover. *Berberis* was selected because it is a dominant, patch-forming species with appropriate size for sampling (average patch size = 12.47 ± 1.01 m<sup>2</sup>), randomly distributed within an open mosaic (Appendix A: Fig. S1).

### Sampling design

Sampling was carried out in 2009 during the July monsoon and the post-monsoon dry period in October in order to record seasonal differences in plant community under and outside shrubs and to assess temporal changes in interaction intensity. Sampled patches were marked, and GPS coordinates were also recorded to ensure that the same patches were sampled both seasons. Seven shrub patches (pure stands of *Berberis*) were randomly selected in each altitudinal belt. Three one square meter (1 × 1 m) plots were sampled in a patch and paired with an adjacent plot in nearby open conditions (Appendix A: Fig. S3). Quadrats were placed completely inside the shrub patch with a minimum distance of 0.5 m from the edge and at least 0.5 m apart. Paired open plots were in an adjacent open area at least 1 m apart from the patch edge to avoid interferences between habitat types. Each plot was further divided into four sub-plots equal in size (i.e., 0.25 m<sup>2</sup>) to ease the recordings of grazing intensity. There were a total of 21 plot pairs across 7 shrub patches per altitude (7 patches × 2 conditions × 3 plots × 3 altitudes = 126 samples per season).

### Plant identification and nomenclature

Plant species were identified using field manuals (Polunin & Stainton, 1984; Stainton, 1988), and taxonomic literature and voucher specimens were deposited at Tribhuvan University Central Herbarium, Nepal. Nomenclature followed Press et al., (2000).



**Fig. 1.** Study area. Map showing the altitudinal belts (sampling sites) in the study area in Langtang valley, Langtang National Park (LNP), Nepal.

### Field data collection and soil analysis

All vascular plant species in each plot, including gymnosperms and pteridophytes, were identified and recorded as binary (presence/absence) data for each taxon. Using a list of all species recorded, we assessed the importance of each species for local people in relation to its medicinal, social, commercial, food and food additives, materials or poisons (see Appendix A: Table S7 for details of each category) based on interviews/discussions with local people and

traditional practitioners ( $n=20$ ), and through consulting secondary sources (Baral & Kurmi, 2006; Ghimire et al., 2008). The assessment was meant to make a list of species which humans valued for uses and services, such as ethno-medicine, food, materials, trade, etc. (see Appendix A: Table S6 for different use categories and their detail explanation). These ethno-botanically useful species are termed as human-valued species throughout the text, and for each plot we compiled a list of total plant species and human-valued species.

**Table 1.** Comparisons of mean  $\pm$  SE, and test of mean difference using t-test, of environmental variables among habitats and seasons [ $n=63$  for all variables per season, except soil organic carbon (SOC;  $n=21$  – measured in dry season only)].

Variables	Monsoon			Dry		
	Shrub	Open	<i>P</i>	Shrub	Open	<i>P</i>
Soil pH	6.56 $\pm$ 0.02	6.46 $\pm$ 0.03	0.002	6.70 $\pm$ 0.01	6.68 $\pm$ 0.03	0.554
SOC (%)	NA	NA	NA	10.95 $\pm$ 0.37	7.89 $\pm$ 0.33	<0.001
Litter thickness (cm)	0.93 $\pm$ 0.07	0	<0.001	0.93 $\pm$ 0.07	0	<0.001
Shrub height (m)	0.61 $\pm$ 0.02	0	NA	0.61 $\pm$ 0.02	0	NA



Different environmental and biotic variables such as altitude, soil pH, litter thickness (cm), and shrub height (m) were recorded in each sampling plot. Soil pH was recorded *in-situ* using a pH meter electrode (Soil PH & Moisture Tester Hygrometer, Takemura Electric Works Ltd., Tokyo, Japan). Soil samples were also collected in each plot for organic carbon content (OC). Soil samples were collected from the top 5 cm of soil from all three plots in each patch and mixed. They were air dried in the field, packed in airtight zipper bags for analyses. Soil OC was analyzed following Walkley and Black's rapid titration method (Walkley & Black, 1934). However, analysis was done for only one season since no marked difference in soil OC was expected in three months' time.

Grazing was identified indirectly by the presence of livestock droppings and trampling (hoof marks) using an ordinal scale of 0–4 whereby zero meant absence of grazing and four meant the presence of grazing in all four sub-plots of a plot (Aryal et al., 2015). Measurement of grazing intensity in an ordinal scale in small (1 m<sup>2</sup>) quadrats using the signs of animal droppings and trampling extent is common in ecological studies in high-elevation pastures in the Himalayas (e.g., Aryal et al., 2015; Ghimire et al., 2006; Zhang & Dong, 2009). Similarly, shrub cover was estimated by measuring the *Berberis* patch area within 100 m<sup>2</sup> plots (n=15). We determined patch area by measuring the largest diameter of the patch and its perpendicular and using the equation for an area of ellipse.

## Statistical analysis

We tested differences in habitat conditions (e.g., soil pH, soil OC, and litter thickness) between shrub and open plots using paired t-test. We quantified the outcome of interactions between *Berberis* shrubs and other plant species using the Relative Interaction Index (RII; Armas et al., 2004). RII ranges from -1 (competition) to 1 (facilitation) and was computed as:  $RII = (S_s - S_o) / (S_s + S_o)$ ; where  $S_s$  is number of species in a shrub plot and  $S_o$  is that of an open plot. RII for overall (total) species ( $RII_{sp}$ ) and human-valued species ( $RII_{hv}$ ) were calculated for each plot pairs for both seasons, as well as differences between seasons. Additionally, we compared  $RII_{sp}$  and  $RII_{hv}$  along the elevation gradient and between seasons using a linear mixed effects model with altitude (a factor with 3 levels: low, mid and high) and season (a factor with 2 levels: monsoon and dry) as fixed factors and plot (with 63 levels) as random factor. Similarly,  $RII_{sp}$  and  $RII_{hv}$  were also compared at different levels of grazing pressure (5 levels: 0–4) for both seasons.

We tested total species richness and richness of human-valued species as a function of altitude, habitat (a factor with 2 levels: open and shrub), season and all two-way interactions with a linear mixed effects model. The data were normally distributed, so we used a Gaussian distribution instead of a Poisson. We used random terms for shrub patch (a

random intercept with 21 levels), plot pair (a random intercept with 63 levels), and patch nested in season (a random intercept with 42 levels). To account for heteroscedasticity between shrubs and open conditions, we fit a separate variance structure for each habitat (see model terms and Wald statistics in Appendix A: Table S1).

We used non-metric multidimensional scaling (NMDS) ordination on a Bray-Curtis dissimilarity matrix to compare species composition between habitats. We included both habitat and elevation in a test of environmental fit on the ordination. We then tested for the fit of the environmental variables such as soil pH, litter depth, and grazing intensity to the NMDS of species composition, and statistical significance was determined using permutation tests (see Appendix A: Table S2).

Data analysis was performed in the statistical software R (version 3.6.3; <http://r-project.org>), and the *vegdist* function in the *vegan* package was used for the calculation of the Bray-Curtis dissimilarity matrix. The NMDS was done using *metaMDS*, whereas the *asreml-R* package (ASReml 4, VSN International, UK) was used for linear mixed effects models.

To assess the positive association or preference of individual species for a specific habitat (shrub or open), we compared differences in frequency of occurrence within or outside *Berberis* using presence/absence data of each species. The indicator species analysis was used, and the statistical significance was tested based on 1000 random iterations using a Monte Carlo procedure (Dufrene & Legendre, 1997) performed with the software *PC-ORD* 7 (<https://www.wildblueberrymedia.net/pcord>). The indicator species analysis permits statistical rigor in assessments of indicator species, that helps to identify the most characteristic species associated with or indicative of a particular habitat type or a group of samples (Bakker, 2008; Dufrene & Legendre, 1997) and use of presence/absence data is generally common (Bakker, 2008; Paudel et al., 2020). Infrequent species (i.e., recorded in less than 10% of plots) were omitted to avoid the bias estimation of habitat preference. Based on the relative frequency of occurrences and statistical significance ( $p$ -value < 0.05), species were categorized into four main categories: a) shrub specialists (SS: species unique to *Berberis* shrubs with occurrence being statistically significant); b) shrub-preferring species (SP: species having significantly higher frequency of occurrence inside *Berberis* shrubs); c) open specialists (OS: species unique to open areas with occurrence being statistically significant); and d) open-preferring species (OP: species having significantly higher frequency of occurrence in open areas).

## Results

### Habitat conditions

Generally, the habitat beneath *Berberis* shrubs had significantly higher values for soil pH, soil organic carbon, and

litter thickness than open areas. The litter accumulation was significantly higher inside the shrubs for both seasons, whereas soil pH was significantly different only during the monsoon season (Table 1). Soil organic carbon (%) was also significantly higher in shrub plots (mean  $\pm$  SE: shrub =  $10.95 \pm 0.37$ ; open =  $7.89 \pm 0.33$ ;  $p < 0.001$ ). However, grazing intensity, as shown by the percentage of plots with different level of grazing (Fig. 2), was found higher in open plots than in *Berberis* patches during both seasons. In about 80% of shrub plots, in both seasons, no traces of grazing activity were observed, whereas in open areas more than 90% of plots had strong evidence of grazing (Fig. 2). Similarly, relatively lower grazing activities were recorded at low elevation than in mid and high elevation belts during both seasons (Appendix A: Fig S4).

### Species richness and richness of human-valued species

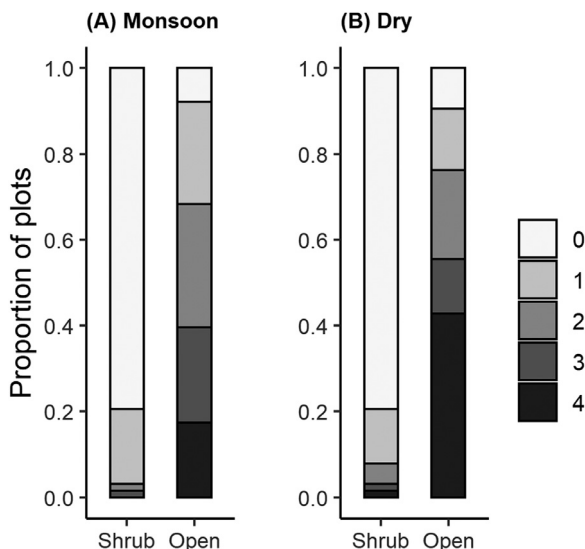
The number of species growing within *Berberis* shrubs was always higher than in adjacent open areas during both monsoon and dry seasons. Shrubs had significantly higher overall species richness (monsoon mean richness = 16.8, 95% CI = 16.1–17.5 and dry mean richness = 14.9, 95% CI = 14.2–15.6) than plots in open areas (monsoon mean richness = 12.7, 95% CI = 12.1–13.4 and dry mean richness = 10.1, 95% CI = 9.5–10.7) regardless of the season (Fig. 3; Appendix A: Table S1). Additionally, richness decreased with increasing altitude, but the decrease was

greater in open sites (difference between low and high = 3.4 species, 95% CI: 2.5–4.3) than under shrubs (difference between low and high = 2.8 species, 95% CI: 1.8–3.8). Overall, species richness was 39% greater under shrubs than in open sites.

The richness of human-valued species was also significantly higher inside *Berberis* (monsoon mean richness = 11.3, 95% CI = 10.8–11.9 and dry mean richness = 8.9, 95% CI = 8.3–9.4) than in open areas (monsoon mean richness = 8.2, 95% CI = 7.7–8.7 and dry mean richness = 5.7, 95% CI = 5.2–6.1) for both seasons (Fig. 3; Appendix A: Table S1). Altitude did not show a clear trend with richness of human-valued species. Overall, richness of human-valued species was 46% greater under shrubs than in open sites.

### Community species richness

Altogether 105 vascular plants species (other than *Berberis*) were documented in this study. During monsoon and dry seasons, 21 (out of 86) and 21 (out of 91) species respectively were recorded from within shrubs only, whereas, for open areas these numbers were five and seven only. Notably, combining both seasons 20 out of 105 species were unique to *Berberis* shrubs, i.e., the entire community richness was enhanced by 19%. Similarly, out of 56 human-valued species recorded during this study, nine species were found only in shrub plots, i.e., 16% increment in community level richness of the human-valued species.



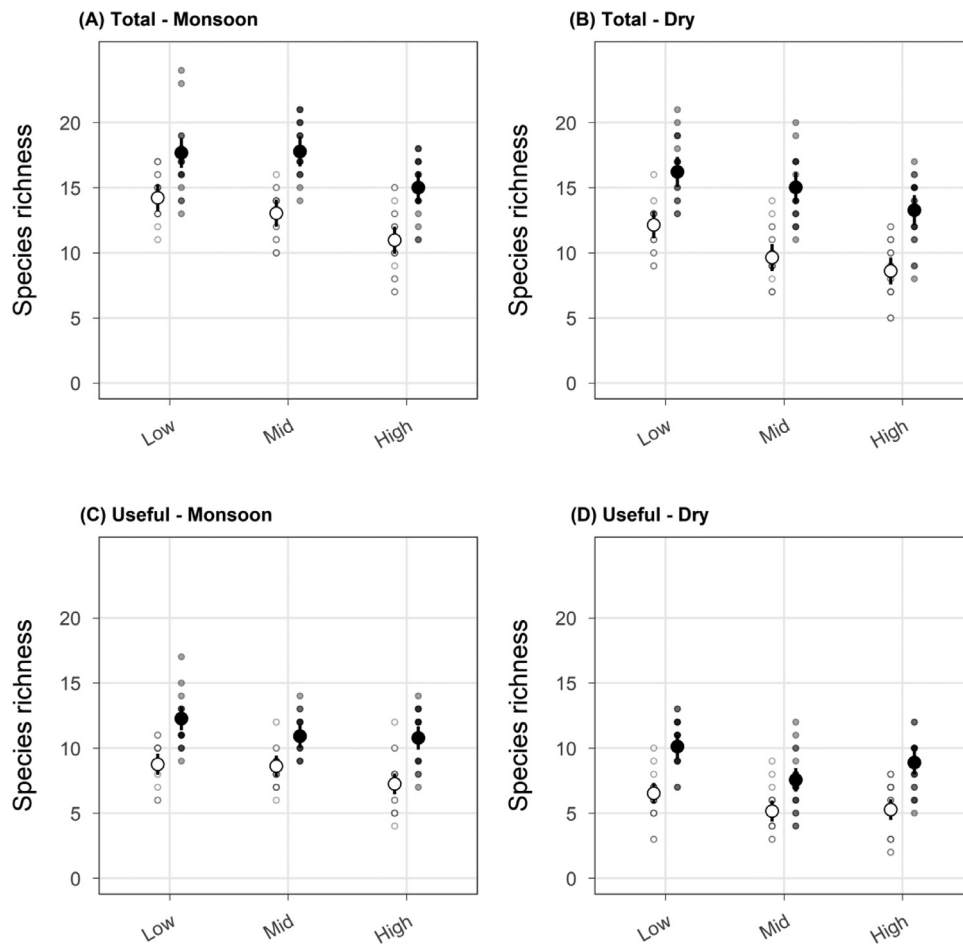
**Fig. 2.** Proportion of plots with different levels of grazing (intensity) in *Berberis* shrubs and open areas during (A) monsoon, and (B) the dry season; where 0=absence of grazing, and 4=grazing recorded in all four subplots of a sampling plot. Graphs shows the high intensity of grazing in open areas compared to shrubs, and grazing intensity increased with season (as shown by greater proportion of plots with high grazing activities).

### Plant-plant interactions

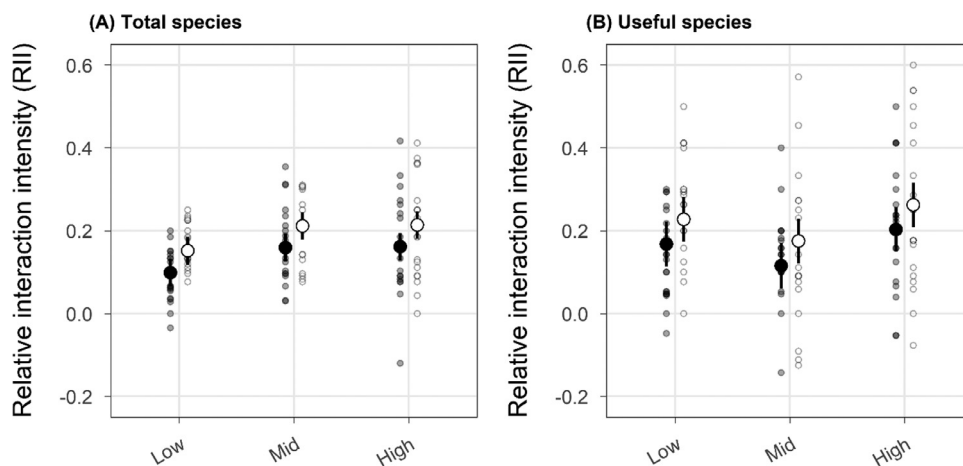
The positive value of RII during both seasons indicated strong facilitation by *Berberis* in the Langtang valley irrespective of seasonality. However, both  $RII_{sp}$  and  $RII_{hv}$  were significantly higher in the dry season (mean  $RII_{sp}$  = 0.19, 95% CI = 0.17–0.22; mean  $RII_{hv}$  = 0.22, 95% CI = 0.18–0.26) than in the monsoon (mean  $RII_{sp}$  = 0.14, 95% CI = 0.12–0.16; mean  $RII_{hv}$  = 0.16, 95% CI = 0.13–0.19), suggesting relatively stronger facilitative effects of *Berberis* shrubs during the post-monsoon dry season (also see Appendix A: Table S5 for results of paired t-test). Importantly, the  $RII_{sp}$  significantly increased with elevation, while  $RII_{hv}$  did not show a clear trend (Fig. 4; Appendix A: Table S6). Similarly,  $RII_{sp}$  had a significant relationship with grazing for both seasons, whereas it was non-significant in the cases of  $RII_{hv}$  (Appendix A: Fig. S5, Table S10).

### Species compositional difference

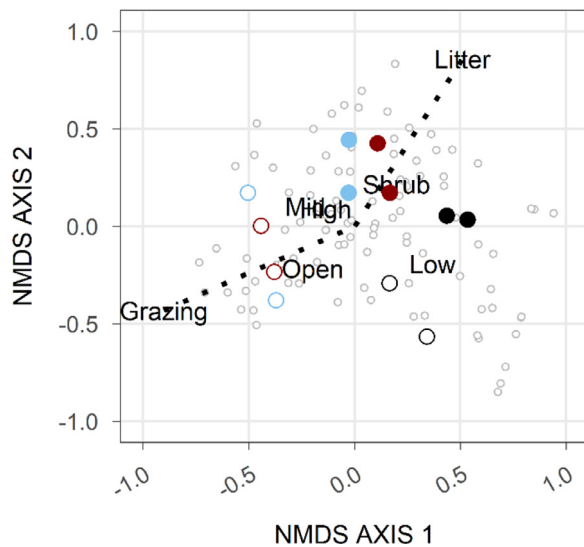
Species composition differed between shrubs and open sites, and among elevations (Fig. 5; Appendix A: Table S2).



**Fig. 3.** Species richness, within and outside the canopy of *Berberis* during the monsoon and dry seasons across elevation. Plant species richness within (closed circles) and outside (open circles) the canopy of *Berberis*. Total species richness (A & B) was always higher within the canopy of *Berberis*. Large points specify model estimates (95% CI), and small points specify plot-level observations. Richness of human-valued (useful) species (C & D) also showed the similar pattern as total species richness.



**Fig. 4.** Outcome of interactions between *Berberis* and other plant species during monsoon and dry season, and along the elevation gradients. Relative interaction intensity (RII) for monsoon (closed black circles) and dry (open circles) seasons for: (A) overall (total) species (RII<sub>sp</sub>), and (B) human-valued (useful) species (RII<sub>hv</sub>). Small circles are the RII values for each pair of plots and big circle represents the mean estimates with bars for 95% confidence interval.



**Fig. 5.** Difference in species composition in plots within and outside the canopy of *Berberis* shrubs. Small circular points represent plot level values, whereas larger circles represent centroids of species composition within *Berberis* (filled circles) and in open areas (open circles), where black circles are for low, sky-blue for mid and dark-red for high elevation.

However, differences in elevation were driven by differences between the low elevation versus the high and mid elevation sites (Fig. 5). Non-metric dimensional scaling axis 1 largely partitioned open and shrub sites while axis 2 showed differences in elevation. Differences among these factors were promoted by a tradeoff between deeper litter under canopies and a higher grazing intensity outside of the *Berberis* shrubs (Appendix A: Table S2).

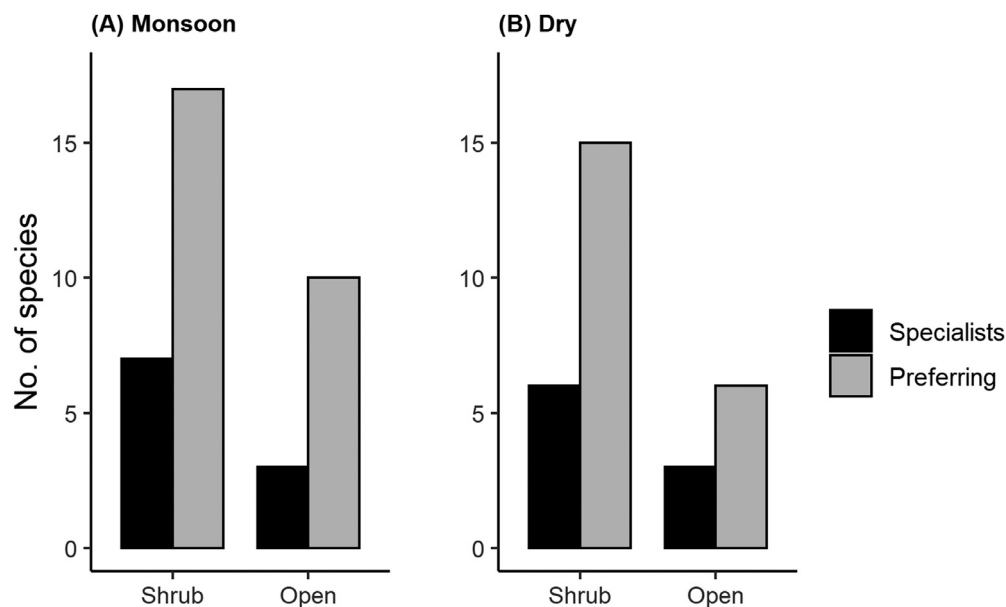
### Individual species' association with *Berberis*

Many species were found to be significantly associated with *Berberis*, thus suggesting a direct benefit from the shrubs' presence. The numbers of shrub specialists (SS) and species preferring shrub (SP) were always higher than those of open specialists (OS) and species preferring open areas (OP) irrespective of season (Fig. 6, Table 2). In both seasons, species significantly associated with *Berberis* (SS+SP: monsoon=7+17, dry=6+15) were almost twice those having spatial association with open areas (OS+OP: monsoon=3+10, dry=3+6) (Fig. 6).

Some medicinally important species, such as *Anaphalis* spp., *Arisaema jacquemontii*, *Avena fatua*, *Bistorta amplexicaulis*, *Parnassia nubicola*, *Polygonatum cirrhifolium*, were only or significantly associated to *Berberis*. Although less frequent (i.e., recorded in less than 10% of plots), the highly important and threatened medicinal species of Nepal, including the critically endangered terrestrial orchid *Dactylorhiza hatagirea*, or *Rheum australe* and *Maharanga emodi* were only recorded under shrubs. Interestingly, there were some species, e.g., *Allium wallichii*, *Anemone rivularis*, *Festuca leptopogon*, *Hedysarum* sp. that did not have significant association with either of the habitats during the monsoon but had a significantly higher occurrence in *Berberis* plots during the dry season (Table 2; Appendix A: Table S3).

### Discussion

We found *Berberis* to be a species facilitating many other species in the high-elevation regions of Nepal's Himalaya.



**Fig. 6.** Number of specialists and species preferring the respective habitat during (A) monsoon and (B) dry seasons. Specialists are the species that are significantly confined (unique) to either of the habitats; whereas, preferring are those species that were present in both habitats but had statistically significant higher frequency of occurrence in either shrub patches or open areas. Number of both specialists and preferring species are higher for shrubs during both seasons.



**Table 2.** Specialist species and species preferring *Berberis* shrubs or open habitats from both seasons. Only those species that exhibited a statistically significant association with either of the habitats are presented in this table (see Appendix A: Table S3 for the full list). The relative frequencies of occurrence in either of the habitats and *p*-value generated by 1000 times randomization using Monte Carlo test are also given for each species. SS= shrub specialists, OS= open specialists, SP= shrub preferring, and OP= open preferring.

Name of the species	Monsoon season				Dry season			
	Relative frequency		<i>p</i>	Species category	Relative frequency		<i>p</i>	Species category
	shrub	open			shrub	open		
Species associated with <i>Berberis</i> shrubs								
<i>Acronema</i> sp.	17	0	<b>0.001</b>	SS	14	0	<b>0.003</b>	SS
<i>Allium wallichii</i>	11	2	0.059		16	3	<b>0.026</b>	SP
<i>Anaphalis busua</i>	78	14	<b>0.001</b>	SP	75	19	<b>0.001</b>	SP
<i>Anaphalis contorta</i>	78	5	<b>0.001</b>	SP	78	19	<b>0.001</b>	SP
<i>Anaphalis triplinervis</i> var. <i>intermedia</i>	19	3	<b>0.008</b>	SP	54	6	<b>0.001</b>	SP
<i>Anaphalis triplinervis</i> var. <i>monocephala</i>	5	0	0.247		13	0	<b>0.006</b>	SS
<i>Androsace sarmentosa</i>	52	27	<b>0.006</b>	SP	48	22	<b>0.005</b>	SP
<i>Anemone rivularis</i>	68	75	0.559		35	14	<b>0.017</b>	SP
<i>Arisaema jacquemontii</i>	73	16	<b>0.001</b>	SP				
<i>Artemisia gmelinii</i>	46	21	<b>0.006</b>	SP	37	22	0.114	
<i>Aster albescens</i>	10	0	<b>0.035</b>	SS	13	2	<b>0.040</b>	SP
<i>Avena fatua</i>	37	0	<b>0.001</b>	SS	38	0	<b>0.001</b>	SS
<i>Bistorta amplexicaulis</i>	40	8	<b>0.001</b>	SP	29	0	<b>0.001</b>	SS
<i>Carex</i> sp.	52	32	<b>0.031</b>	SP	14	24	0.244	
<i>Cotoneaster microphyllus</i>	44	5	<b>0.001</b>	SP	41	16	<b>0.004</b>	SP
<i>Delphinium kamaonense</i>	13	2	<b>0.041</b>	SP	6	8	1.000	
<i>Festuca leptopogon</i>	48	37	0.269		41	17	<b>0.005</b>	SP
<i>Hedysarum</i> sp.	14	5	0.129		24	3	<b>0.002</b>	SP
<i>Helictotrichon virescens</i>	62	30	<b>0.001</b>	SP	70	17	<b>0.001</b>	SP
<i>Morina longifolia</i>	38	11	<b>0.001</b>	SP	40	10	<b>0.001</b>	SP
<i>Notholirion macrophyllum</i>	37	16	<b>0.014</b>	SP	10	2	0.107	
<i>Parnassia nubicola</i>	10	0	<b>0.030</b>	SS	11	0	<b>0.014</b>	SS
Poaceae	3	0	0.517		27	5	<b>0.002</b>	SP
<i>Polygonatum cirrhifolium</i>	52	25	<b>0.005</b>	SP	5	0	0.249	
<i>Roscoeia</i> sp.	30	0	<b>0.001</b>	SS	2	0	1.000	
<i>Selinum striatum</i>	25	0	<b>0.001</b>	SS	24	8	<b>0.023</b>	SP
<i>Stellaria patens</i>	78	8	<b>0.001</b>	SP	90	14	<b>0.001</b>	SP
<i>Thalictrum reniforme</i>	19	0	<b>0.001</b>	SS	16	0	<b>0.002</b>	SS
<i>Typhonium diversifolium</i>	49	25	<b>0.011</b>	SP				
<i>Veronica himalensis</i>	16	2	<b>0.007</b>	SP				
Species associated with Open areas								
<i>Bistorta milletii</i>	21	43	<b>0.012</b>	OP	2	33	<b>0.001</b>	OP
<i>Cortia depressa</i>	3	25	<b>0.003</b>	OP	2	5	0.621	
<i>Echinochloa colona</i>	25	81	<b>0.001</b>	OP	10	41	<b>0.001</b>	OP
<i>Elsholtzia</i> sp.	0	3	0.496		0	10	<b>0.028</b>	OS
<i>Gueldenstaedtia himalaica</i>	2	44	<b>0.001</b>	OP	0	5	0.246	
<i>Gypsophila cerastioides</i>	3	16	<b>0.025</b>	OP	2	0	1.000	
<i>Habenaria</i> sp.	37	60	<b>0.016</b>	OP	8	17	0.174	
<i>Juncus thomsonii</i>	3	19	<b>0.007</b>	OP	2	13	<b>0.030</b>	OP
<i>Leontopodium jacotianum</i>	0	32	<b>0.001</b>	OS	5	35	<b>0.001</b>	OP
<i>Parochetus communis</i>	5	24	<b>0.005</b>	OP	6	71	<b>0.001</b>	OP
<i>Plantago himalaica</i>	0	10	<b>0.031</b>	OS	0	3	0.475	
<i>Plantago depressa</i>	0	8	0.065		0	29	<b>0.001</b>	OS
<i>Potentilla argyrophylla</i> var. <i>atrosanguinea</i>	30	67	<b>0.001</b>	OP	30	56	<b>0.008</b>	OP
<i>Primula primulina</i>	0	24	<b>0.001</b>	OS	0	11	<b>0.008</b>	OS
<i>Roscoeia alpina</i>	33	75	<b>0.001</b>	OP	2	3	1.000	

The *Berberis* shrubs not only enhanced plant diversity at the plot or landscape level irrespective of seasons and elevations, but also promoted richness of human-valued species, and protected plants having medicinal, social, and conservation importance thus increasing ecosystem services. The species composition also significantly differed between shrubs and open plots, and the difference was also consistent across seasons. Our results agree with several studies from alpine and high-elevation environments that documented similar facilitative effects of shrubs (Ballantyne & Pickering, 2015; Iyengar et al., 2017; Pistón et al., 2016) and cushions (Cavieres & Badano, 2009; Cavieres et al., 2014; Chen et al., 2015; Pugnaire et al., 2015; Schöb, Armas et al., 2013, but see Dvorsky et al., 2013). Importantly, this might be the first research reporting this Himalayan endemic shrub as a nurse species and exploring the valuable contribution of facilitation as providing ecosystem services by protecting highly medicinal and human-valued plant species.

The facilitative role of *Berberis* shrubs is likely caused by habitat amelioration through resource enhancement and protection against grazing within their canopies, thus facilitating growth, survival and reproduction of beneficiary species (Callaway, 2007; Howard et al., 2012; Pistón et al., 2016; Schöb, Armas et al., 2013; Tirado et al., 2015). Soils beneath shrubs had significantly higher litter accumulation and soil organic carbon content than open plots (Table 1). The organic matter and litter accumulation under the shrub canopy preserve soil moisture (Callaway, 2007; Pugnaire et al., 2004) that, in addition to directly benefiting understory herbaceous species, plays a crucial role in nutrient enrichment through decomposition and nutrient cycling (Callaway, 2007; Callaway & Nadkarni, 1991; Shumway, 2000). Furthermore, shrub canopy can buffer extreme environmental conditions such as radiation intensity, temperature, strong winds, frost, and snow damage, and influence soil evaporation and understory plants' transpiration (Körner, 2003).

The facilitative effect of *Berberis* shrubs can equally be attributed to its protective role against intensive livestock grazing in the Langtang valley. Vegetation beneath shrub patches is less accessible to herbivores, therefore experiencing low grazing pressure (Fig. 2) as pointed out for Langtang valley and similar regions (Aryal, 2009; Aryal et al., 2015; Sharma et al., 2014). Therefore, *Berberis*, being a thorny shrub (Adhikari et al., 2012), protects other palatable species from grazing as reported elsewhere for nurse plants (Howard et al., 2012; Rebollo, Milchunas, Noy-Meir, & Chapman, 2002; Tirado et al., 2015). Avoidance is the only survival strategy for grazing-intolerant species in highly grazed plant communities (Milchunas & Noy-Meir, 2002) where spiny plant acts as an important natural refuge from herbivores (Rebollo et al., 2002; Tirado et al., 2015). As such, we found that most of the species having significantly higher occurrence beneath *Berberis* canopies (SS and SP), for e.g., *Acronema* sp., *Allium wallichii*, *Avena fatua*, *Carex* sp., *Helictotrichon virescens*, *Parnassia nubicola*,

*Polygonatum cirrhifolium*, *Selinum striatum*, *Stellaria patens*, were generally delicate, grazing intolerant, and palatable (Aryal, 2009; Pokharel et al., 2007; RP & BT personal observation and interaction with herders). In contrast, open specialist and species preferring open areas (OS and OP) such as *Plantago himalaica*, *P. depressa*, *Primula primulina*, *Bistorta milletii*, *Potentilla argyrophylla* var. *atrosanguinea*, *Roscoea alpina* are mostly unpalatable or undesirable, grazing and trampling resistant, and nitrophilous species (Aryal, 2009; Aryal et al., 2015; Ghimire et al., 2006; Paudel et al., 2020; Pokharel et al., 2007).

Agro-pastoralism involving transhumance i.e., rotational movement of herds between pastures to maximize seasonal resources for grazing, has been for centuries an integral part of the socio-economic life of peoples living in high mountain regions of the Himalayas including within the Langtang valley (Aryal et al., 2014). The U-shaped Langtang valley floor, being the confluence of all herds of the region before they spread out to different pastures upward and downward twice a year (May-June and September-October), is among the most heavily grazed areas of the region (Aryal et al., 2014). Therefore, in addition to abiotic stress of typical high-elevation habitats, grazing further increases the stress levels in the Langtang valley, and hence, the interaction between nurse plant and other species is generally expected to be positive (Ale et al., 2018; Bertness & Callaway, 1994; Pugnaire et al., 2015, but see Dvorsky et al., 2013; Liancourt et al., 2017). Furthermore, as expected by the original stress gradient hypothesis (SGH), and in concurrence with previous studies (e.g., Kikvidze et al., 2006; Veblen, 2008), we found stronger facilitation by shrubs during the dry season than during the monsoon as shown by significantly higher values of  $R_{II_{sp}}$  and  $R_{II_{hv}}$  (Fig. 4; Appendix A: Table S5), and the larger difference in both mean total species richness (difference between shrub and open in monsoon = 4.1 species, and dry = 4.8 species) and human-valued species richness (monsoon = 3.1 species, and dry = 3.2 species). Such a trend can potentially be explained by the relatively more stressful climatic conditions (i.e., low mean temperature, precipitation, and relative humidity) of post-monsoon (October) dry season, and high grazing pressure, as the October sampling coincided with the last week of the grazing season. Additionally, this change in biotic and abiotic stress may be the reason for change in habitat associations for some species, such as *Allium wallichii*, *Anemone rivularis*, *Festuca leptopogon*, and *Hedysarum* sp. These species did not have statistically significant association with either of the habitats during the monsoon season, however, they had significantly higher relative frequency beneath shrubs during the dry season (Table 2; Appendix A: Table S3). Such a temporal change in association, especially during the fruiting period (September-October) of most of the alpine species (Polunin & Stainton, 1984; Stainton, 1988), is indicative of shrubs as “source site” (Dias, 1996) and/or “seed refuge” (Giladi et al., 2013) that contributes to species

coexistence. However, further experimental research would be needed to better understand this phenomenon.

The significant difference in community composition between plots within *Berberis* shrubs and open areas suggests that herbaceous species in Langtang potentially differ in their niche space because of differences in their ability to withstand abiotic and biotic stresses. The role of nurse shrubs to ameliorate abiotic conditions and protection from grazing is crucial to the extension of the niche space of species that are less stress-tolerant (Howard et al., 2012; Kikvidze et al., 2015; O'Brien et al., 2019), as suggested by the high number of unique species (specialists) beneath the *Berberis* canopy, which otherwise would have been excluded from the community. As a result, the richness of human-valued species, which are usually less stress-tolerant and palatable, was significantly higher in shrub understories during both seasons. Indeed, the presence of several commercially threatened medicinal species such as *Dactylorhiza hatagirea* (CITES Appendix II, Critically Endangered in Nepal's Himalaya), *Rheum australe* (Vulnerable in Nepal's Himalaya), *Parnassia nubicola* (locally Vulnerable in a few Himalayan regions of Nepal), *Maharanga emodi* (data deficit at national level and locally Vulnerable in Langtang region) (Ghimire et al., 2006, 2008; Shrestha & Shrestha, 2012) found only beneath the canopy of *Berberis* illustrates the importance of facilitation in conserving socio-ecologically important species in the valley.

Small patches in grassland ecosystems increase spatial heterogeneity, contribute to heterogeneous vegetation and lead to high community diversity (Begon et al., 2006), playing a critical role in biodiversity conservation (Wintle et al., 2019). Small yet intact and less livestock accessible habitat patches of shrubs could buffer habitat fragmentation and climatic adversities thus providing favorable niche for understory species. Therefore, the nurse effect of Himalayan endemic *Berberis* shrubs can potentially be pivotal for the conservation of Himalayan biodiversity in the face of climate change.

## Conclusions

Our results suggest that *Berberis* shrubs act as nurse plant and play a critical role in structuring plant communities in the Langtang valley of Nepal's Himalayas. The facilitation by *Berberis* enhanced community diversity of overall plant species and human-valued species, combining both seasons by 19% and 16% respectively. The high number of unique species found only under shrubs, often palatable, delicate, and demanding species, indicates that *Berberis* facilitates the presence of less stress-tolerant species which otherwise would have been excluded from the community (Kikvidze et al., 2015; O'Brien et al., 2019). Similarly, the high frequency of low- or unpalatable species in open plots suggests that vegetation in the Langtang valley without nurse shrub patches would have been quite different, made up by an assemblage

of stress-tolerant, unpalatable species (Howard et al., 2012; Pugnaire & Luque, 2001). We evidenced facilitation promoting ecosystems services, and suggest considering facilitation in future conservation policies and management strategies to contribute to healthy and diverse grassland ecosystems, ultimately promoting biodiversity conservation and sustainable livelihoods in the Himalayas.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Supplementary materials

Supplementary material associated with this article can be found in the online version at doi:[10.1016/j.baae.2021.04.004](https://doi.org/10.1016/j.baae.2021.04.004).

## References

- Adhikari, B., Pendry, C. A., Pennington, R. T., & Milne, R. I. (2012). A revision of berberis S.S. (Berberidaceae) in Nepal. *Edinburgh Journal of Botany*, 69(03), 447–522. doi:[10.1017/S0960428612000261](https://doi.org/10.1017/S0960428612000261).
- Ale, R., Zhang, L., Li, X., Raskoti, B. B., Pugnaire, F. I., & Luo, T. (2018). Water shortage drives interactions between

- cushion and beneficiary species along elevation gradients in dry Himalayas. *Journal of Geophysical Research: Biogeosciences*, 123(1), 226–238. doi:10.1002/2017JG004365.
- Armas, C., Ordiales, R., & Pugnaire, F. I. (2004). Measuring plant interactions: A new comparative index. *Ecology*, 85(10), 2682–2686. doi:10.1890/03-0650.
- Armas, C., & Pugnaire, F. I. (2005). Plant interactions govern population dynamics in a semi-arid plant community. *Journal of Ecology*, 93(5), 978–989. doi:10.1111/j.1365-2745.2005.01033.x.
- Arroyo, M. T. K., Cavieres, L. A., Peñaloza, A., & Arroyo-Kalin, M. A. (2003). Positive associations between the cushion plant *Azorella monantha* (Apiaceae) and alpine plant species in the Chilean Patagonian Andes. *Plant Ecology*, 169(1), 121–129.
- Aryal, S. (2009). *Effect of Transhumance in Species Richness and Composition in a High-Altitude Landscape, Langtang National Park, Nepal*. Tribhuvan University and University of Bergen.
- Aryal, S., Cockfield, G., & Maraseni, T. N. (2015). Effect of summer livestock grazing on plant species richness and composition in the Himalayan rangelands. *The Rangeland Journal*, 37(3), 309–321.
- Aryal, S., Maraseni, T. N., & Cockfield, G. (2014). Sustainability of transhumance grazing systems under socio-economic threats in Langtang, Nepal. *Journal of Mountain Science*, 11(4), 1023–1034.
- Bakker, E. S., Olff, H., Vandenbergh, C., De Maeyer, K., Smit, R., Gleichman, J. M., & Vera, F. W. M. (2004). Ecological anachronisms in the recruitment of temperate light-demanding tree species in wooded pastures. *Journal of Applied Ecology*, 41(3), 571–582.
- Bakker, J. D. (2008). Increasing the utility of indicator species analysis. *Journal of Applied Ecology*, 45(6), 1829–1835.
- Ballantyne, M., & Pickering, C. M. (2015). Shrub facilitation is an important driver of alpine plant community diversity and functional composition. *Biodiversity and Conservation*, 24(8), 1859–1875. doi:10.1007/s10531-015-0910-z.
- Baral, S. R., & Kurmi, P. P. (2006). *A compendium of medicinal plants in Nepal*. Kathmandu, Nepal: Mrs. Rachana Sharma.
- Begon, M., Townsend, C. R., & Harper, J. L. (2006). *Ecology: From individuals to ecosystems*. Oxford, UK: Blackwell Publishing Ltd.
- Bertness, M. D., & Callaway, R. M. (1994). Positive interactions in communities. *Trends in Ecology and Evolution*, 9, 191–193. doi:10.1201/9780203738559.
- Bhatta, K. P., Grytnes, J., & Vetaas, O. R. (2018). Downhill shift of alpine plant assemblages under contemporary climate and land-use changes. *Ecosphere*, 9(1), e02084.
- Billings, W. D., & Mooney, H. A. (1968). The ecology of arctic and alpine plants. *Biological Reviews*, 43(4), 481–529.
- Brooker, R. W., Maestre, F. T., Callaway, R. M., Lortie, C. L., Cavieres, L. A., Kunstler, G., ... Michalet, R. (2008). Facilitation in plant communities: The past, the present, and the future. *Journal of Ecology*, 96(1), 18–34. doi:10.1111/j.1365-2745.2007.01295.x.
- Bruno, J. F., Stachowicz, J. J., & Bertness, M. D. (2003). Inclusion of facilitation into ecological theory. *Trends in Ecology and Evolution*, 18(3), 119–125. doi:10.1016/S0169-5347(02)00045-9.
- Butterfield, B. J., Cavieres, L. A., Callaway, R. M., Cook, B. J., Kikvidze, Z., Lortie, C. J., ... Brooker, R. W. (2013). Alpine cushion plants inhibit the loss of phylogenetic diversity in severe environments. *Ecology Letters*, 16(4), 478–486. doi:10.1111/ele.12070.
- Callaway, R. M. (2007). *Positive interactions and interdependence in plant communities*. . doi:10.1007/978-1-4020-6224-7 https://doi.org/.
- Callaway, R. M., Brooker, R. W., Choler, P., Kikvidze, Z., Lortie, C. J., Michalet, R., & Armas, C. (2002). Positive interactions among alpine plants increase with stress. *Nature*, 417(6891), 844–848.
- Callaway, R. M., & Nadkarni, N. M. (1991). Seasonal patterns of nutrient deposition in a *Quercus douglasii* woodland in central California. *Plant and Soil*, 137(2), 209–222.
- Cavieres, L. A., & Badano, E. I. (2009). Do facilitative interactions increase species richness at the entire community level? *Journal of Ecology*, 97(6), 1181–1191. doi:10.1111/j.1365-2745.2009.01579.x.
- Cavieres, L. A., Brooker, R. W., Butterfield, B. J., Cook, B. J., Kikvidze, Z., Lortie, C. J., ... Callaway, R. M. (2014). Facilitative plant interactions and climate simultaneously drive alpine plant diversity. *Ecology Letters*, 17(2), 193–202. doi:10.1111/ele.12217.
- Chaudhary, R. P. (1998). *Biodiversity in Nepal: Status and conservation*. Sharanpur: S. Devi.
- Chen, J., Schöb, C., Zhou, Z., Gong, Q., Li, X., Yang, Y., ... Sun, H. (2015). Cushion plants can have a positive effect on diversity at high elevations in the Himalayan Hengduan Mountains. *Journal of Vegetation Science*, 26(4), 768–777. doi:10.1111/jvs.12275.
- Connell, J. H. (1983). On the prevalence and relative importance of interspecific competition: Evidence from field experiments. *The American Naturalist*, 122(5), 661–696.
- Dhar, U. (2002). Conservation implications of plant endemism in high-altitude Himalaya. *Current Science*, 141–148.
- Dias, P. C. (1996). Sources and sinks in population biology. *Trends in Ecology & Evolution*, 11(8), 326–330.
- Dufrene, M., & Legendre, P. (1997). Species assemblages and indicator species: The need for a flexible asymmetrical approach. *Ecological Monograph*, 67, 345–366.
- Dvorsky, M., Dolezal, J., Kopecky, M., Chlumska, Z., Janatkova, K., Altman, J., ... Rehakova, K. (2013). Testing the stress-gradient hypothesis at the roof of the world: Effects of the cushion plant *thylacospermum caespitosum* on species assemblages. *PLoS ONE*, 8(1), e53514. doi:10.1371/journal.pone.0053514.
- Flores, J., & Jurado, E. (2003). Are nurse-protégé interactions more common among plants from arid environments. *Journal of Vegetation Science*, 14(3), 911–916.
- Ghimire, S. K., Mckey, D., & Aumeeruddy-Thomas, Y. (2006). Himalayan medicinal plant diversity in an ecologically complex high altitude anthropogenic landscape, Dolpo, Nepal. *Environmental Conservation*, 33(2), 128–140.
- Ghimire, S. K., Sapkota, I. B., Oli, B. R., & Parajuli-Rai, R. (2008). *Non-timber forest products of Nepal Himalaya: Database of some important species found in the mountain protected areas and surrounding regions*. Kathmandu, Nepal: WWF Nepal.
- Giladi, I., Segoli, M., & Ungar, E. D. (2013). Shrubs and herbaceous seed flow in a semi-arid landscape: Dual functioning of shrubs as trap and barrier. *Journal of Ecology*, 101(1), 97–106.



- Grime, J. P. P. (1973). Competitive exclusion In herbaceous vegetation. *Nature (London)*, 242(5396), 344–347. doi:10.1038/242344a0.
- Hacker, S. D., & Gaines, S. D. (1997). Some implications of direct positive interactions for community species diversity. *Ecology*, 78(7), 1990–2003. doi:10.1890/0012-9658(1997)078[1990:SIODPI]2.0.CO;2.
- Howard, K. S. C., Eldridge, D. J., & Soliveres, S. (2012). Positive effects of shrubs on plant species diversity do not change along a gradient in grazing pressure in an arid shrubland. *Basic and Applied Ecology*, 13(2), 159–168. doi:10.1016/j.baae.2012.02.008.
- Iyengar, S. B., Bagchi, S., Barua, D., Mishra, C., & Sankaran, M. (2017). A dominant dwarf shrub increases diversity of herbaceous plant communities in a Trans-Himalayan rangeland. *Plant Ecology*, 218(7), 843–854. doi:10.1007/s11258-017-0734-x.
- Kikvidze, Z., Brooker, R. W., Butterfield, B. J., Callaway, R. M., Cavieres, L. A., Cook, B. J., ... Schob, C. (2015). The effects of foundation species on community assembly: A global study on alpine cushion plant communities. *Ecology*, 96(8), 2064–2069. doi:10.1890/14-2443.1.
- Kikvidze, Z., Khetsuriani, L., Kikodze, D., & Callaway, R. M. (2006). Seasonal shifts in competition and facilitation in subalpine plant communities of the central Caucasus. *Journal of Vegetation Science*, 17(1), 77–82. doi:10.1111/j.1654-1103.2006.tb02425.x.
- Körner, C. (2003). *Alpine plant life: Functional plant ecology of high mountain ecosystems*. Springer Science & Business Media.
- Liancourt, P., Le Bagousse-Pinguet, Y., Rixen, C., & Dolezal, J. (2017). SGH: Stress or strain gradient hypothesis? Insights from an elevation gradient on the roof of the world. *Annals of Botany*, 120(1), 29–38. doi:10.1093/aob/mcx037.
- Miehe, G., Miehe, S., Böhner, J., Bäumler, R., Ghimire, S. K., Bhattarai, K., ... Pendry, C. (2015). Vegetation ecology. In Georg Miehe, C. Pendry, R. P. Chaudhary (Eds.), *Nepal: An introduction to the natural history, ecology and human environment of the Himalayas* (pp. 385–472). Royal Botanic Garden Edinburgh, Edinburgh, UK: Royal Botanic Garden Edinburgh.
- Milchunas, D. G., & Noy-Meir, I. (2002). Grazing refuges, external avoidance of herbivory and plant diversity. *Oikos*, 99(1), 113–130.
- Myers, N., Mittermeier, R. A., Mittermeier, C. G., Da Fonseca, G. A. B., & Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature*, 403(6772), 853.
- O'Brien, M. J., de Menezes, L. F. T., Bräthen, K. A., Losapio, G., & Pugnaire, F. I. (2019). Facilitation mediates species presence beyond their environmental optimum. *Perspectives in Plant Ecology, Evolution and Systematics*, 38, 24–30.
- O'Brien, M. J., Pugnaire, F. I., Armas, C., Rodríguez-Echeverría, S., & Schöb, C. (2017). The shift from plant–plant facilitation to competition under severe water deficit is spatially explicit. *Ecology and Evolution*, 7(7), 2441–2448. doi:10.1002/ece3.2875.
- Paudel, A., Markwith, S. H., Konchar, K., Shrestha, M., & Ghimire, S. K. (2020). Anthropogenic fire, vegetation structure and ethnobotanical uses in an alpine shrubland of Nepal's Himalaya. *International Journal of Wildland Fire*, 29(3), 201–214.
- Pistón, N., Schöb, C., Armas, C., Prieto, I., & Pugnaire, F. I. (2016). Contribution of co-occurring shrub species to community richness and phylogenetic diversity along an environmental gradient. *Perspectives in Plant Ecology, Evolution and Systematics*, 19(FEBRUARY), 30–39. doi:10.1016/j.ppees.2016.02.002.
- Pokharel, A., Chhetri, M., & Upadhyaya, C. P. (2007). Effects of grazing on plant species diversity and above ground biomass in a trans-Himalayan Rangeland. *Banko Janakari*, 17(1), 25–31.
- Polunin, O., & Stainton, J. D. A. (1984). *Flowers of the Himalaya*. New Delhi, India: Oxford University Press.
- Press, J. R., Shrestha, K. K., & Sutton, D. A. (2000). *Annotated Checklist of the Flowering Plants of Nepal*. London, UK: The Natural History Museum.
- Pugnaire, F. I., Armas, C., & Valladares, F. (2004). Soil as a mediator in plant–plant interactions in a semi-arid community. *Journal of Vegetation Science*, 15(1), 85–92. doi:10.1111/j.1654-1103.2004.tb02240.x.
- Pugnaire, F. I., & Luque, M. T. (2001). Changes in plant interactions along a gradient of environmental stress. *Oikos*, 93(1), 42–49.
- Pugnaire, F. I., Zhang, L., Li, R., & Luo, T. (2015). No evidence of facilitation collapse in the Tibetan plateau. *Journal of Vegetation Science*, 26(2), 233–242. doi:10.1111/jvs.12233.
- Rebollo, S., Milchunas, D. G., Noy-Meir, I., & Chapman, P. L. (2002). The role of a spiny plant refuge in structuring grazed shortgrass steppe plant communities. *Oikos*, 98(1), 53–64.
- Schöb, C., Armas, C., Guler, M., Prieto, I., & Pugnaire, F. I. (2013). Variability in functional traits mediates plant interactions along stress gradients. *Journal of Ecology*, 101(3), 753–762. doi:10.1111/1365-2745.12062.
- Schöb, C., Armas, C., & Pugnaire, F. I. (2013). Direct and indirect interactions co-determine species composition in nurse plant systems. *Oikos*, 122(9), 1371–1379.
- Sharma, L. N., Vetaas, O. R., Chaudhary, R. P., & Mären, I. E. (2014). Pastoral abandonment, shrub proliferation and landscape changes: A case study from Gorkha, Nepal. *Landscape Research*, 39(1), 53–69.
- Shrestha, N., & Shrestha, K. K. (2012). Vulnerability assessment of high-valued medicinal plants in Langtang National Park, Central Nepal. *Biodiversity*, 13(1), 24–36.
- Shrestha, U. B., Gautam, S., & Bawa, K. S. (2012). Widespread climate change in the Himalayas and associated changes in local ecosystems. *PloS One*, 7(5), e36741.
- Shumway, S. W. (2000). Facilitative effects of a sand dune shrub on species growing beneath the shrub canopy. *Oecologia*, 124(1), 138–148. doi:10.1007/s004420050033.
- Stainton, A. (1988). *Flowers of the Himalaya: A Supplement*. New Delhi, India: Oxford University Press.
- Stainton, J. (1972). *Forests of Nepal*. London, UK: John Murray.
- Tirado, R., Bräthen, K. A., & Pugnaire, F. I. (2015). Mutual positive effects between shrubs in an arid ecosystem. *Scientific Reports*, 5, 14710.
- Tylianakis, J. M., Didham, R. K., Bascompte, J., & Wardle, D. A. (2008). Global change and species interactions in terrestrial ecosystems. *Ecology Letters*, 11(12), 1351–1363. doi:10.1111/j.1461-0248.2008.01250.x.
- Veblen, K. E. (2008). Season-and herbivore-dependent competition and facilitation in a semiarid savanna. *Ecology*, 89(6), 1532–1540. doi:10.1890/07-0973.1.
- Walkley, A., & Black, I. A. (1934). An examination of Degtjareff method for determining soil organic matter and a proposed



- modification of the chromic acid titration method. *Soil Science*, 37, 29–37.
- Wintle, B. A., Kujala, H., Whitehead, A., Cameron, A., Veloz, S., Kukkala, A., . . . Cadenhead, N. C. R. (2019). Global synthesis of conservation studies reveals the importance of small habitat patches for biodiversity. *Proceedings of the National Academy of Sciences*, 116(3), 909–914.
- Xu, J., Grumbine, R. E., Shrestha, A., Eriksson, M., Yang, X., Wang, Y. U. N., & Wilkes, A. (2009). The melting Himalayas: Cascading effects of climate change on water, biodiversity, and livelihoods. *Conservation Biology*, 23(3), 520–530.
- Zhang, J. T., & Dong, Y. (2009). Effects of grazing intensity, soil variables, and topography on vegetation diversity in the subalpine meadows of the Zhongtiao Mountains, China. *The Rangeland Journal*, 31(3), 353–360. doi:10.1071/RJ08051.

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