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Facilitation by an endemic shrub as a nature-based approach to conserve taxonomic and phylogenetic diversities of high-value plants in the Himalayas

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Abstract

Background Plant-plant positive interactions are among the main drivers of plant community structure, especially in stressful environments. While the ecological dynamics of such facilitation are increasingly understood, studies evaluating the importance of nurse plants in preserving phylogenetic diversity and protecting species of medicinal value and conservation concern are still limited. Here, we investigated the nurse effects of a Himalayan endemic shrub, *Berberis angulosa*, in promoting taxonomic richness, composition and phylogenetic diversity of overall and highly valued species in the high-elevation mountain landscape of Langtang National Park, Nepal. Using pair-wise sampling design, we recorded plant communities within the patches of *Berberis* shrubs and in open gaps at three altitudinal belts.

Results Compared to adjacent open areas, *Berberis* patches were found to harbor compositionally distinct and evolutionarily diverse lineage plant communities with significantly higher average overall and human-valued species richness. Relative interaction indices showed clear patterns along an elevation gradient with the strongest facilitation observed at highest elevations. Comparisons of phylogenetic diversity across elevations showed inconsistent patterns, whereas overall metrics indicated higher phylogenetic diversity in shrub habitats for human-valued species. Facilitation by *Berberis* enhanced community-level richness by 40% (39 species; total = 97), including 19 human-valued species (~ 36%; total = 53) that occurred exclusively within shrub canopies. Many medicinal, endemic and conservation priority species were either shrub specialists or had significant association with *Berberis* patches, illustrating the protective role of the nurse shrub.

Conclusions Our results demonstrate that the facilitative effect of *Berberis* is not only crucial in maintaining plant communities with diverse evolutionary histories but also equally contributing to local beta and landscape-scale gamma biodiversity, sustaining valuable ecosystem services and benefits to human communities in the Himalayas. These findings suggest that appropriate management of such nurse plants may constitute a nature-based approach to biodiversity conservation, that should be considered in policies for sustainability, resilience, and ecosystem functioning in this high-elevation alpine system.

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Keywords Biodiversity conservation, Functional trait, Evolutionary relationship, High-elevation mountain, Ecosystem services

Introduction

Facilitation shapes community structure across environmental and geographic scales, affecting biological diversity across taxonomic, phylogenetic, and functional dimensions (Callaway 2007; Valiente-Banuet and Verdú 2007; Butterfield et al. 2013; Cavieres et al. 2014; Losapio et al. 2021; Bashirzadeh et al. 2022). Among plants, these interactions manifest such that one or more species, often called nurse plants, promote the fitness of other, less environmentally tolerant (i.e. stress-sensitive) species, mostly in severe environmental conditions (*sensu* stress gradient hypothesis—SGH, Bertness and Callaway 1994). Nurse plants ameliorate bio-physical stresses and create favorable micro-habitats beneath or beside their canopies, facilitating the growth, survival and recruitment of other species, thus supporting the formation of unique phylogenetic and plant community structure (Callaway 2007; Valiente-Banuet and Verdú 2007; Butterfield et al. 2013; Kikvidze et al. 2015; Pistón et al. 2016; Constantinou et al. 2023).

Phylogenetic diversity (PD) quantifies the evolutionary relationships among species within a community and serves as a fundamental metric to understand biodiversity patterns from a historical perspective and their contributions to ecosystem stability and resilience (Faith 1992). Conserving PD is therefore essential to preserve the evolutionary history of an ecosystem, maintain adaptability to environmental change, support critical ecosystem services, and preserve units of evolutionary history (Srivastava et al. 2012). Facilitation by nurse plants is effective in maintaining phylogenetic diversity in stressful environments, including alpine ecosystems, by creating microhabitats that support the coexistence of phylogenetically distinct species under harsh conditions (Butterfield et al. 2013; Navarro-Cano et al. 2016; Pistón et al. 2016; Dolezal et al. 2019). The extent of facilitation in conserving PD, however, varies across ecosystem types (Bashirzadeh et al. 2022), underscoring the need to extend research across a wider geographic region.

The Himalayas, the youngest and highest mountain range on Earth (Roy and Purohit 2018), remain among the least explored systems, where the implications of plant facilitation on phylogenetic diversity in these extreme montane environments remain poorly studied. They harbor unique ecosystems and diverse habitats exhibiting high endemism and encompassing distinct evolutionary lineages, thereby contributing to

remarkable phylogenetic diversity (Ahmad et al. 2025). However, the Himalayan mountains are vulnerable to biodiversity loss due to the ongoing climate change, habitat fragmentation, and intensifying resource exploitation (Myers et al. 2000; Xu et al. 2009). It is therefore critical to safeguard this diversity against various global and local stressors (Ahmad et al. 2025), and facilitation by nurse shrubs may offer one of the nature-based conservation strategy to this end, while providing opportunities for better understanding this ecological phenomenon (Parajuli et al. 2021). Despite increasing knowledge on how facilitation shapes the phylogenetic diversity in other critical ecosystems (Valiente-Banuet and Verdú 2007; Butterfield et al. 2013; Navarro-Cano et al. 2016; Le Bagousse-Pinguet et al. 2018; Bashirzadeh et al. 2022), the Himalayan region remains a major knowledge gap in the geographically biased corpus of literature on this topic, necessitating research to better understand and safeguard its biological heritage (Ahmad et al. 2025).

Importantly, there is some debate and uncertainty regarding the prevalence of facilitative interactions and their importance in structuring the plant communities in the Himalayan and Karakoram mountain regions (e.g., Bello et al. 2011; Dvorský et al. 2013; Liancourt et al. 2017; Ram and Chawla 2024). For instance, Bello et al. (2011), Dvorský et al. (2013) and Liancourt et al. (2017) showed that competitive interactions, rather than facilitative ones, were more common in the environmentally severe western arid trans-Himalayas and Karakoram in Ladakh, India, contradicting the SGH. Similarly, Ram and Chawla (2024) found no evidence of facilitation by several dwarf shrubs (*Caragana versicolor*, *Juniperus polycarpus* and *Rhododendron anthopogon*) on herbaceous plant communities in alpine regions of the western Himalayas of India. However, Iyengar et al. (2017) found that a dwarf compact shrub (*Caragana versicolor*) facilitated rare species and increased local herbaceous plant communities in the western trans-Himalayan region of Spiti, India. Likewise, in the central and eastern Himalayas (including the Hengduan mountains) and Tibetan Plateau, facilitation by cushion plants and shrubs strongly influenced plant community structure, with increasing interaction intensity observed where environmental stresses were higher (e.g., Yang et al. 2010; Pugnaire et al. 2015; Chen et al. 2015; Ale et al. 2018, 2023; Parajuli et al. 2021).

Characterized by high cultural diversity (Chaudhary 1998; Xu et al. 2009; Negi et al. 2025), the Himalayan region hosts unique ethnoecological interactions due to local communities' reliance on natural resources for socio-ecological resilience and sustainability (Chaudhary 1998; Ghimire et al. 2004, 2008a; Aryal et al. 2014; Negi et al. 2025). In Nepal, people depend heavily on plant resources such as medicinal herbs, and pastures used in transhumance—a traditional practice involving the seasonal movement of livestock between high- and low-elevation pastures to optimize grazing, as integral parts of their livelihood (Ghimire et al. 2004; Aryal et al. 2014). These landscapes are culturally shaped by anthropogenic disturbances, such as transhumance, which act as ecological drivers of plant diversity (Aryal et al. 2015). In this system, for example, both overgrazing and the complete absence of grazing can lead to declines in plant diversity (Sharma et al. 2014; Aryal et al. 2015). In addition to changing anthropogenic influences on the landscape, alpine ecosystems like the Himalayas are experiencing the most severe impacts of climate change and its cascading effects on biodiversity and ecosystem functioning (Xu et al. 2009; Bhattarai et al. 2022; Ahmad et al. 2025). Moreover, by altering the availability of resources, including medicinal and high-value plants, climate and land use changes may impact local livelihood and ultimately threaten socioeconomic sustainability and resilience (Xu et al. 2009; Aryal et al. 2014; Aryal 2015; Negi et al. 2025).

Facilitation may play an important role as a nature-based conservation measure in these imperiled Himalayan socio-ecological systems, where microhabitats created by nurse plants provide shelter for culturally or economically valuable herbs and species of conservation concern (Kikvidze et al. 2015; Cavieres et al. 2016; Parajuli et al. 2021). Despite the potential for such studies, research on facilitation as a nature-based tool to maintain biodiversity across multiple dimensions, sustain ethnoecological ties, contribute to local livelihoods, and enrich ecosystem services remains limited. Limited research concerning the implications of facilitation in the phylogenetic diversity of plant communities, including high value plants, along with debate over its prevalence in this system, necessitates further exploration to better understand how facilitation influences plant communities and their evolutionary relationships in the Himalayas.

Here, we investigated the role of facilitation by a Himalayan endemic dwarf shrub, *Berberis angulosa* (hereafter, *Berberis*), on plant community composition, and taxonomic and phylogenetic diversities of both overall and human-valued species, including medicinal herbs, endemic species and conservation priority taxa. We predicted that facilitation by *Berberis* supports compositionally and phylogenetically distinct taxa, thus conserving

plant diversity and ecosystem functioning in the human-adapted high-elevation alpine mountains. While testing our prediction, we specifically address the following questions:

- a) What are the patterns of plant-plant interactions along an elevation gradient in the study region?
- b) Are there more high-value medicinal, endemic, and conservation priority species associated with *Berberis* patches than open gaps?
- c) Does facilitation by native nurse shrubs contribute to conserving phylogenetic diversity in Nepal's Himalaya?

Materials and methods

Study area

The study was conducted in the Gosaikunda sector, a Himalayan eco-cultural landscape within Langtang National Park (LNP) of central Nepal (Fig. 1). LNP is one of the most biodiverse areas of the country, with high species richness and endemism, harboring a high number of rare and medicinal species (Ghimire et al. 2008b; Joshi and Joshi 2022). Of the 47 endemic plant species recorded in the park, 18 are found only in the Gosaikunda sector (Ghimire et al. 2008b), highlighting the critical importance of research encompassing various facets of biodiversity in the region. The unique geography, diverse topography, and rich assemblage of flora and fauna, combined with human interactions with the natural ecosystem, make this area socio-ecologically significant. In addition to being a protected area, Gosaikunda holds cultural and religious significance, with traditional indigenous peoples' settlements within the park. Herding is a major livelihood practice among the local community, and transhumance is adopted for generations as a strategy for harnessing the resources among the herders (Aryal et al. 2014). The Gosikunda sector of LNP receives much higher rainfall (1972–2009 average annual rainfall at Dhunche, Rasuwa—the nearest metrological station at an elevation 2065 m asl: ~1885 mm) compared to drier rain-shadowed inner Himalayan Langtang-Kyangjing valley (average annual rainfall: ~650 mm) (Chaudhary 1998; Tripathi et al. 2014).

Focal species (nurse plant)

Berberis angulosa is a spiny dwarf shrub endemic to the Himalayas and is among the dominant patch-forming shrubs in the region with around 15% cover (Adhikari et al. 2012; Miede et al. 2015; Parajuli et al. 2021). Distinguished by its bright red and usually solitary fruit, *B. angulosa* is a low stature shrub up to two meters tall (Adhikari et al. 2012). As erect and profusely branched

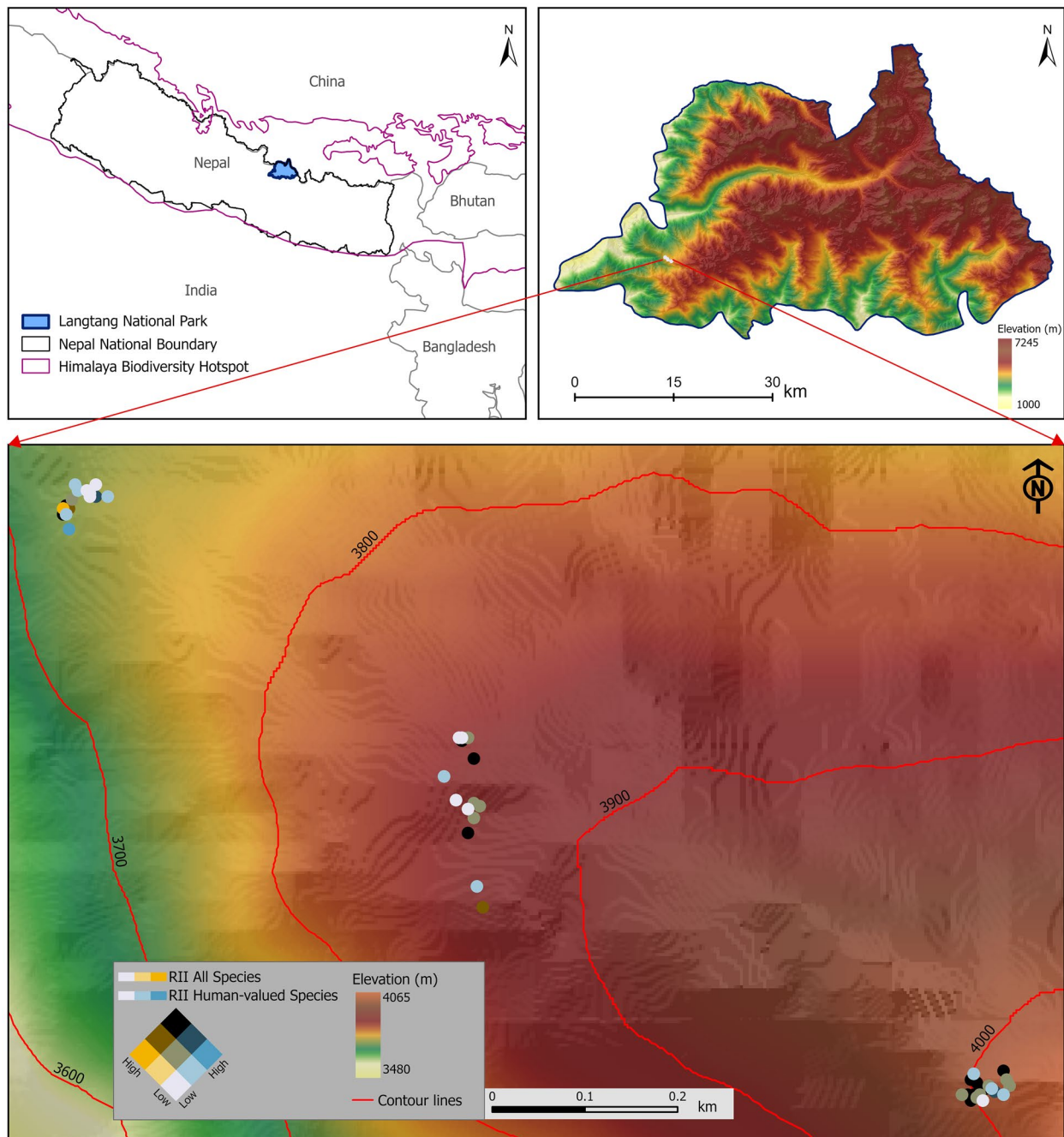


Fig. 1 Study area map showing 21 paired plots sampled in each of three elevation belts. The bivariate colors symbolize the values of relative interaction intensity (RII) of both all and human-valued species, where dark circles represent plots with high-high values and light circles represent low-low values. Note the greater number of dark plots around 4000 m asl (high elevation), illustrating the stronger facilitation by *Berberis* shrubs for both overall and human-valued species at higher elevation

from base, this shrub has coriaceous leaves with 1–3 spinulose teeth on each side of lamina, along with both central (1–3 cm) and lateral (0.5–1.5 cm) spines on the stem (Adhikari et al. 2012), thus largely preventing

livestock browsing within its canopies (Parajuli et al. 2021; RP and KA personal observations). *B. angulosa* was selected because its mosaic of distinct patches interspersed with open gaps is well suited to the pairwise sampling design employed in this study. For a

more in-depth botanical description of this shrub, we refer to Adhikari et al. (2012).

Sampling design

Pairwise sampling was conducted in patches of *Berberis* shrubs and corresponding open gaps randomly selected in three altitudinal belts: low (~3730 m), mid (~3870 m), and high (~4010 m), from just above Cholangpati to Lauribina areas of the Gosainkunda sector in Langtang National Park, central Nepal. In each elevational transect, we selected patches of *Berberis* shrubs with an adjacent open area without shrubs. A total of 21 pairs of $1 \times 1 \text{ m}^2$ shrub and open plots were sampled at each of the three elevational belts, for a total of 63 paired plots (i.e., 21 plots $\times$ 2 habitats $\times$ 3 elevations = 126 plots altogether). The shrub plots were laid completely within the canopy of *Berberis* at least 0.5 m from the edge, whereas the open plots were sampled at around one meter from the shrub edge in the open gaps to eliminate possible bias due to edge effects (Parajuli et al. 2021). Each plot was further divided into four equally sized subplots to facilitate the estimation of % covers of plant functional groups within the plot and to assess grazing (signs of livestock browsing, hoofmarks and droppings) intensity (Parajuli et al. 2021). The purpose of the sampling was to examine the spatial effect of the presence of *Berberis* shrubs along an elevation-mediated environmental gradient. Geographic positioning system coordinates (GPS locations) were marked, one for each paired plot, to visualize the geospatial pattern of the shrub's facilitative effect on understory species, including along the elevation gradient (Fig. 1).

All vascular species present within sampled plots were recorded. Species were identified on site by consulting the field manuals (Polunin and Stainton 1984). Unidentified species were collected, and herbarium voucher specimens were prepared. All species were later identified and confirmed by expert plant systematists at the National Herbarium and Plant Laboratories (KATH). Nomenclature followed national checklists such as (Rajbhandari et al. 2017, 2019, 2021, 2022, 2025; Shrestha et al. 2022a). Geographic distributions in these publications, along with the plants of the world online database by Royal Botanic Gardens Kew (<https://powo.science.kew.org/>), were used to determine the endemic status of each species.

Field data recording

In each of the sampling plots, all vascular plants were documented based on their presence or absence. The percent covers of plant functional groups such as herbs and grasses were also recorded separately based on visual estimates and logged on a scale of 0–100%. To maintain

consistency, the same researcher estimated the cover % for all functional groups and throughout the study. Additionally, we also documented environmental variables like elevation, slope, and aspect for each plot. Litter thickness was measured in centimeters using a steel ruler. Similarly, the height of shrubs was recorded using measuring tape. Observations were made regarding browsing, trampling, signs of plant harvest, and traces of fires within each plot. Because harvesting and fires were infrequent, we removed those from analysis. A composite 'grazing' disturbance variable was determined based on signs of browsing and trampling on a scale of 0–4, where 0 is absence of grazing and 4 means heavy grazing (Parajuli et al. 2021).

Plants known to have various ethnobotanical uses such as medicinal values or other socio-cultural significance were termed as human-valued species (i.e., plants useful to humans). To enhance generalizability across geographies and socio-cultural context, we categorized these plants into eight major categories following an established taxonomy (Parajuli et al. 2021). Briefly, some of the key categories were medicinal, food, additive, social, commercial, and fodder values (see full details in SI Table S1). We identified ethnobotanical use values of the species recorded in this study by consulting: (a) local peoples, herders and traditional healers ($n=23$) and (b) relevant published literature (e.g., Manandhar 2002; Baral and Kurmi 2006; Ghimire et al. 2008a). Verbal consent was obtained prior to the consultation and all local resource persons voluntarily shared their traditional knowledge about plant use values. The conservation status of species were based on Ghimire et al. (2008a) and Bachman et al. (2024).

Statistical analysis

We employed the relative interaction indices as proposed by Armas et al. (2004), to assess the extent of interaction between the shrub and different species. The index is calculated using the equation $\text{RII} = (S_s - S_o) / (S_s + S_o)$, where S_s represents the number of species occurring within the shrub plot and S_o represents the number of species in the open plot. We calculated relative interaction indices for all species and human-valued species, i.e., RII of total species (RII_{tsp}) and RII using a dataset with human-valued species only (RII_{hvsp}). These indices were computed for each pair of sampling plots.

To test the patterns of RIIs along the elevation gradient, we first fitted a linear regression model (LM) with the Gaussian family, because RIIs followed the normal distribution, using *lm()* function in the R statistical environment (R Core Team 2022). We also included other predictors such as litter thickness measured in shrub plots and grazing disturbance recorded in open areas.

We tested heterogeneity using Levene's test and fitted a generalized least square regression (GLS) model as an additional attempt to check for the potential heterogeneity inherently associated with ecological data using different variance structures (Zuur et al. 2009). Because both Levene's test and the model comparisons using *anova()* were non-significant, we ruled out the GLS. However, given the nested sampling design (21 pairs of plots sampled within each elevation belt), we also did fit linear mixed-effects models (LMMs) to analyze the variation of RII_{tsp} and RII_{hvsp} along the elevation gradient using *lme()* function from the *nlme* package (Pinheiro et al. 2025). Elevation (a factor with three levels: low, mid, and high), litter thickness and grazing (a factor with five levels: 0–4) were treated as a fixed factors, while plot (random intercept with 63 levels) was considered as a random term to account for variability in RII values for both total species and human-valued species across plots, which is specifically important to consider in the hierarchical sampling structure like this. The LMMs were fitted with 'ML' (maximum likelihood) and compared with fixed-effects only model, a common practice of model selection process suggested and applied in ecology (Zuur et al. 2009; Bolker et al. 2009).

The non-significant likelihood ratio test, along with higher AIC and BIC, indicated that LMMs didn't perform better than LMs. Since there were no apparent signs of heterogeneity and both GLS and LMMs failed to improve the model fit over LMs, we decided to use linear models although all plots were not completely independent due to our nested sampling design. Because the overall effects of elevation, our fixed factor of primary interest, on RIIs were consistent regardless of the model used and LMs diagnostics showed the good sign of model fit (i.e., the residuals were normally distributed and fit vs residuals were random without any visible patterns), the conclusions from the LMs should be robust enough to draw overall patterns of RIIs along elevation gradients. Finally, we also compared the mean differences in RIIs computed with covers of herbs and grasses between the elevation bands using ANOVA and calculating the mean and 95% confidence intervals (CIs). All visual comparisons were made using point and whisker plots with mean and 95% CIs using the *ggplot2* package.

We conducted Nonmetric Multidimensional Scaling (NMDS) ordination using a Bray–Curtis dissimilarity matrix to visualize differences in species composition between areas under *Berberis* shrubs and adjacent open areas along an altitudinal gradient. We employed Permutational Multivariate Analysis of Variance (PERMANOVA) with 999 permutations to test for overall difference in species composition between habitat types (under shrubs vs. open) and altitudinal levels (low, mid,

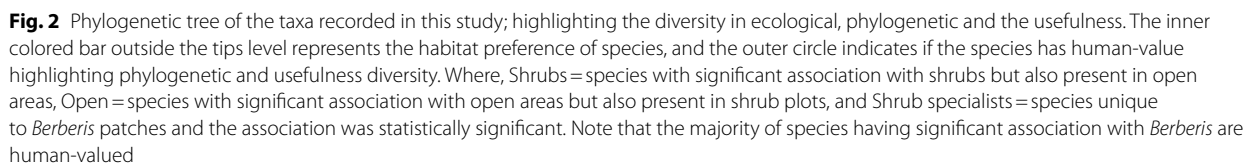
high). Similarly, we performed pairwise PERMANOVA to compare the compositional difference between each of the habitat types and elevation, adopting a similar approach. To analyze the effect of grazing and litter content in species composition, we fitted these variables to NMDS objects using the *env_fit()* function in the *vegan* package (Oksanen et al. 2025), with 999 permutations and created the plots with *ggplot2* package.

Indicator species analysis

We used indicator species analysis (ISA) to test the association of species with a habitat (shrubs vs open) and statistical significance was tested using a Monte Carlo 9999 permutation procedure using *multipatt()* function in R package *indicspecies* (Cáceres and Legendre 2009). We used group equalized association function (Indicator Value Index, IndVal.g) method to identify whether a species has an ecological association with either shrubs or open areas. The association statistics in IndVal is a product of two quantities, namely 'A' and 'B' (Dufrêne and Legendre 1997; Cáceres and Legendre 2009), where, for presence–absence data, component A is “the relative frequency of the species in the target site group divided by the sum of relative frequencies over all groups”, whereas B is “the relative frequency of occurrence of the species inside the target site group” (Cáceres and Legendre 2009). The indicator species analysis is commonly used in facilitation and other community ecological research to identify most characteristic species representing habitat of interests using both presence-absence and abundance data (Dufrêne and Legendre 1997; De Cáceres and Legendre 2009; Parajuli et al. 2021).

Phylogenetic diversity

We generated the phylogenetic tree (Fig. 2) using the *VPhyloMaker2* package (Jin and Qian 2022) based on the GBOTB.extended backbone tree. To incorporate species missing from the backbone, we employed Scenario 3 (S3), which binds missing taxa to the phylogeny based on the relative branch lengths of their respective genera or families. This approach ensures the resulting tree is ultrametric while maintaining representative evolutionary distances. Finally, the tree was resolved into a fully bifurcating structure using the *multi2di()* function in the *ape* package to meet the requirements for downstream phylogenetic diversity analyses. Using this tree, we quantified phylogenetic community structure using mean pairwise distance (MPD), mean nearest taxon distance (MNTD), and their standardized indices. Based on these metrics, we calculated the Net Relatedness Index (NRI) and Nearest Taxon Index (NTI), which quantify the standardized deviation of



matrices were generated from the regional species pool, and the resulting distributions were used to calculate the standardized effect sizes of PD, MPD, and MNTD. The generalized equation for estimating the phylogenetic matrix is:

where PM (phylogenetic matrix)=either SES.PD or MNTD or MPD, PM_{obs} =observed total value of the PM connecting species in the community, $\mu(PM_{\text{null}})$ = mean value of the PM from randomized communities, $\sigma(PM)$ =standard deviation of null PM.

The diversity metrics were calculated using *Picante* package (Kembel et al. 2010). We used a two-way ANOVA to test the effects of elevation, habitat type,

and their interaction on phylogenetic structure (NRI, NTI and SES.PD). Post-hoc comparisons were performed using Tukey's Honestly Significant Difference (TukeyHSD) test. Pairwise *t*-tests were conducted to compare the phylogenetic indices between open and shrub habitats at each elevation. All the analyses were done in R statistical environment (R Core Team 2022).

Results

Higher community and plot level richness beneath *Berberis*

A total of 97 vascular plant species were recorded in this study (Supplementary Information, SI, Table S4). Of these, 39 species were exclusively recorded from underneath the *Berberis* canopies, whereas only two species were confined to open areas. Similarly, 53 (out of 97) species were documented to be human valued species, which included 19 species unique to shrub plots compared to only one from open gaps. The mean richness of both total species and human-valued species was significantly higher within shrub canopies than in adjacent open gaps (total species: $t=14.56$, $p<0.001$; human-valued species: $t=9.5$, $p<0.001$). On average, shrub plots have greater than 50% more species (mean richness of total species: 16.05, 95% CIs 15.2–16.9; human-valued species: 11.03, 95% CIs 10.36–11.7) than in open plots (mean richness of total species: 10.25, 95% CIs 9.7–10.8; human-valued species: 6.9, 95% CIs 6.5–7.3). Likewise, the % cover of herbaceous plants was significantly higher underneath *Berberis* (mean=58.94, 95% CIs 53.4–64.5) than in open (mean=47.48, 95% CIs 43.2–51.7), whereas grass coverage was higher in open (mean=8.68, 95% CIs 6.9–10.4) than in shrub plots (mean=3.58, 95% CIs 2.5–4.8).

Berberis patches offered comparatively more favorable habitat conditions

Habitat conditions within *Berberis* patches were comparatively better than open areas in terms of both abiotic (litter thickness, a proxy of nutrient availability) and biotic (protection from grazing) factors. Litter thickness within shrubs (mean=1.87 cm; 95% CIs 1.65–2.09) was significantly higher compared to open (mean=0.02 cm; 95% CIs –0.002 to 0.04). Likewise, shrub plots were generally excluded from grazing, in contrast to the frequent signs of high grazing pressure observed in open areas (Supplementary Information Fig. S1), and patterns of grazing were largely similar in all three elevation bands.

Increase in relative interaction intensity along the elevation gradient

The average RII of both all and human-valued species were positive and significantly different from zero (RII_{tsp} : mean=0.22, 95% CIs 0.19–0.25; RII_{hvsp} : mean=0.22,

95% CIs 0.19–0.26) suggesting a facilitative role of *Berberis* shrubs on understory species in Gosaikunda sector of LNP, Nepal. Our test of trends of facilitatory effects of *Berberis* shrubs along the elevation gradient showed an interesting pattern, albeit the facilitation intensity was the strongest at the highest elevation for both all and human-valued species. The difference in RII_{tsp} was statistically significant between low and high elevation, however, it was non-significant when compared mid-elevation with both low and high elevations (Fig. 3A; SI Table S2). The pattern was similar for human-valued species (RII_{hvsp}) too.

The mean RIIs values of % covers of herbs and grasses revealed varied patterns in their interactions with *Berberis* shrubs. Overall, as illustrated by the RII computed with % covers, herbaceous plants (mean=0.09, 95% CIs 0.02–0.16) had significantly positive interactions with *Berberis* shrubs, whereas the grasses exhibited strong competition (mean=–0.36, 95% CIs –0.48 to –0.24). Per elevation-wise comparisons, while the facilitative effects of shrubs on covers of herbs and the competitive effects on grass were strongest at high-elevation, these interactions were neutral, i.e., non-significantly different from zero, at low-elevation (Fig. 3B).

Difference in species composition between shrub and open habitats

Overall, species composition differed significantly between plots in open areas and under shrubs for both all species ($F=24.77$, $p=0.001$) and human valued species ($F=29.21$, $p=0.001$). It varied significantly between open gaps and shrub canopies across all three elevations as well for both all ($F=21.96$, $p=0.001$; Fig. 4A) and human-valued species ($F=26.41$, $p<0.001$; Fig. 4B). Post-hoc pairwise comparison between the habitat types at low, mid, and high elevations also showed significant difference in composition for both all species ($F=17.23$, $p_{adj}=0.01$; $F=16.32$, $p_{adj}=0.01$; $F=21.0$, $p_{adj}=0.01$) and human-valued species ($F=22.79$, $p_{adj}=0.01$; $F=17.76$, $p_{adj}=0.01$; $F=25.31$, $p_{adj}=0.01$). Community composition in open plots was significantly correlated with grazing disturbance (all species: $R^2=0.42$, $p=0.001$; human-valued: $R^2=0.42$, $p=0.001$), while in shrub plots it was significantly correlated with litter thickness (all species: $R^2=0.57$, $p=0.001$; human-valued: $R^2=0.55$, $p=0.001$).

More high value plants associated with shrub patches than open gaps

We found around one third of characteristic species (30 out of 97) that had statistically significant association with either of the habitats (Table 1). A total of 25 species (i.e., 83%) had significant association with shrubs

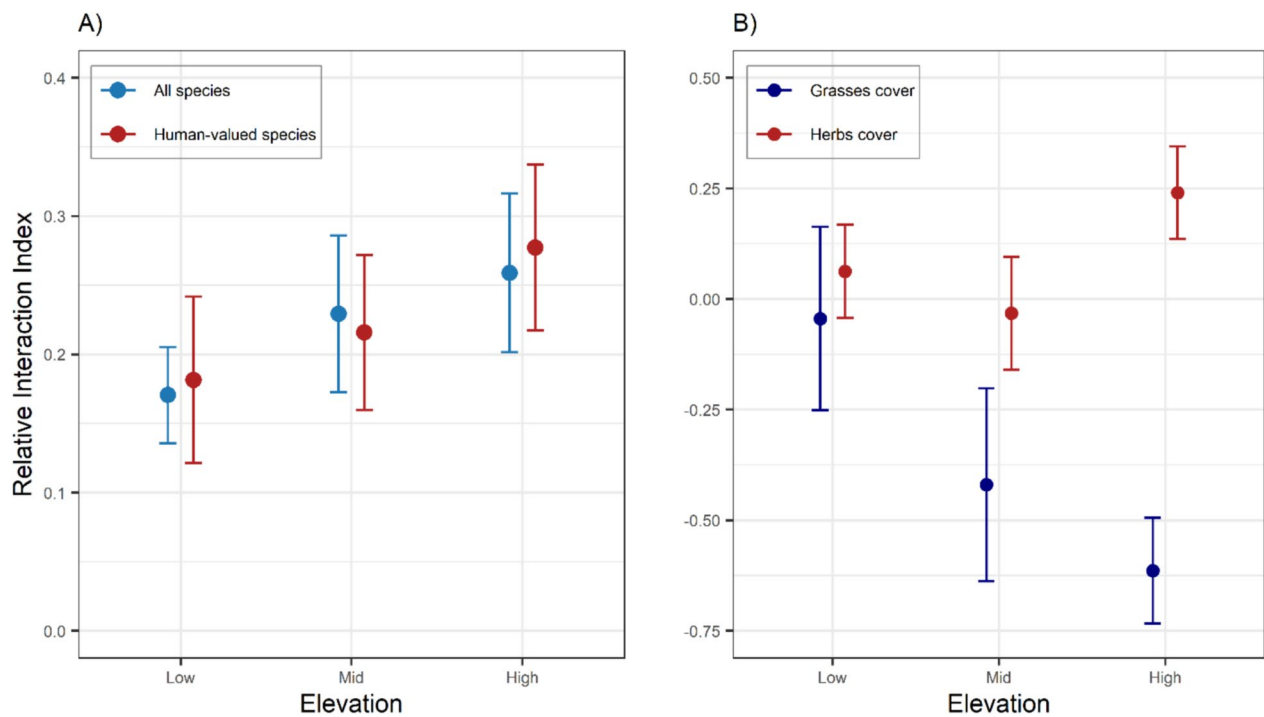


Fig. 3 Comparisons of RII along the elevation gradient. **A** Dot and whisker (mean $\pm$ 95% CIs) plots showing the patterns of interactions between *Berberis* shrubs and understory species, both all (RII_{tsp}) and human-valued (RII_{hvsp}); with highest intensity of facilitations by *Berberis* shrubs for both total and human-valued species evident at high-elevation. **B** Overall trends of RIs computed with % covers of different functional groups; note the significantly strong positive interactions between *Berberis* shrubs and herbs at high-elevation, non-significant in the case of grasses and herbs at low-elevation, and significantly negative interaction (i.e., competition) with grasses at mid- and high-elevations

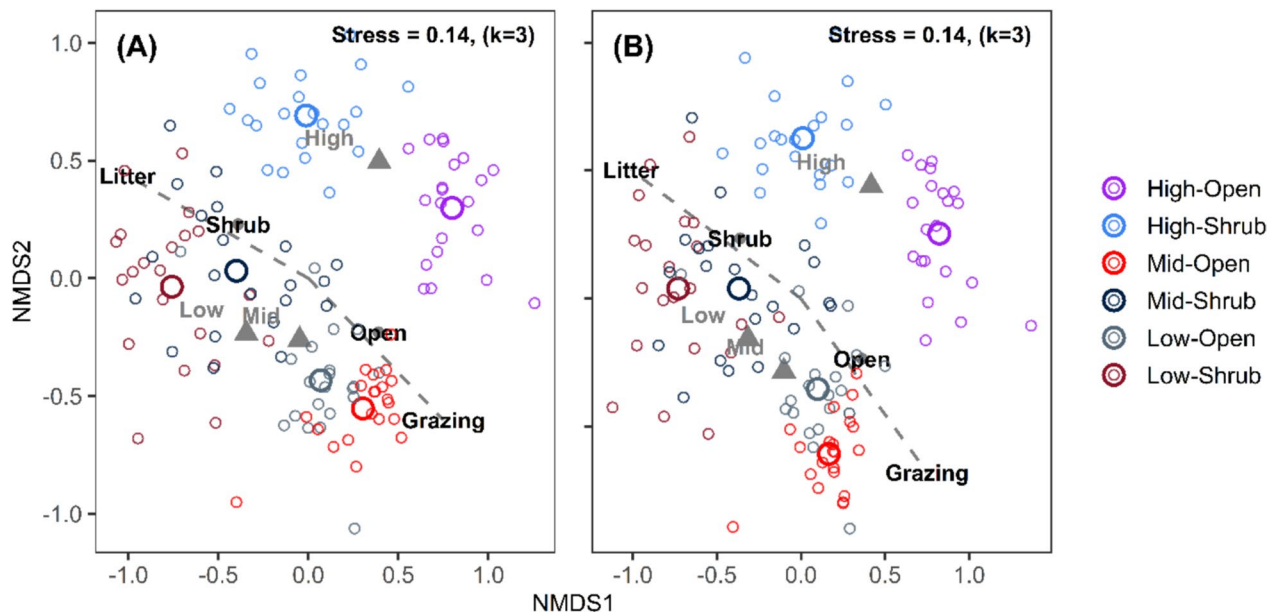


Fig. 4 NMDS plots illustrating differences in taxonomic composition between open and shrub habitats across the altitudinal range for **A** all species and **B** human-valued species. Small colored circles represent plot-level values and bigger colored circles represent the centroid of habitat types in different elevations. Grey triangles are the centroids of pooled (shrub + open) species composition at three different elevations

Table 1 Results of tests of species' habitat association with shrubs and open areas

Species name	Association statistics	P-value	Habitat association	Usefulness	Endemism	Conservation status
<i>Saxifraga diversifolia</i>	0.77	0.0001	Shrubs	Human valued		
<i>Potentilla daltoniana</i>	0.77	0.0001	Shrubs	Human valued		
<i>Themeda triandra</i>	0.66	0.0001	Shrubs	Human valued		
<i>Calamagrostis pseudophragmites</i>	0.65	0.0001	Open			
<i>Anaphalis nepalensis</i>	0.65	0.0001	Shrubs	Human valued		
<i>Corydalis juncea</i>	0.59	0.0001	Shrubs	Human valued	Himalayan endemic	
<i>Stellaria patens</i>	0.58	0.0001	Shrubs		Himalayan endemic	
<i>Valeriana hardwickii</i>	0.53	0.0001	Shrub specialist	Human valued		
<i>Impatiens</i> sp.	0.47	0.0001	Shrubs			
<i>Tetrataenium wallichii</i>	0.47	0.0001	Shrub specialist	Human valued	Himalayan endemic	Threatened
<i>Cyperus</i> sp.	0.49	0.0002	Open			
<i>Cyanaea</i> sp.	0.44	0.0002	Shrub specialist			
<i>Caltha palustris</i>	0.53	0.0004	Open	Human valued		
<i>Gentiana depressa</i>	0.51	0.0004	Shrubs	Human valued		
<i>Hemiphragma heterophyllum</i>	0.44	0.0004	Shrub specialist	Human valued		
<i>Pedicularis megalantha</i>	0.48	0.0006	Shrubs	Human valued	Himalayan endemic	
<i>Cyananthus himalaicus</i>	0.47	0.0006	Shrubs		Nepal endemic	Threatened
<i>Euphorbia stracheyi</i>	0.46	0.0011	Shrubs	Human valued		
<i>Aster</i> sp.	0.40	0.0014	Shrub specialist			
<i>Androsace sarmentosa</i>	0.40	0.0024	Shrub specialist	Human valued	Himalayan endemic	
<i>Sporobolus fertilis</i>	0.49	0.0029	Open	Human valued		
<i>Epilobium</i> sp.	0.38	0.0029	Shrub specialist			
<i>Galium</i> sp.	0.38	0.0034	Shrub specialist			
<i>Delphinium himalayae</i>	0.36	0.0055	Shrub specialist	Human valued	Himalayan endemic	Threatened
<i>Calamagrostis scabrescens</i>	0.41	0.0130	Shrubs			
Unknown1	0.33	0.0131	Shrub specialist			
<i>Arisaema jacquemontii</i>	0.38	0.0136	Shrubs	Human valued		
<i>Rheum acuminatum</i>	0.33	0.0138	Shrub specialist	Human valued	Himalayan endemic	
<i>Plantago</i> sp.	0.38	0.0178	Open			
<i>Arisaema</i> sp.1	0.31	0.0270	Shrub specialist			

Only species with statistically significant association with either of the habitats are presented here. Association statistics are the indicator value test statistics obtained from ISA using *IndVal.g* function and *p*-values were generated by Monte Carlo permutation procedure with 9999 random resampling. Species used in various local indigenous traditional practices are marked as 'Human valued'. Habitat association terms, Shrubs = species with significant association with shrubs but also present in open areas, Open = species with significant association with open areas but also present in shrubs plots, and Shrub specialists = species unique to *Berberis* patches and the association was statistically significant. A full list of species with their association statistics and corresponding *p*-values is given in SI Table S3

compared to only five (i.e., 17%) species in the case of open areas. Of these, 12 species were shrub specialists, i.e., species unique to *Berberis* shrubs with their association being statistically significant, whereas none of the species were found to be open specialists. Likewise, the proportion of human-valued species having significant association with shrubs was much higher (15 out of 17) than those associated with open areas (2 out of 17). Some commercially important medicinal herbs, e.g., *Delphinium himalayae* (Nationally and globally threatened, Himalayan endemic), *Rheum acuminatum*

(Himalayan endemic), and *Valeriana hardwickii*, were shrub specialists and hence protected within the patches of *Berberis*. Some other high-value medicinal plants with conservation importance such as, *Allium wallichii* (Nationally threatened), *Parnassia nubicola* (Locally vulnerable), *Aconitum ferox* (Nationally and globally threatened, Himalayan endemic), though were less frequent and statistically non-significant, were only recorded from underneath *Berberis* shrubs.

Shrubs offer phylogenetic refuge for human-valued plant lineages

Phylogenetic structure varied along the elevational gradient as illustrated by all diversity metrics computed in this study. Both NRI and NTI increased with elevation, with significantly lower values at low and mid elevations compared to high elevation for both all species and human-valued species ($p < 0.001$ for all comparisons).

Standardized size effect of phylogenetic diversity (SES.PD) showed opposite pattern along the elevation compared to NRI and NTI, with higher values at low elevation that declined significantly toward high elevation ($p < 0.01$ for all elevation wise comparisons). Overall, SES.PD was significantly higher for human valued species in shrub ($p = 0.002$, $F = 10.017$), while the Nearest Taxon Index (NTI) was lower ($p = 0.001$, $F = 11.23$). However, when compared in each of the elevation belts, the habitat effects were inconsistent. Shrub plots had

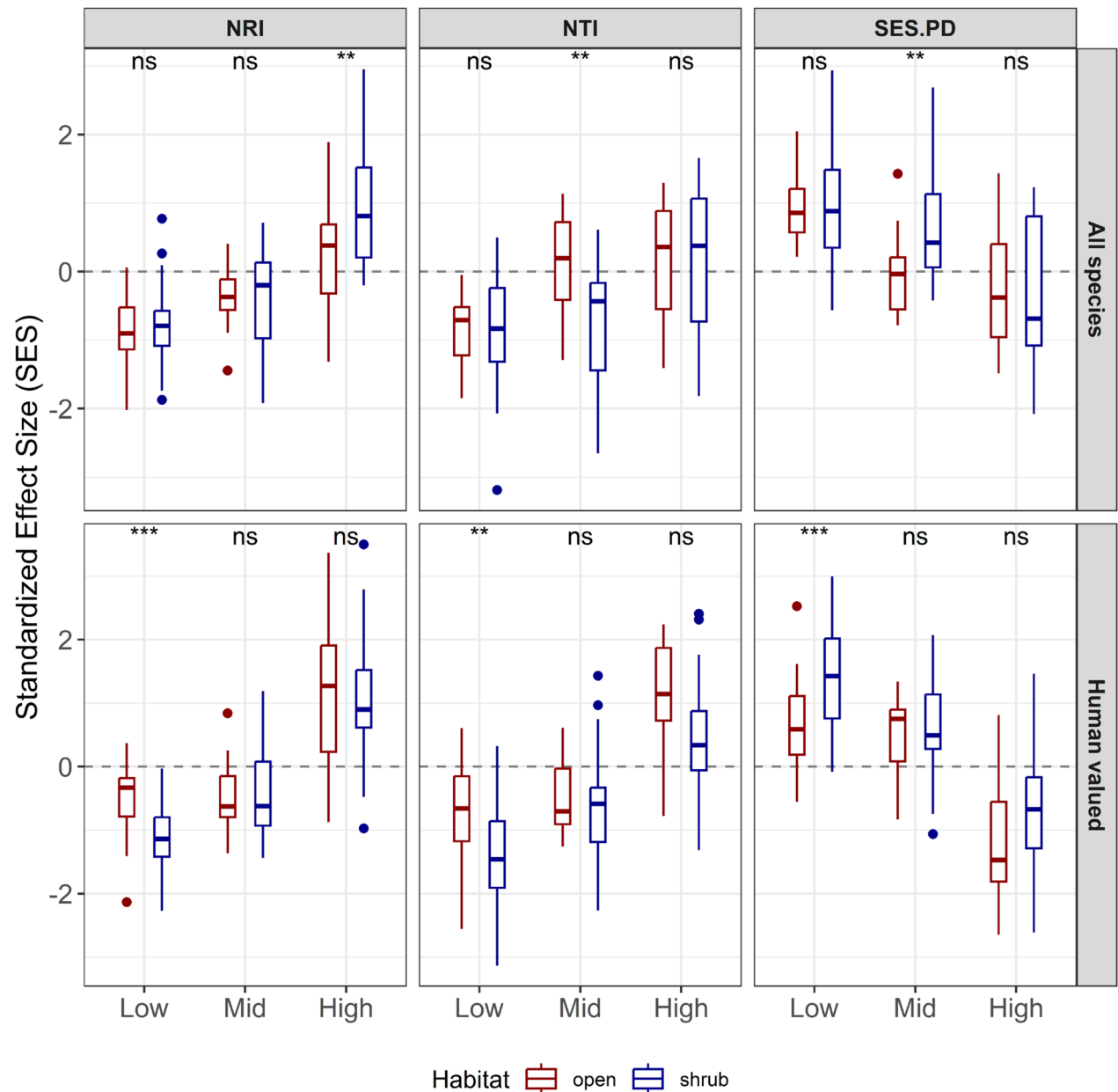


Fig. 5 Comparison of net relatedness index (NRI), nearest taxon index (NTI) and standardized effect size of phylogenetic diversity (SES.PD) between open and shrub habitats across elevation range for all species and human-valued species

significantly higher NRI than open plots at high elevation for all species ($p=0.005$), but significantly lower than that of open plots at low elevation in the case of human valued species ($p<0.001$) (Fig. 5). NTI was lower at mid elevation for all species in shrub plots ($p=0.001$), while it was significantly lower in the low elevation for human valued species ($p=0.002$) (Fig. 5). Compared to open plots, shrub plots found to have significantly higher SES.PD for all species at mid elevation ($p=0.006$) and for human valued species at low elevation ($p<0.007$) (Fig. 5).

Discussion

Our results demonstrate that facilitation by *Berberis* plays a critical role in promoting the taxonomic and phylogenetic diversity of alpine plants in Nepal's Himalaya. Previous studies also reported a strong role of facilitation by shrubs and cushion plants in maintaining plant diversity and structuring plant communities in the high-elevation mountains characterized for both abiotic and biotic stressors (e.g., Yang et al. 2010; Chen et al. 2015; Ale et al. 2018, 2023; Parajuli et al. 2021; but see Ram and Chawla 2024). Our findings support the idea of nurse plant-created microsites as conservation refugia of plant taxonomic and phylogenetic biodiversity in the Himalayas (Parajuli et al. 2021; Rasray et al. 2024). Moreover, this study may be the first to demonstrate that facilitation by shrubs contributes to preserving phylogenetic diversity of high-value medicinal species and other species of societal and conservation importance. The facilitative effects of *Berberis* can be attributed to both direct and indirect mechanisms, particularly its role in modifying microhabitats beneath its canopy through abiotic stress amelioration and protection from grazing (Parajuli et al. 2021).

We observed the strongest facilitation by *Berberis* at the highest elevation for both the overall plant community and for human-valued species. These findings align with the predictions of the stress gradient hypothesis (SGH; Bertness and Callaway 1994) and are consistent with reports from previous studies conducted in the Himalayan region (e.g., Yang et al. 2010; Ale et al. 2018; Parajuli et al. 2021; but see contrasting findings from Karakoram mountain: Bello et al. 2011; Dvorský et al. 2013). In this study, elevation was considered as an integrative proxy for the stress gradient, and interpretations are made accordingly. In the Himalayas and other alpine mountain systems, environmental stress typically increases with an increase in elevation due to declining temperature, shortening growing seasons and increasing exposure to radiation (Körner 2007, 2021; Sundqvist et al. 2013). For instance, the average temperature lapse rate in Nepal's Himalaya is $-0.5\text{ }^{\circ}\text{C}$ to $-0.7\text{ }^{\circ}\text{C}$ per 100 m of elevation gain (Kattel et al. 2013; Khadka et al. 2023). Given

the elevation difference of approximately 300 m between the low- and high-elevation transects in our study, this translates to decline of about $2\text{ }^{\circ}\text{C}$ in mean surface air temperature, resulting in more stressful climatic conditions at higher elevations. These increments in climatic and other associated environmental severities could explain the strongest facilitation observed at the high-elevation sites, in line with the general predictions of SGH (Bertness and Callaway 1994). Notably, with only a 200 m elevation gain, Yang et al. (2010) documented a stronger facilitative effect at higher site (4700 m) compared to the lower one (4500 m) in the Hengduan alpine mountains of the Sino-Himalayas, underscoring how small changes in elevation can influence plant-plant interactions patterns in these youngest mountain systems. Although previous studies have tested the SGH across elevation ranges that are narrower (e.g., Yang et al. 2010), similar to (e.g., Parajuli et al. 2021), or even wider (e.g., Pugnaire et al. 2015; Chen et al. 2015), than those considered here, we emphasize the need for additional studies incorporating longer gradients and multiple environmental stressors in the Himalayas to better understand the generality of this hypothesis.

Per our expectations, unique species were observed in both habitats, albeit the proportion was much higher underneath *Berberis* canopies (40.2% of total species, 35.9% of total human-valued) than open gaps (2.1% of total species, 1.9% of total human-valued), leading to a significant difference in community compositions of both overall and human-valued species between these two contrasting habitats. Since livestock browsing, as a part of centuries long transhumance agropastoral practice, is common in Nepal's Himalayan landscapes including Langtang region (Aryal et al. 2014, 2015), largely palatable yet grazing intolerant species were benefitted from protection by the patches of *Berberis* (Parajuli et al. 2021; RP and KA personal observations and interactions with local herders), an erect thorny dwarf shrub (Adhikari et al. 2012). Nurse shrubs, specifically spiny ones, are generally found to be effective in protecting palatable species in heavily grazed landscapes (Soliveres et al. 2012; Tirado et al. 2015; Parajuli et al. 2021). The indicator species of open areas were mostly grazing-tolerant but shade-intolerant perennial grasses, such as *Calamagrostis pseudophragmites*, *Sporobolus fertilis*, *Cyperus* sp., *Kobresia* sp. or generally undesirable to livestock or unpalatable forbs, e.g., *Caltha palustris*, *Plantago* sp. (Aryal et al. 2015; Paudel et al. 2020; Parajuli et al. 2021; RP and KA personal observations and interactions with local herders). This could be the reason for a strong competitive interaction between grasses and *Berberis* as shown by significantly negative RII (mean = -0.36 , 95% CIs -0.48 to -0.24) when computed with % cover

values of grasses. In contrast, *Berberis*-specialist species were dominantly forbs with low to moderate tolerance to livestock browsing and highly valued because of their medicinal and other societal uses, endemism and conservation status such as *Delphinium himalayae*, *Rheum acuminatum*, *Tetrataenium wallichii*, *Valeriana hardwickii* (Ghimire et al. 2008a; Paudel et al. 2020; Parajuli et al. 2021; RP and KA personal observations and interactions with local healers).

Our findings showed variable effects on phylogenetic diversification within shrubs for both all species and the human-valued species recorded in the study area. *Berberis* supports communities with diverse evolutionary relationships specifically in the lower elevations, particularly for human-valued taxa, with shrub patches supporting more evolutionary diverse assemblages across both deep and shallow phylogenetic scales. This pattern is reflected in lower NRI and NTI values at low elevations, indicating reduced phylogenetic clustering among both distant and closely related taxa, which is further supported by the higher value of SES.PD. Nurse plants are known to promote phylogenetic diversity in environmentally severe ecosystems such as alpine, arid and dryland sites on several continents (Pistón et al. 2016; Pashirzad et al. 2019; Bashirzadeh et al. 2022), as well as degraded lands like mining fields in Spain (Navarro-Cano et al. 2016). *Berberis* is recognized for its botanical nursing effects enhancing species richness in stressful environments of the Himalayas, including more sensitive subsets of plant diversity such as the human-valued commercial and conservation priority species (Parajuli et al. 2021). Our finding evidenced that facilitation by nurse shrubs is effective in preserving phylogenetic diversity particularly in the lower elevation alpine areas, implying its critical role in conserving evolutionary legacies and adaptations unique to the Himalayan environments. However, our results also suggest that at high elevation, where more stressful conditions prevail, environmental filtering probably was more dominant resulting into phylogenetic clustering within nursed microhabitats underneath *Berberis*. Our findings are consistent with Le Bagousse-Pinguet et al. (2018), who also reported random patterns in highly stressful environments of Karakoram Mountain Range, including tendencies of phylogenetic evenness with increasing elevation.

In addition to protection from herbivory, facilitation by *Berberis* shrubs may also result from abiotic facilitation due to microhabitat amelioration within its canopies. Compared to adjacent open areas, habitat patches created by *Berberis* tend to be comparatively richer in nutrients with higher litter accumulation beneath their canopies (Parajuli et al. 2021), thus preserving soil moisture content and maintaining nutrient cycling (Callaway

2007). The higher litter thickness within *Berberis* canopies often directly translates into higher soil organic carbon contents (Parajuli et al. 2021), therefore create favorable microhabitats for beneficiary species. Those nutrient rich microenvironment facilitate the growth and survival of unique assemblage of species, thereby maintaining phylogenetic diversity in high-elevation mountains that experience a variety of abiotic and biotic stressors (Körner 2021). Phylogenetic dispersion reflects the assembly of taxa with different traits over time (Webb et al. 2002). Taxa recorded from outside of *Berberis* patches were adapted to generally uniform habitat conditions common in open areas across landscape such as low nutrient availability and high grazing pressure (Parajuli et al. 2021; RP and KA personal observations), resulting in their being more similar in their traits due to habitat filtering (Webb et al. 2002, 2006), whereas nurse shrubs facilitate species coexistence (Callaway 2007; Bulleri et al. 2016) and conserve regeneration niche of distantly related species that support higher phylogenetic diversity (Valiente-Banuet and Verdú 2007; Pistón et al. 2016).

Since at a global scale cushion plants have been found to serve as micro-refugia by facilitating less stress-tolerant lineages in severe alpine environments (Butterfield et al. 2013), the phylogenetically diverse assemblage of species found in this study (specifically in the lower alpine environment), including high value plants, beneath *Berberis* confirms that nurse shrubs perform that important role in the Nepal's Himalayas. Maintaining phylogenetic diversity is crucial for conserving evolutionary traits that are suited to diverse microclimates and, importantly, can withstand adverse conditions prevalent in the high mountain ecosystems (Faith 1992; Körner 2021). Moreover, preserving high phylogenetic diversity, specifically those of the habitat specialists, medicinal, endemic and endangered species that tend to have narrow niche space (Ahmad et al. 2021; Shrestha et al. 2022b), is critically important in the context of ongoing climate change and its some of the worsts impacts experienced in the Himalayas (Xu et al. 2009; Ahmad et al. 2025). Additionally, high-value medicinal and aromatic plants in Nepal's Himalayas are experiencing extreme pressure due to overexploitation, triggering population decline and increased extinction risk (Shrestha et al. 2022b; Khakurel et al. 2024) which further reinforces the need to conserve phylogenetically diverse communities supported by nurse shrub.

Conclusions

Our findings clearly show that facilitation by nurse shrubs functions as a nature-based approach to conserving valuable plant diversity, while also sustaining the human-nature relationships that have been established

in mountain environments for centuries. Facilitation by *Berberis* not only enhances plant diversity, contributing to local, beta, and landscape-scale gamma diversity, but also helps conserve taxa endemic to the Himalayas and those of high value to humans, while supporting sustainable ecosystem services in this region. Our results highlight the importance of the facilitative effects of shrubs in maintaining phylogenetic diversity, particularly in lower elevation Himalayan alpine region. Phylogenetically diverse communities preserve evolutionary history and adaptive potential, both of which are important for maintaining resilient ecosystems in rapidly changing environments (Faith 1992), and also maintain known and unknown biodiversity functions that may hold ecological or utilitarian value while providing provisioning or cultural services to people (Cardillo 2023). *Berberis* promotes more evolutionarily diverse communities, especially at lower elevations, by maintaining assemblages that capture a wider span of the phylogenetic tree, particularly among human-valued taxa across both closely and distantly related species. These patterns imply that *Berberis* shrubs create important microhabitats that facilitate the persistence of phylogenetically diverse communities across multiple evolutionary scales. *Berberis*, therefore, by protecting phylogenetically diverse taxa under its canopy and conserving the evolutionary history shaped by plant-environment interactions in the Himalayan region, also helps maintain human-nature relationships in cultural landscapes such as those found in Langtang National Park.

Supplementary Information

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Supplementary material 1.

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Author contributions

RP and BT conceived the ideas, designed methodology and led formal analyses; RP and KA conducted field works and collected primary data; RC identified plants; RP, BT, RC and PB collated and curated data; RP and BT drafted original manuscript and CBvR led the review and editing. All authors contributed critically to the drafts and gave final approval for publication.

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Data availability

The datasets used and/or analyzed during the current study are available from the corresponding authors on reasonable request.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

We declare no competing interests.

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