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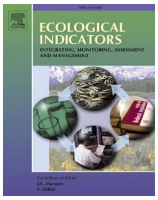

Topography mediated effect of canopy cover and light intensity explain trait variability among shrub species in Western Himalayan Forest ecosystem

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ABSTRACT

This study examines how topography (elevation and slope aspect) shapes shrub diversity and functional traits in Western Himalayan Forests. We recorded 777 individuals from nine species across 90 plots between 1500–3000 m asl. Shrub density declined significantly with elevation on north-facing slopes, while species richness and diversity peaked at mid-elevations (~2226 m asl), with higher beta diversity at higher elevations and northern aspects. Six dominant shrub species (*Sarcococca saligna*, *Prinsepia utilis*, *Berberis aristata*, *Cotoneaster bacillaris*, *Rubus ellipticus* and *Daphne papyraceae*) were selected to identify important environmental factor(s) affecting twelve plant functional traits. Trait variation revealed distinct strategies between deciduous and evergreen shrubs. Deciduous species exhibited acquisitive traits, including higher Specific Leaf Area (SLA), Leaf Phosphorus Content (LPC), and Leaf Potassium Content (LKC), while evergreen species showed conservative traits such as higher Leaf Thickness (LT), Leaf Dry Matter Content (LDMC), and Leaf Relative Water Content (LRWC), while evergreen species showed conservative traits (higher LT, LDMC, LRWC), especially at higher elevations, reflecting adaptation to environmental stress. Linear mixed-effects models explained 5–61 % of trait variability through fixed effects (stand canopy cover, light intensity, soil moisture). Structural equation models revealed that deciduous traits were more indirectly shaped via vegetation and soil feedback, while evergreen traits were tightly constrained by topography and stand canopy cover. Environmental predictors explained 63 % of vegetation structure and 50 % of trait variation. Our findings highlight the role of topography and associated environmental variables in shaping shrub communities and highlight the importance of functional trait perspectives for conservation planning in mountain ecosystems.

1. Introduction

The shrub layer plays an important role in biodiversity conservation and ecosystem functions in temperate forests (Zhou et al. 2022). While temperate forests account for around 16 % of the world's total forest cover (Hansen et al. 2010), their understorey vegetation contributes more than 80 % of the biodiversity in such ecosystems (Gilliam 2007). Shrub species influence key ecosystem processes such as nutrient cycling, soil stabilization, and microclimatic regulation (George and Bazzaz 2014), and serve as indicators for site characteristics, overstorey regeneration patterns, and plant–soil interactions (Small and McCarthy 2002). Understorey shrub species compete with overstorey tree species for essential nutrients and resources (Coll et al. 2011). The structure and composition of understorey shrub communities are shaped by complex interactions among topography, overstorey canopy, edaphic conditions, and microclimate (North et al. 2005; Gracia et al. 2007). In montane forest ecosystems, topography (elevation and slope aspect) is a key determinant of understorey species composition and diversity (Taylor et al. 2015). Slope aspect and elevation create contrasting thermal and moisture regimes that drive fine-scale variation in species distribution and functional adaptations. North-facing slopes tend to be cooler and moister with denser canopies, while south-facing slopes are warmer and drier, often supporting more light-demanding understorey species (Sternberg and Shoshany 2001; Singh 2018). Overstorey canopy cover significantly limits light penetration, especially during the summer season allowing only 0.7 to 7 % of light to reach the ground layer

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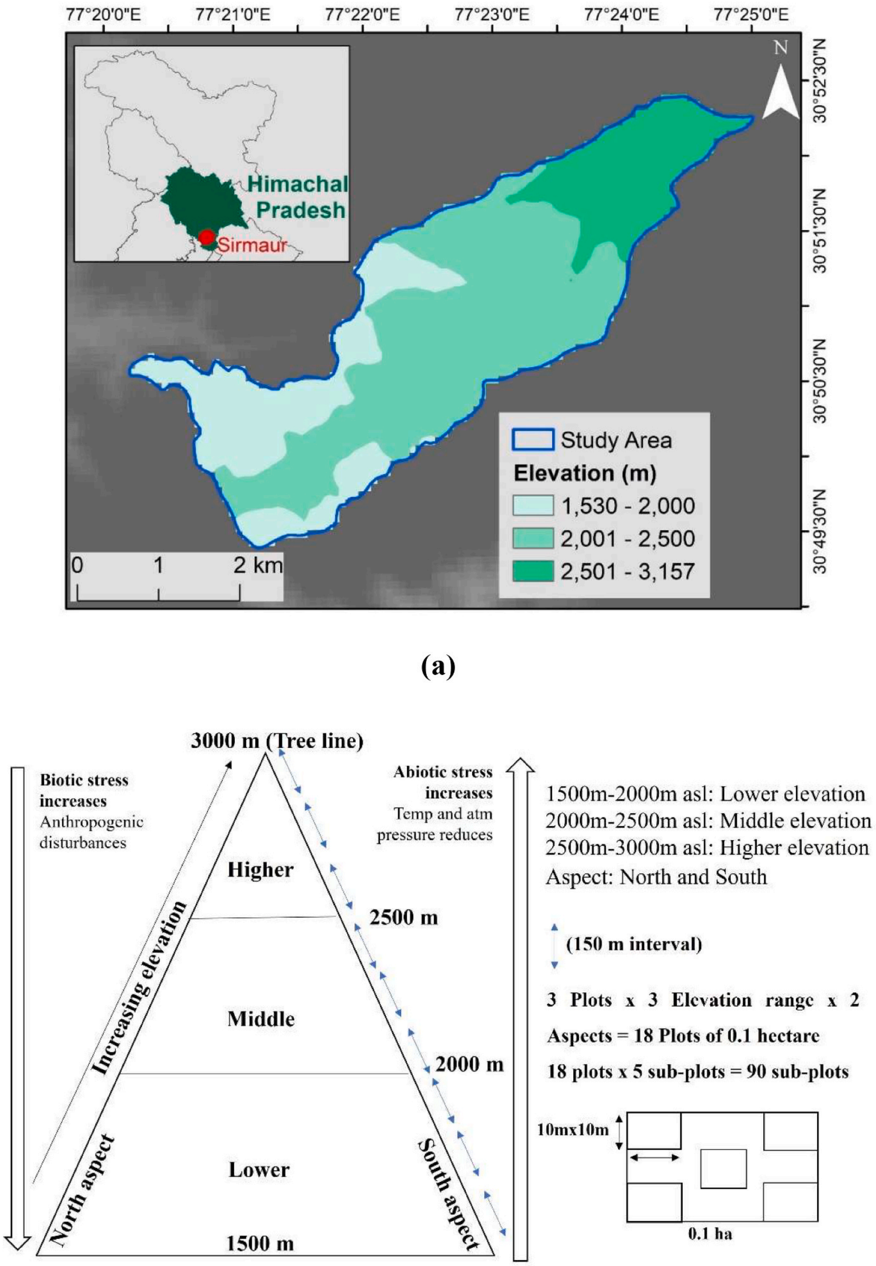
(Neufeld and Young 2003), thereby filtering understorey community composition and trait variability (Depauw et al. 2019).

Recent ecological research emphasizes the integration of functional traits with taxonomic composition to understand species–environment relationships and ecosystem functioning (Violle et al. 2007; Bruelheide et al. 2018). Functional traits link plant responses to environmental drivers and provide mechanistic insight into resource-use efficiency and resilience under environmental change (Hofhansl et al. 2020; Maes et al. 2020). Species adapt to these environmental gradients via contrasting trait strategies. Evergreen shrubs typically adopt a conservative strategy with higher leaf thickness (LT), leaf dry matter content (LDMC), and lower specific leaf area (SLA), conferring tolerance to low-resource, high-stress environments (Givnish 2002; Wright et al. 2004;). In contrast, deciduous shrubs exhibit acquisitive traits such as higher SLA and greater nutrient concentrations (LNC, LPC, LKC), facilitating rapid growth under favorable conditions (Cornwell and Ackerly 2009; Díaz et al. 2016; Shipley et al. 2006). These functional strategies are central to understanding community assembly, particularly under topographic and canopy-driven environmental filters. This approach is especially relevant in mountainous regions, where sharp gradients in climate and soil conditions produce high biodiversity and trait variability over small spatial scales (Bjorkman et al. 2018).

The Western Himalaya, part of a global biodiversity hotspot, hosts numerous endemic and rare species that are particularly sensitive to environmental changes (Tewari et al. 2017; Pandey et al. 2024). Despite its ecological significance, research on the functional responses of understorey shrub species to topographic heterogeneity remains limited. Few studies have examined how deciduous and evergreen shrub species



(a)

(b)

Fig. 1. (a). Study area in Swana Reserved Forest in Sirmour district, Himachal Pradesh, India. **(b).** Schematic diagram representing the stratified sampling design across three elevational zones: lower (1500–2000 m), middle (2000–2500 m), and higher (2500–3000 m) elevations, on both north- and south-facing aspects.

differ in their trait-environment relationships along elevational and aspect gradients (Kermavnar and Kutnar 2020). This limits our ability to generalize how vegetation responds to climate change across mountain ecosystems. To address these gaps, we investigated how topography, stand structure, and resource availability shape shrub community composition and functional trait variability in temperate forests of the Western Himalaya. The specific objectives were to: (i) assess patterns of shrub species composition and diversity across topographical gradients (changing elevation and slope aspect), (ii) analyze plant trait variability in response to changing elevation and slope aspect, and (iii) identify the key environmental factors driving trait variability and the assembly of shrub communities, with particular focus on evergreen vs. deciduous functional strategies. We hypothesized that shrub species diversity and distribution patterns would be highly responsive to local-scale topographical variations. Furthermore, we hypothesized that local heterogeneity in resource availability, coupled with associated topographical features, would play a substantial role in driving the taxonomic diversity and functional trait composition of understorey shrub species (Cheng et al. 2022; Cuesta et al. 2023). We further expected evergreen and deciduous shrubs to exhibit distinct functional responses reflecting their respective conservative and acquisitive strategies, consistent with the leaf economics spectrum (Díaz et al. 2007). By combining taxonomic and trait-based approaches across topographic gradients, this study offers new insights into the ecological strategies governing understorey plant communities in Himalayan forests. These findings contribute to a broader understanding of plant adaptation in mountain ecosystems and provide a foundation for biodiversity conservation and trait-informed forest management under global change.

2. Materials and methods

2.1. Study area

The present study was conducted in the Swana Reserved Forest (30° 86'N – 31°01́ N and 77° 38' E - 77°49́ E), a protected area in the Rajgarh range of Sirmour district, Himachal Pradesh (Fig. 1). The climate of the study site exhibits considerable variability, transitioning from moderate to cold at mid-elevations and extremely cold at higher elevations. Temperatures typically vary from a minimum of around 2 °C during winter to a maximum of approximately 30 °C during summer, with annual precipitation averaging about 1250 mm (Fig. S1) (District Survey Report 2016). The elevation ranges from around 1500 m to 3100 m asl. At elevations less than 2000 m, the parent rock materials predominantly consist of phyllite, schist, and quartzite, resulting in soil types ranging from clayey to sandy loam. In contrast, elevations greater than 2000 m are characterized by dominant rock types such as granite, gneiss, micaceous, and schist, accompanied by soil types that vary from shallow to moderately deep clay loam. Higher elevations, typically above 2000 m, exhibit brown and podzol soils (Rawat et al. 2010). The study area is classified as Group 12- Himalayan moist-temperate forest (Champion and Seth 1968**)**. *Cedrus deodara*, *Pinus roxburghii*, *Quercus floribunda, Q. leucotrichophora*, *Abies pindrow, Picea smithiana,* and *Rhododendron arboreum* are dominant vegetation, with *Q. semecarpifolia* forming the treeline community (~3000 m) (Singh et al. 2023).

2.2. Sampling design

Shrubs were defined as woody species with several branches arising from the base or absence of a distinct main axis (Saxena and Singh 1982). Shrub species were sampled in August-September 2019, during their peak growth period. A stratified sampling approach was used to study shrub floristic composition, diversity and trait variation along a topographical gradient in the study area. Eighteen stands were selected along elevational gradients and contrasting slope aspects (north and south). Stands of 0.1 ha (~31.62 m × 31.62 m) were established at an elevational distance of 150 m (Fig. 1). Tree density, basal area and diversity indices were calculated for each stand following (Curtis and Mcintosh 1950;Shannon and Weaver 1949, Margalef 1973).Within each stand, five plots of 10 m × 10 m were laid around every four corners and one at the centre (total = 90 plots) to determine shrub species composition and abundance. Slope angles were determined using a clinometer and ranged from 14° to 40°. Elevation and geographical coordinates were determined using Garmin GPS device. Slope aspect azimuth measurements were conducted using a magnetic compass. Stand canopy cover was estimated using a spherical densiometer, following Lemmon (1956), while Relative radiation intensity (RI) was calculated using Vetaas (1992). Detailed stand-level information are provided in Table 1.

2.3. Shrub species composition and trait analysis

Species identification was conducted using the Glossary of Forest Flora available at the Sirmour district Forest Department at the Forest Division, Rajgarh (Kaur and Sharma, 2004). Within each plot, shrub individuals were recorded, and the diameter of each individual was measured 8 cm above ground level using a vernier caliper. Density, frequency, and abundance were determined following Curtis and McIntosh (1950). Shannon-Wiener diversity index (H') was calculated following Shannon and Weaver (1963), Species evenness or equitability (SE) following Pielou (1966), while species richness (SR) was determined using Margalef's index given by (Magurran, 1988). The rank abundance curve was plotted for the pooled site data using BiodiversityR package (Kindt 2020) (Fig. S2). The six most dominant shrub species viz., *Sarcococca saligna* (SS), *Prinsepia utilis* (PU), *Berberis aristata* (BA), *Cotoneaster bacillaris* (CB), *Rubus ellipticus* (RE), and *Daphne papyraceae* (DP) were selected to further analyze key environmental factors driving trait variability and associated vegetation attributes. Shrub species were grouped as evergreen (*Sarcococca saligna*, *Daphne papyracea*, *Berberis aristata*) and deciduous (*Prinsepia utilis*, *Cotoneaster bacillaris*, *Rubus ellipticus*) based on their leaf-shedding behaviour. For each dominant shrub species, five individuals were sampled per plot, resulting in 327 individuals from 90 plots (18 stands). Twelve plant traits were assessed for each individual which were expected to respond to environmental condition along the altitudinal gradient. Plant Height (HT) was measured using a measuring tape, and Crown Cover (CC) was determined using the line-intercept method (Gray et al. 2021). From each shrub individual, ten fully expanded leaves with minimal herbivore or pathogen damage were sampled. Fresh weight of the samples was determined using a portable weighing balance after drying the leaves with blotting paper to eliminate moisture. Leaf Area (LA) was measured using a leaf area meter (LICOR, LI-3000C). Leaf samples were then oven-dried at 60 °C for 72 h to determine dry weight, which was used to calculate Specific Leaf Area (SLA) and Leaf Dry Matter Content (LDMC). Leaf Thickness (LT) of fresh leaf samples was measured using a screw gauge micrometer. Leaf Relative Water Content (LRWC) was determined following Stocker's method (Anderson and McNaughton 1973) in which weighed leaves were saturated for four hours by keeping in water at room temperature, and weight of leaf was taken again. After oven drying leaves at 60 °C for 72 h, the dry weight was taken and LWC was calculated as:

$$\mathrm{LRWC} = \frac{\text{fresh weight} - \text{dry weight}}{\text{saturated weight} - \text{dry weight}} \, X\,100$$

Leaf pH was calculated following Jackson (1973) in which dried leaves were grinded to a fine powder. Five grams of the dried leaf powder was diluted with 25 ml double distilled water and was shaken on a shaker for 30 min. Further, Leaf pH was calculated using pH meter. To analyze Leaf Nitrogen and Phosphorous Content, dried leaves were grinded into a fine powder. Leaf Carbon and Nitrogen Content (LCC and LNC) was analyzed using the Dumas combustion technique with an elemental analyzer CHNS (Euro, EA-3000). Leaf Potassium Content (LKC) were analyzed using flame photometer (766 nm) (Okalebo et al. 2002). Leaf Phosphorus Content (LPC) was measured following

Table 1

Plot-level information from the study site. Elevation in meters (m), Relative Radiation Intensity: Light Intensity (RI, unitless), Water availability as a proxy to Soil Moisture Content (SMC, %), Stand Canopy Cover in %, Slope Angle, Aspect azimuth, Latitude and Longitude in degree (°), Tree Density (ind ha^{-1}), Tree Basal Area (m^2 ha^{-1}) and Tree Shannon diversity (H') and Species richness (SR).

Plot	Elevation (m asl)	Aspect	Slope	Aspect azimuth	Latitude	Longitude	Relative Radiation Intensity	SMC	Stand Canopy Cover	Tree Density	Tree Basal Area	Tree H'	Tree SR
1	1592	North	26	327°NW	30°51′51′’N	77°21′37′’E	0.87	10.33	56.68	430	10.81	0.11	2
2	1684	South	27	186°S	30°51′16′’N	77°21′41′’E	−0.9	11.88	48.57	340	27.71	0.22	2
3	1785	North	37	14°N	30°51′33.30′’N	77°21′41.79′’E	0.028	22.82	88.9	660	40.07	0.49	2
4	1785	South	40	210°S	30°51′31.04′’N	77°21′41.18′’E	−0.5	21.86	28.08	530	53.65	0.87	7
5	1980	North	29	307°NW	30°51′41.51′’N	77°22′05.87′’E	−0.34	19.58	49.23	740	35.63	0.01	1
6	2007	South	31	169°S	30°51′43.40′’N	77°22′12.52′’E	0.56	31.25	81.25	580	19.48	0.58	9
7	2144	North	18	315°NW	30°51′37.02′’N	77°22′35′’E	−0.18	13.99	86.23	850	61.35	0.88	2
8	2149	South	27	180°S	30°51′54.30′’N	77°22′39.30′’E	−0.93	12.69	81.65	360	15.07	1.15	4
9	2260	North	14	348°N	30°51′55.80′’N	77°22′68.70′’E	0.14	24.57	88.63	860	58.3	1.14	4
10	2226	South	28	278°S	30°51′54.40′’N	77°22′6720′’E	−0.46	15.9	89.25	320	17.86	1.96	6
11	2400	North	37	349°N	30°51′61.30′’N	77°23′0070″E	0.87	9.66	86.58	780	70.66	0.59	2
12	2400	South	32	170°S	30°51′61.30′’N	77°23′0070″E	0.87	11.87	87.52	740	67.92	0.66	2
13	2562	North	28	352°N	30°51′48.6′’N	77°23′20.04′’E	−0.44	35.88	92.55	630	59.4	0.58	2
14	2562	South	29	198°S	30°51′48.6′’N	77°23′20.04′’E	−0.11	17.04	87.74	580	57.31	0.51	2
15	2703	North	27	340°N	30°51′8270′’N	77°23′5240′’E	0.55	23.18	94.67	950	81.39	0.82	3
16	2700	South	28	219°SW	30°51′7900′’N	77°23′5700′’E	−0.65	21.62	82.55	880	52.07	0.95	3
17	2850	North	31	205°NW	30°52′02.20′’N	77°23′79.60′’E	0.88	38.42	93.16	930	71.35	0.42	1
18	2850	South	27	138°SE	30°51′95.60′’N	77°23′76.20′’E	0.12	32.15	94.56	1040	47.56	0.01	1

digestion with a tri-acid mixture (conc. H_2SO_4, HNO_3 and $HClO_4$ in 1:5:1 ratio) heated at 90 °C until a milky white slurry formed (Allen et al. 1986). Samples were then rinsed with 5 ml of a 1:1 HCl and distilled water solution. LPC was quantified colorimetrically by digesting samples with nitric acid and perchloric acid (3:1 ratio), with absorbance measured after 10 min at 420 nm using a spectrophotometer (blue filter) (John 1970).

2.4. Edaphic variables

Soil core samples were collected from each plot at depths of 0–10, 10–20, and 20–30 cm using a soil corer with an inner diameter of 5 cm and transported to the laboratory. Soil moisture content (SMC) was determined gravimetrically by oven drying 10 g of soil at 105 °C for 48 h (Misra 1968). Soil bulk density (BD) was determined from the undisturbed core segments as dry soil mass per unit volume (Ingram and Anderson 1993). Soil pH was measured using a multi-parameter ion meter (pH/Cond 340i SET 1) in a 1:2.5 dry soil: water solution ratio (Jackson 1973). Particle size distribution was analyzed using the Bouyoucos hydrometer method, employing a 10 % Calgon solution (sodium hexametaphosphate) as described by (Okalebo et al. 2002). Soil organic carbon (OC) was estimated through the dichromate oxidation method, using a 1 g air-dried soil sample and subsequent titration with ferrous sulfate ($FeSO_4$), following modification to the Walkley and Black procedure (1943). Total nitrogen (TN) content was quantified by digesting a 3 g soil sample with concentrated sulfuric acid (H_2SO_4) and a catalyst mixture of K2SO4:CuSO4, following which analysis was performed using a Micro-Kjeldahl apparatus (Jackson 1973). Available potassium (K) was extracted using the neutral ammonium acetate method (Morwin and Peach 1951) and measured with a flame photometer. Available phosphorus (AP) was quantified colorimetrically by treating the soil with Bray reagent (0.025 N HCl mixed with 0.03 N NH4F in a 1 N sulfuric acid solution), and absorbance was recorded spectrophotometrically at 420 nm (blue filter) (Bray and Kurtz 1945).

2.5. Data analysis

Data normality was assessed using the Shapiro–Wilk test, and homogeneity of variance using Levene's test. Additionally, assumptions of linearity and homoscedasticity were checked prior to performing linear regression analyses. To analyze the effect of topography (slope aspect and elevation) on shrub species composition and diversity (Objective 1), we used linear regression models. Significant differences were reported at $p < 0.05$ and visualized using ggplot2 package. Trait variation along the elevational gradient (Objective 2) was also analyzed using linear regression models, with the Benjamini-Hochberg procedure employed to control the false discovery rate, minimizing Type I errors (Benjamini and Hochberg 1995). Principal Component Analysis (PCA) was used to analyze the effect of species on trait variation and to reduce data dimensionality. The ggfortify package was used to select important traits based on PCA loadings (Table S1). To identify the biotic/abiotic factor(s) that explained shrub species distribution in the region (Objective 3), linear mixed models (LMMs) were applied, with plant functional traits as the response variable, environmental factors as explanatory variables, and plots as random variable. Multicollinearity among environmental and soil variables was assessed using the Variance Inflation Factor (vif) test (threshold: vif < 5) through the car package. The selected environmental variables included functional group, light intensity (RI), stand canopy cover, soil phosphorous and soil water availability (SMC) (Table 1). Starting with a saturated model that included all parameters, predictors were sequentially removed until arriving at a final model with the lowest Akaike Information Criterion (AIC) value. The contributions of fixed effects alone (R^2_m, marginal R^2) and combined fixed and random effects (R^2c, conditional R^2) in explaining variability in functional traits were evaluated using coefficients of determination calculated via the MuMIn package (Nakagawa and Schielzeth 2013). To mechanistically explain the direct and indirect effects of environmental variables on plant traits, structural equation modeling (SEM) was conducted using piecewiseSEM package (Lefcheck et al. 2016). Principal Component Analysis (PCA) was conducted to derive the first principal component axis representing plant traits for both deciduous and evergreen species separately. An additional PCA was performed to minimize multicollinearity among soil and vegetation variables along environmental gradients, resulting in derived principal components used in subsequent SEM analyses. Vegetation structure and soil traits were grouped according to whether the plot was dominated by deciduous or evergreen shrub species, to match trait-based analyses. The best model was selected based on lowest AIC value. The model was used to investigate statistically significant relationships among ecological pathways, partitioning direct and indirect relationships using path analysis (Bu et al. 2019). The model was consistent with the data if the chi-squared test of Fisher's C statistic did not indicate significance ($p < 0.05$). All statistical analyses were conducted using R version 4.3.2 (R Core Team 2018).

3. Results

3.1. Spatial pattern of understorey shrub abundance and diversity

A total of 777 individuals belonging to nine species were recorded across ninety plots in the study area. Shrub density declined significantly with elevation ($R^2 = 0.48$, $p = 0.03$) on the northern aspect with maximum density recorded at 1980 m (1350 ind ha^{-1}) and minimum at 2850 m (50 ind ha^{-1}). H' ($R^2 = 0.47$, $p = 0.03$) and SR ($R^2 = 0.38$, $p = 0.03$) increased significantly with elevation on northern aspect. Southern aspect exhibited higher H' (1.08) and SR (2.6), with peak values at 2226 m asl (Fig. 2). Beta diversity (β-diversity) was highest at higher elevations, 2500–3000 m (0.52), followed by lower, 1500–2000 m (0.38) and middle elevations, 2000–2500 m (0.35). Aspect-wise, β-diversity was significantly greater on the northern aspect (0.56) compared to the southern aspect (0.45) (Fig. S3). Soil properties exhibited contrasting responses to elevation, aspect, and depth (Fig. S4). On north-facing slopes, SMC showed a strong positive relationship with elevation ($R^2 = 0.36$, $p < 0.001$), OC and Na content significantly increased with elevation on both aspects (OC: $R^2 = 0.40$–0.47, $p < 0.001$; Na: $R^2 = 0.42$–0.48, $p < 0.001$) and decreased with soil depth. Available K increased significantly with elevation on north-facing slopes ($R^2 = 0.45$, $p < 0.001$), and decreased with increasing depth, while Available P increased significantly only on south-facing slopes ($R^2 = 0.18$, $p = 0.02$). Other soil properties, including bulk density (BD), pH, sand, silt, clay, and total nitrogen, did not show significant trends with elevation across either aspect, suggesting limited elevational influence.

3.2. Plant trait variation along elevational gradient

Functional trait variation along the elevational gradient revealed distinct patterns between deciduous and evergreen shrubs and across north- and south-facing aspects (Fig. 3). Deciduous shrubs exhibited a significant increase in HT with elevation ($R^2 = 0.11$, $p < 0.01$), while evergreens showed a decline ($R^2 = 0.10$, $p < 0.01$). CC declined significantly in deciduous species ($R^2 = 0.07$, $p < 0.01$) and marginally in evergreens ($R^2 = 0.08$, $p = 0.014$) with highest coefficient of variation (CV) in *Sarcococca saligna* (121.83 %) and the lowest in *Daphne papyraceae* (19.45 %) (Table S2). Similarly, LA decreased significantly with elevation in deciduous species ($R^2 = 0.31$, $p < 0.01$), particularly on the south-facing slope ($R^2 = 0.16$, $p < 0.001$) (Table S3). LT increased in both deciduous and evergreen ($R^2 = 0.46$ and 0.27, $p < 0.01$) shrubs, with stronger trends on the north-facing slope. SLA increased with elevation in evergreens ($R^2 = 0.14$, $p < 0.01$) and deciduous species (R^2

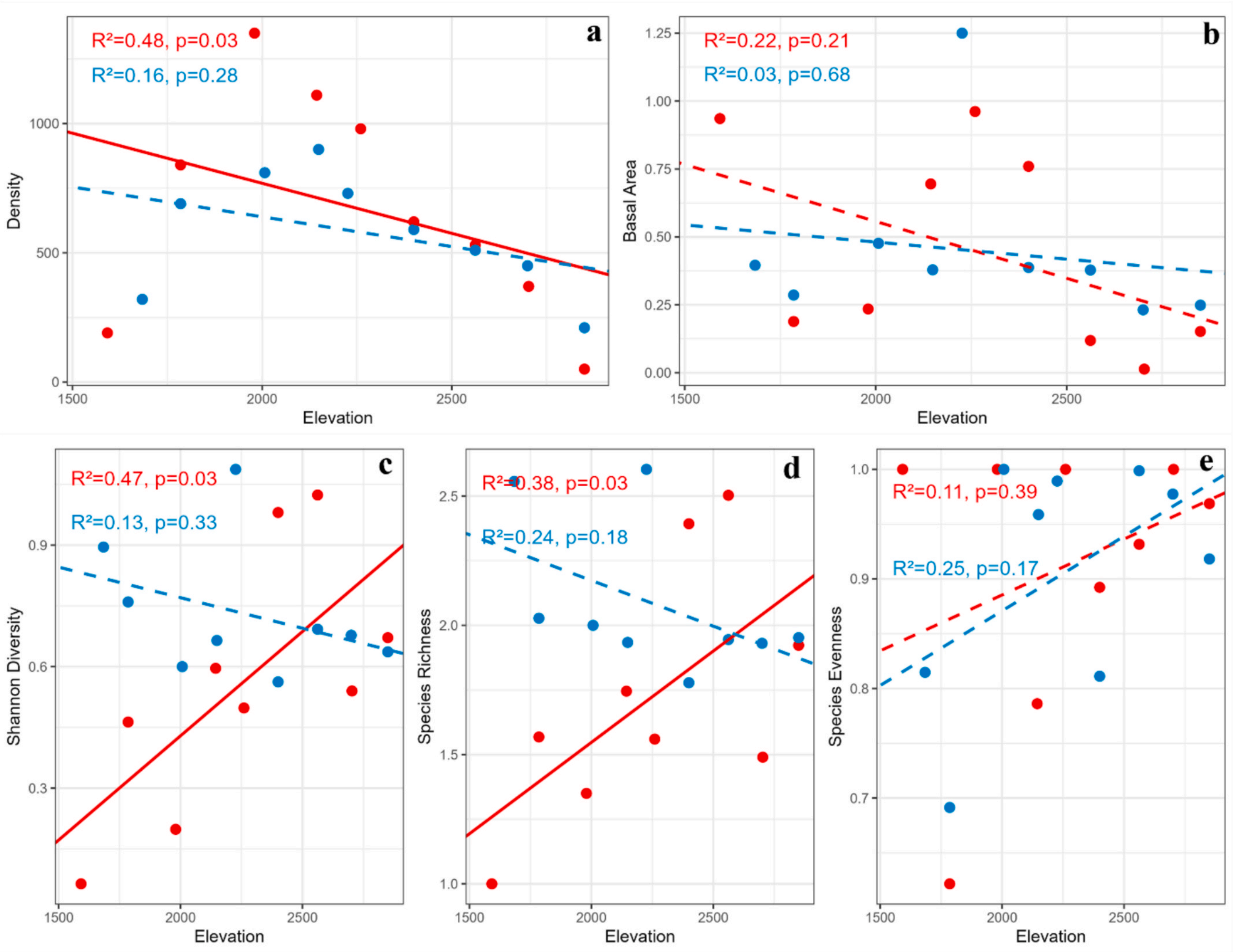


Fig. 2. Variation in shrub Density (individuals ha^{-1}), Basal Area (m2 ha^{-1}), and diversity indices: Shannon Diversity (H′), Species Richness, and Species Evenness, along an elevational gradient (1500–3000 m asl) across slope aspects: north-facing (red) and south-facing (blue) slopes. Solid lines represent significant trends ($p < 0.05$), and dashed lines indicate non-significant relationships. R^2 and p-values for each aspect are shown within each panel. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

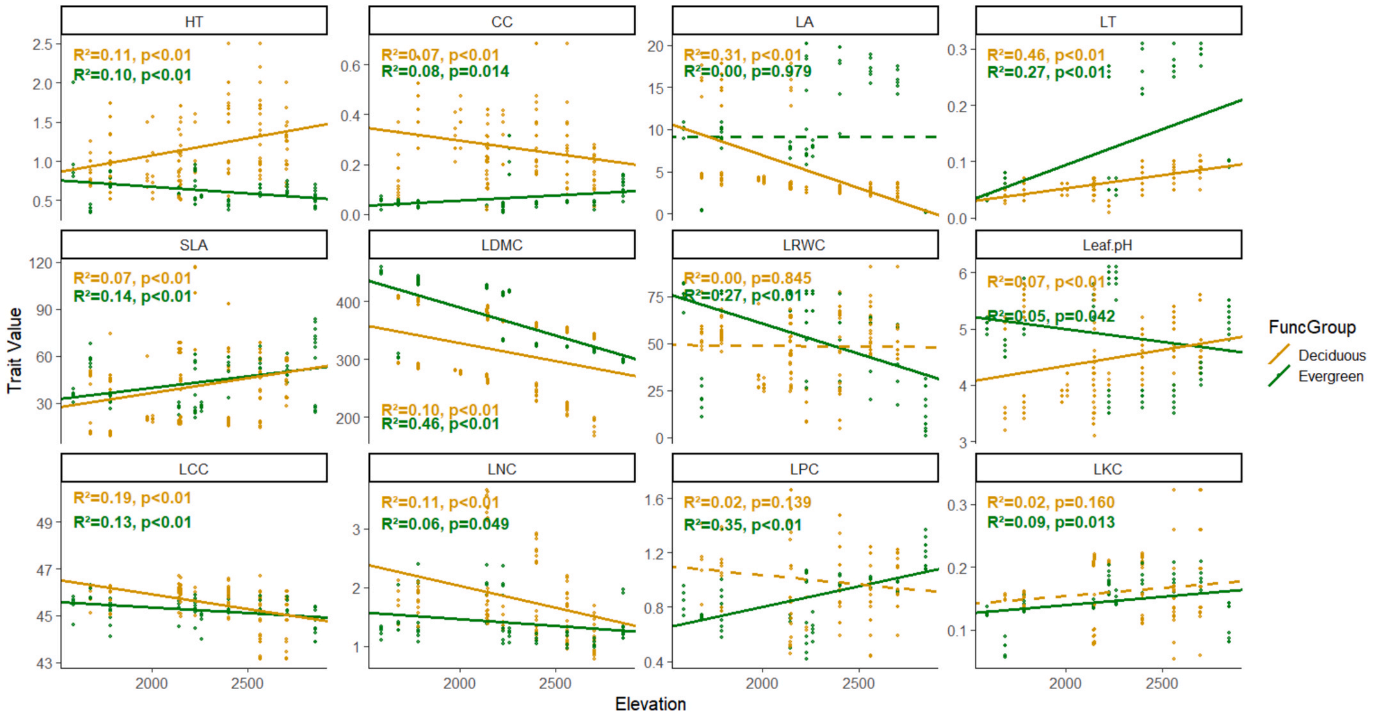


Fig. 3. Trait variation of dominant shrub species across increasing elevation (1500–3000 m asl) and functional groups (FuncGroup): Deciduous (orange) and Evergreen (green). Traits include: Plant Height (HT; m), Crown Cover (CC; m^2), Leaf Area (LA; cm^2), Leaf Thickness (LT; mm), Specific Leaf Area (SLA; $cm^2\ g^{-1}$), Leaf Dry Matter Content (LDMC; mg g^{-1}), Leaf Relative Water Content (LRWC; %), Leaf pH (unitless), Leaf Carbon Content (LCC; %), Leaf Nitrogen Content (LNC; %), Leaf Phosphorus Content (LPC; %), and Leaf Potassium Content (LKC; %). Solid lines denote significant ($p < 0.05$) and dashed lines non-significant trends from linear models; R^2 and p-values are displayed accordingly for each group. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

$= 0.07$, $p < 0.01$) notably on north-facing slope ($R^2 = 0.18$, $p < 0.001$) ranging from 49.34 in *B. aristata* to 180.5 in *C. bacillaris*. LRWC declined only in evergreen shrubs ($R^2 = 0.27$, $p < 0.01$), with a significant trend on the north-facing slope ($R^2 = 0.18$, $p < 0.001$). Leaf pH showed a decreasing trend with elevation in evergreen ($R^2 = 0.05$, $p = 0.04$) and increasing trend in deciduous species ($R^2 = 0.07$, $p < 0.01$). Among chemical traits, LCC declined significantly with elevation in both deciduous ($R^2 = 0.19$, $p < 0.01$) and evergreen ($R^2 = 0.13$, $p < 0.01$) species. This trend was most pronounced on the south-facing slope ($R^2 = 0.29$, $p < 0.001$). LCC showed the strongest decline in *C. bacillaris* and *B. aristata*. Similarly, LNC showed a decreasing trend, more evident in deciduous shrubs and on the north-facing slope ($R^2 = 0.08$, $p = 0.008$). In contrast, LPC and LKC increased significantly only in evergreens species ($R^2 = 0.35$, $p < 0.01$) and ($R^2 = 0.09$, $p = 0.013$). Principal Component Analysis (PCA) further confirmed the functional divergence between deciduous and evergreen shrubs (Fig. 4). The first two PCA axes explained 39.8 % of the total trait variance, with deciduous species clustering around traits such as SLA, LPC, LNC and LKC, while evergreens aligned with traits like LDMC, LA, LT, LRWC, and Leaf pH. These variations in species level and group level responses across topographical gradient reflect ecophysiological adaptations with changing environment.

3.3. *Determinants of plant functional trait variation*

The fitted LMMs explained a significant proportion of functional trait variability through the environmental predictors and the functional group (Table 2). Fixed effects (R^2_{marginal}) ranged from 5 % (LPC) to 61 % (CC), while both fixed and plot (random) effects ($R^2_{\text{conditional}}$) varied between 19 % (SLA) and 84 % (CC), indicating significant influences of functional group and environmental predictors on shrub functional traits. Evergreen species had significantly lower HT (–0.26 ± 0.01, $p < 0.001$), CC (–1.8 ± 0.05, $p < 0.001$), LNC (–0.02 ± 0.004, $p < 0.001$), and LPC (–0.011 ± 0.002, $p < 0.001$), but higher LA (0.52 ± 0.05, $p < 0.001$), SLA (0.18 ± 0.05, $p < 0.001$), LDMC (0.11 ± 0.02, $p < 0.001$), and LT (0.67 ± 0.04, $p < 0.001$). Stand Canopy Cover negatively influenced LA (–0.32 ± 0.15, $p < 0.05$), SLA (0.12 ± 0.06, $p < 0.05$), LDMC (–0.06 ± 0.03, $p < 0.01$), and LT (0.23 ± 0.11, $p < 0.01$). Additionally, Available Phosphorus positively affected SLA (0.07 ± 0.01, $p < 0.05$), though with relatively modest explanatory power (6 %/19 %). The models showed the highest explanatory power for CC (R^2m/c = 61 %/84 %) and LT (32 %/67 %), underscoring strong trait–environment interactions linked to functional group and Stand Canopy Cover, with soil moisture and phosphorus availability contributing to specific traits like SLA. Structural Equation Modeling (SEM) revealed distinct pathways driving trait variation in deciduous and evergreen shrub species (Fig. 5a and b). In deciduous species, vegetation structure (Veg_PC1) was negatively influenced by Topography ($\beta = –0.54$, $p < 0.001$) and positively by Stand Canopy Cover ($\beta = 0.38$, $p < 0.001$), with indirect effects from soil properties (Soil_PC1; $\beta = –0.14$, $p < 0.05$). Topography also had a direct positive effect on soil properties ($\beta = 0.44$, $p < 0.001$). In contrast, evergreens showed stronger responses. Topography ($\beta = –0.92$, $p < 0.001$) and Stand Canopy Cover ($\beta = 0.99$, $p < 0.001$) together explained 63 % of variation in vegetation structure. Trait expression (Trait_PC1) was positively associated with Topography ($\beta = 0.38$, $p < 0.001$) and Veg_PC1 ($\beta = 0.48$, $p < 0.001$), but negatively with Stand Canopy Cover ($\beta = –0.96$, $p < 0.001$). Soil properties were shaped by Topography ($\beta = 0.73$ and Stand Canopy Cover ($\beta = –0.19$), together explaining 50 % of variation. These findings highlight contrasting strategies that deciduous species respond more to vegetation and soil feedback, while evergreen traits are tightly linked to topography and overstorey conditions.

4. Discussion

Forest structure and diversity exhibited divergent responses to

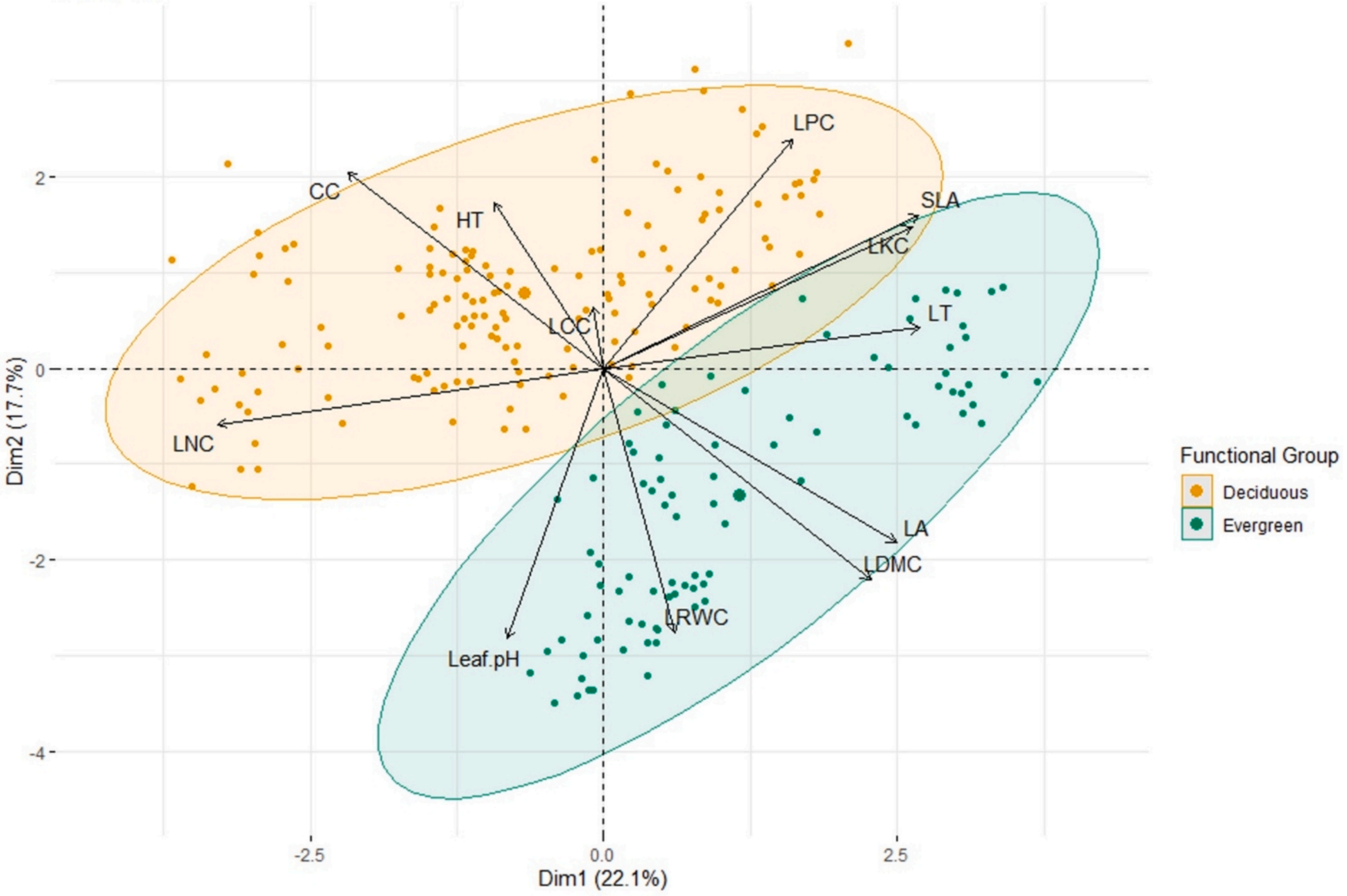


Fig. 4. Principal Component Analysis (PCA) biplot showing the functional trait space of dominant shrub species, grouped by functional type, deciduous (orange) and evergreen (green). Trait vectors represent correlations between traits and PCA axes. Deciduous species cluster around acquisitive traits such as specific leaf area (SLA), leaf phosphorus content (LPC), leaf potassium content (LKC), crown cover (CC), height (HT), and leaf nitrogen content (LNC), while evergreen species are associated with conservative traits like leaf area (LA), leaf dry matter content (LDMC), leaf thickness (LT), leaf relative water content (LRWC), and leaf pH. Ellipses indicate 95% confidence intervals for each functional group. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

elevation across slope aspects. North-facing slopes showed a sharper decline in shrub density and basal area with elevation, suggesting stronger environmental filtering (Candeias and Fraterrigo 2020). In contrast, south-facing slopes displayed greater structural and compositional stability, reflecting more favorable microclimatic conditions. This likely results from microclimatic and edaphic differences between aspects influencing community assemblage, species turnover and productivity (Pauw et al. 2021). Functional trait patterns further revealed contrasting strategies across topographic gradients: evergreens at higher elevations showed conservative traits (higher LT, LDMC, and LRWC), whereas deciduous shrubs at lower elevations exhibited acquisitive traits (higher SLA, LPC, and LKC), reflecting distinct ecophysiological adaptations along topographic and environmental gradients (Bai et al. 2015).

Shrub basal area and density peaked at mid-elevation sites, suggesting that both low- and high-elevation sites present harsher conditions for shrub growth. At lower elevations, increased anthropogenic pressure and grazing negatively impact shrub abundance, while at higher elevations, lower temperatures and reduced atmospheric pressure constrain growth (Moles et al. 2014; Singh et al. 2021). Lower atmospheric pressure at higher elevations can constrain shrub species growth through its negative effects on plant ecophysiological processes. Reduced atmospheric pressure decreases the partial pressure of CO_2, which in turn lowers the rate of photosynthesis, reduces stomatal conductance efficiency, and can hamper aboveground biomass production, ultimately affecting plant growth and survival, especially in species with limited physiological plasticity (Körner 2007). At the same time dense overstorey canopy cover limits light availability further constraining shrub species growth. Although direct assessment of disturbance was beyond the study’s scope, these results align with the intermediate disturbance hypothesis (Connell 1978), which proposes that species richness and productivity are maximized at moderate disturbance levels. Higher elevations showed the lowest values for density and basal area, despite high levels of organic carbon and soil nutrients (Singh et al. 1994; Singh 2021). This could be attributed to inadequate sunlight availability due to increased stand canopy cover formed by higher tree density (Måren et al. 2015; Singh 2023). These results are consistent with a study conducted in sub-alpine forests, which reported a decrease in density with increasing elevation (Gairola et al. 2010). Also, slope aspect did not significantly influence vegetation attributes (basal area), likely because the dense canopy hindered light penetration to the ground layer (Sharma et al. 2009). SR and H’ followed a unimodal trend, peaking around 2226 m asl, before declining at higher elevations. This pattern likely reflects stable species coexistence and favorable resource availability at mid-elevations (Dias 1996). Additionally, increasing geographic distance among sampling sites contributed to higher beta diversity (decreased similarity in plant species composition), attributed to the growing topographic and edaphic heterogeneity (Prada et al. 2017). Together, these results underscore the combined influence of elevation, slope aspect, light intensity and soil

Table 2
Summary of linear mixed-effects models examining the influence of environmental predictors and functional group on each plant functional traits. Each model includes Plot as a random effect. Shown are model coefficients (Estimate ± SE), significance levels ($p < 0.001$ ‘***’, <0.01 ‘**’, <0.05 ‘*’, 0.01 ‘.’), and marginal/conditional R^2 values [R^2(m/c)], representing variance explained by fixed effects alone and by the full model (fixed + random effects), respectively.

Trait	Predictor	Estimate ± SE	Significance	R^2 (m/c)
HT	Intercept	0.75 ± 0.02	***	33/49
	FuncGroup (Evergreen)	−0.26 ± 0.01	***	
	Light Intensity × Stand Canopy Cover	0.01 ± 0.02	n.s.	
CC	Intercept	−1.2 ± 0.13	***	61/84
	FuncGroup (Evergreen)	−1.8 ± 0.05	***	
	Light Intensity × Stand Canopy Cover	0.15 ± 0.16	n.s.	
LA	Intercept	1.52 ± 0.13	***	21/63
	FuncGroup (Evergreen)	0.52 ± 0.05	***	
	Stand Canopy Cover	−0.32 ± 0.15	*	
	Light Intensity	0.22 ± 0.15	n.s.	
SLA	Intercept	3.49 ± 0.05	***	6/19
	FuncGroup (Evergreen)	0.18 ± 0.05	***	
	SMC	−0.10 ± 0.03	.	
	Stand Canopy Cover	0.12 ± 0.06	*	
	Available Phosphorous	0.07 ± 0.01	*	
LDMC	Intercept	5.77 ± 0.02	***	15/42
	FuncGroup (Evergreen)	0.11 ± 0.02	***	
	Stand Canopy Cover	−0.06 ± 0.03	**	
LT	Intercept	−2.9 ± 0.1	***	32/67
	FuncGroup (Evergreen)	0.67 ± 0.04	***	
	Stand Canopy Cover	0.23 ± 0.11	**	
	Light Intensity	2.74 ± 0.8	.	
	Light Intensity × SMC	−0.01 ± 0.04	.	
LNC	Intercept	2.47 ± 0.006	***	12/36
	FuncGroup (Evergreen)	−0.02 ± 0.004	***	
	Light Intensity	−0.008 ± 0.006	n.s.	
LPC	Intercept	2.39 ± 0.03	***	5/25
	FuncGroup (Evergreen)	−0.011 ± 0.002	***	
	SMC	0.001 ± 0.001	n.s.	

Abbreviations: Predictor abbreviations: FuncGroup: Functional Group, SMC: Soil Moisture Content. Trait abbreviations: HT: Plant Height, CC: Crown Cover, LA: Leaf Area, SLA: Specific Leaf Area, LDMC: Leaf Dry Matter Content, LT: Leaf Thickness, LNC: Leaf Nitrogen Content, LPC: Leaf Phosphorous Content, n.s.: non-significant.

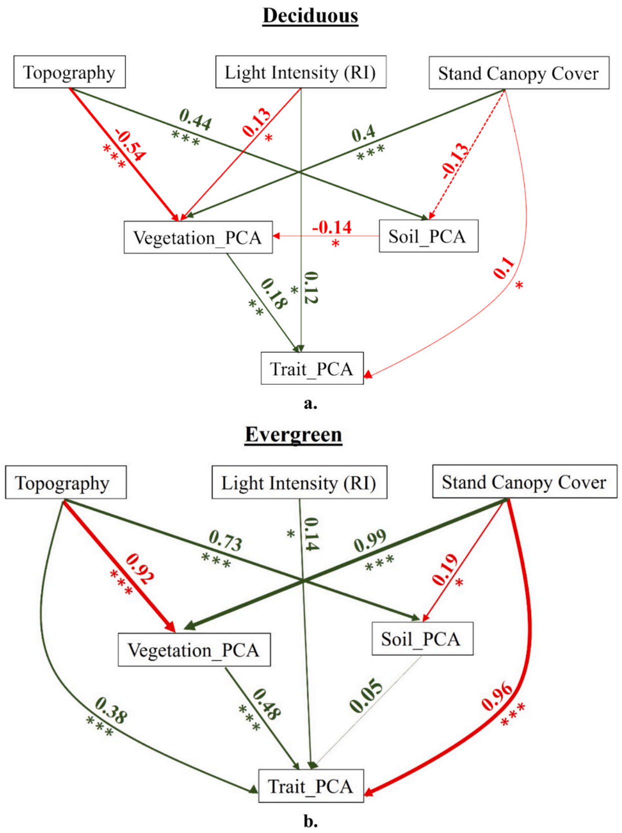


Fig. 5. Structural Equation Model framework for **a.** deciduous and **b.** evergreen shrubs showing relation between environmental gradients and vegetation parameters using plant functional traits (Trait_PC1). The model incorporates Topography (elevation, aspect), Light Intensity (RI), Stand Canopy Cover, Veg_PC1 and Soil_PC1. Red arrow indicates negative relation whereas green arrow indicates positive relation. Arrow width indicates effect strength, and numbers are significant standardized path coefficients. Asterisks denote significance levels (*$p < 0.05$; **$p < 0.01$; ***$p < 0.001$). Dashed lines indicate non-significant paths. Model fit statistics: **a.** Deciduous: Fisher’s C = 6.18, df = 6, p = 0.403; AIC = 36.18. R2 values: Trait_PC1 = 0.05, Soil_PC1 = 0.13, Veg_PC1 = 0.24. **b.** Evergreen: Fisher’s C = 7.29, df = 6, p = 0.295; AIC = 43.29. R2 values: Trait_PC1 = 0.50, Soil_PC1 = 0.50, Veg_PC1 = 0.63. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

resource gradients in shaping shrub distribution and diversity across temperate Himalayan forests.

The selection of twelve plant traits, spanning morphological (HT, CC, LA, LT), physiological (SLA, LDMC, LRWC), and chemical attributes (LCC, LNC, LPC, LKC, Leaf pH), are widely recognized to capture plant resource use strategies and responses to environmental stress. These traits are indicators of acquisitive vs. conservative strategies across environmental gradients (Díaz et al. 2022; Wright et al. 2004). Trait variation differed markedly between deciduous and evergreen shrubs, reinforcing their contrasting ecological strategies. Trait–environment relationships revealed consistent patterns across deciduous and evergreen groups. Evergreen species like *Cotoneaster bacillaris* and *Berberis aristata* showed high LDMC, LT, and LRWC, thriving under high-elevation conservative strategy suited to resource-poor and stressful environments (Rawat et al. 2020). In contrast, deciduous species such as *Sarcococca saligna* and *Rubus ellipticus* demonstrated high SLA and nutrient-rich leaf chemistry (LNC, LPC), reflecting opportunistic growth in lower elevation zones associated with resource-acquisitive strategies. Such species are adapted to maximize rapid growth and resource uptake under favorable conditions. Elevational filtering significantly shaped trait distributions. LA decreased with elevation, reflecting a global trend of smaller leaves in cooler and harsh environments to reduce thermal and mechanical stress (Wright et al. 2002). SLA was notably lower at lower elevations, where soil moisture was more limiting, indicating trait convergence under strong environmental filtering (Wellstein et al. 2017). LT increased with elevation, especially in evergreens, suggesting structural reinforcement to withstand frost and UV radiation (Vitasse et al. 2014). LNC declined with increasing light and soil moisture, indicating increased nutrient turnover under elevated irradiance and water availability (Hu et al. 2023). LPC was higher in deciduous species and associated with phosphorus-rich soils at mid elevations. LKC was generally higher in deciduous species and showed a weak positive relationship with elevation, suggesting its role in maintaining osmotic balance and metabolic flexibility under increasing abiotic stress (Li et al.

2021). This pattern supports the acquisitive strategy of deciduous shrubs, where elevated K^+ concentrations enhance stomatal regulation and photosynthetic efficiency, particularly under fluctuating light and moisture conditions commonly observed along elevational gradients (Tripler et al. 2006).

LMMs demonstrated that a substantial proportion of trait variability was explained by fixed effects such as functional group, stand canopy cover, topography, and soil variables, with marginal R^2 values ranging from 5 % (LPC) to 61 % (CC), and conditional R^2 extending up to 84 % (CC). This indicates that in addition to environmental filtering, local-scale plot heterogeneity, possibly arising from microsite variability, contributes significantly to trait variation (Shipley et al. 2006; Laughlin et al. 2021). Evergreen shrubs consistently exhibited trait values associated with resource conservation (e.g., higher LDMC, LT), while deciduous species showed traits aligned with acquisitive strategies (e.g., higher SLA, LNC, LPC). The strong negative effect of stand canopy cover on LA, SLA, and LT further supports light limitation as a key structuring force in these understorey communities (Healy et al. 2008; Wellstein et al. 2017). The SEM results revealed distinct causal pathways governing trait expression in deciduous versus evergreen functional groups. In deciduous species, trait expression was indirectly regulated by topography via its influence on soil properties and vegetation structure. This suggests that deciduous shrubs are more responsive to biotic feedbacks and microsite resource variation, consistent with their opportunistic growth and acquisitive resource-use strategy (Wright et al. 2004; Díaz et al. 2016). For instance, increased stand canopy cover enhanced structural complexity (Veg_PC1), which in turn influenced trait responses, highlighting the role of feedback-mediated niche construction in deciduous assemblages (Boyer et al. 2009; Suding et al. 2008). In contrast, trait variability in evergreen shrubs was primarily governed by abiotic drivers, particularly elevation and stand canopy cover, with limited mediation through soil or vegetation structure. The direct negative effect of canopy cover on trait expression ($\beta = -0.96$) in evergreens emphasizes their sensitivity to overstorey competition and suggests lower trait plasticity in response to environmental gradients (Givnish 2002; Körner 2012). The positive path coefficient between elevation and Trait_PC1 ($\beta = 0.38$) further underscores the role of topographic filtering in shaping evergreen strategies, likely due to physiological constraints under cooler, low-light conditions typical of high-elevation habitats (Vitasse et al. 2014; Lenoir et al. 2017). Overall, our results highlight that deciduous species adjust more flexibly to their environment through strong links between soil, vegetation, and traits, while evergreen species respond more rigidly, mainly to elevation and canopy-induced stress. These findings advance our understanding of how plant strategies are modulated by both abiotic filters and vegetation-mediated microenvironmental variation across complex topography.

5. Conclusion

The study concluded that topography (elevation and aspect) and resource gradients (light, canopy, and, nutrients) jointly shape shrub community composition and trait variation in the Western Himalayan temperate forests. Our findings indicate that deciduous and evergreen shrubs employ contrasting resource strategies, with evergreens being more strongly constrained by abiotic stress and overstorey stand canopy cover. While canopy and light are strong mediators, they are together influenced by elevation and slope aspect. Given the complexity of trait-environment relationships, we recommend long-term monitoring under climate change scenarios, with additional focus on anthropogenic factors (e.g. grazing, road building) and the integration of phylogenetic frameworks, to better predict functional responses and enhance conservation strategies in these ecosystems. Furthermore, since not all shrub species occurred across all elevations, future studies should integrate intraspecific trait variation across elevation zones to disentangle plasticity from community compositional effects. Such integrative approaches are crucial to inform conservation strategies that maintain biodiversity and ecosystem function amid environmental change.

CRediT authorship contribution statement

Shipra Singh: Writing – original draft, Visualization, Formal analysis, Data curation, Conceptualization. **Abhishek K. Verma:** Writing – review & editing, Visualization, Supervision.

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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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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2025.114000.

Data availability

Data will be made available on request.

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