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Ecological filtering explains species distribution pattern and regeneration potential in Western Himalayan forests

Shipra Singh [a,b,*], Abhishek K. Verma [b,c], Rajendra Kumar Joshi [b], Florian Hofhansl [a]

[a] International Institute for Applied Systems Analysis, Schlossplatz 1, A-2361 Laxenburg, Austria
[b] School of Environmental Sciences, Jawaharlal Nehru University, New Delhi 110067, India
[c] Forest Ecology and Climate Change Division, ICFRE- Forest Research Institute, Dehradun, Uttarakhand 248006, India

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ABSTRACT

Understanding how environmental heterogeneity shapes species composition is essential for managing fragile Himalayan ecosystems. We assessed patterns of tree and shrub diversity, forest structure, regeneration dynamics, and soil physicochemical properties along an elevation gradient and across north- and south-facing slopes in 36 forest stands of Western Himalaya. We recorded 3,486 individuals from 47 tree and 34 shrub species. Floristic composition revealed four distinct forest community types along elevation: sub-tropical Sal-dominated (300-900 m), sub-tropical Pine (900–1500 m), lower temperate mixed (1500–2400 m), and upper temperate mixed (2400–3000 m) forests, indicating a strong species turnover. Tree density and basal area increased with elevation, peaking in upper temperate forests (~1128 ind ha^{-1}; ~68 m^2 ha^{-1}), whereas species richness and Shannon diversity peaked in Sal forests. Shrub density showed a unimodal response, peaking at mid-elevations (~1600 m). Tree seedling density was greater on north-facing slopes, whereas sapling density peaked at mid-elevations (~1200 m). Soil moisture, organic carbon, and available potassium increased with elevation, with higher values on north-facing slopes. However, bulk density was greater on south-facing slopes. Multivariate ordination identified soil nutrients and elevation as the main drivers of community composition. Redundancy Analysis explained 53% of variance (adj. $R^2 = 0.59$, $p < 0.001$), with elevation, soil moisture, organic carbon, and available potassium emerging as the strongest predictors. Climatic variables primarily influenced Sal forests. This study highlights the dominant role of soil and topography in governing community composition in Western Himalaya, with climate exerting as secondary but reinforcing driver at lower elevations.

1. Introduction

Mountain forest ecosystems serve as natural laboratories for understanding the biotic and abiotic factors that shape species composition and biodiversity at both local and global scales (Kattel, 2022; Sangry et al., 2024). Among these factors, topography, particularly elevation and slope aspect are considered key factors driving spatial biodiversity patterns in mountain forest ecosystems (Singh, 2018; Wang et al. 2024). In these systems, elevation acts as a composite bioclimatic control, integrating gradients in temperature, moisture availability, and solar radiation that collectively govern soil development trajectories and nutrient cycling processes. These bioclimatic gradients directly mediate soil formation, organic matter decomposition rates, and nutrient availability, which in turn structure plant community composition, functional diversity, and ecosystem productivity (Méndez-Toribio et al., 2016; Wang et al., 2022; Zhou et al., 2025). Similarly, slope aspect modifies these microclimatic conditions by altering incoming solar radiation and subsequently influencing temperature and moisture regimes. North-facing slopes are generally cooler and moister, while south-facing slopes tend to be warmer and drier due to differences in solar radiation exposure (Måren et al., 2015; Singh and Verma, 2025). Collectively, these aspect-mediated microclimatic variations create distinct edaphic conditions that control soil moisture retention, nutrient mineralization, and organic matter accumulation, thereby shaping differential vegetation assemblages and regeneration patterns (Fartyal et al., 2024; Ram and Chawla, 2024).

The interplay between topography, climate, and edaphic factors creates complex vegetation patterns along elevational gradients, which emerge from the interactions between these abiotic drivers and biotic processes (McCain and Grytnes, 2010; Wang et al., 2024). Numerous

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* Correspondence author at. International Institute for Applied Systems Analysis (IIASA), Schlossplatz, A-2361, Laxenburg, Austria.
E-mail address: shipra91singh@gmail.com (S. Singh).

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studies have reported that species richness often peaks at mid-elevation, which is attributed to optimal energy, moisture availability, and reduced competition or disturbance (Ao et al., 2024; Fraser et al., 2015; Stein et al., 2014). However, this pattern is not universal, and the extent to which slope aspect (north- vs. south-facing) and edaphic factors modulate these biodiversity patterns remains poorly quantified in the Himalayas, particularly when considering both overstory and understory vegetation components. Beyond species diversity, forest regeneration processes, particularly seedling and sapling dynamics, are critical for ecosystem resilience and are also strongly influenced by elevation, aspect, and dominant vegetation types that regulate light and soil conditions (Díaz-Yáñez et al., 2024; Negi et al., 2025). Underlying these vegetation patterns are systematic variations in soil properties, such as moisture content, organic carbon, total nitrogen, and nutrient availability, which vary significantly across elevational gradients. In montane systems, cooler temperatures and slower decomposition rates at higher elevations typically result in greater organic matter accumulation, improved soil structure, and increased nutrient retention (Jozedaemi and Golchin, 2024; Måren et al., 2015), creating a feedback loop where these soil attributes influence vegetation composition, productivity, and diversity.

The Himalayas are recognized as one of the global biodiversity hotspots, harboring high levels of endemism and varying forest types due to microclimatic variations and topographical heterogeneity (Champion and Seth, 1968; Haq et al., 2022). The Western Himalaya, located in the Indian state of Himachal Pradesh, represents a diverse physiographic region with forest types ranging from sub-tropical Sal forests at lower elevations to temperate coniferous and oak forests at mid- to high elevations (Champion and Seth, 1968). This progression from subtropical Sal forests to temperate coniferous and oak forests along the elevation gradient represents not merely a floristic shift but a systematic reorganization of ecosystem structure driven by elevation-mediated changes in temperature and precipitation regimes. These climatic gradients control soil moisture dynamics, organic matter decomposition rates, and nutrient cycling, which collectively determine species composition, community assembly rules, and regeneration potential across the landscape (Fan et al., 2025). Despite the ecological importance of these montane ecosystems, comprehensive assessments of how elevation and topographic variability influence forest diversity, community composition, and soil properties across this region remain limited (Sangry et al., 2024; Sharma et al., 2025; Verma and Garkoti, 2019). This knowledge gap is particularly critical because understanding how these environmental gradients affect both overstorey (trees) and understorey (shrubs, seedlings, saplings) components of forest ecosystems is essential for predicting ecosystem responses to climate change and for developing effective forest management and conservation strategies that can maintain ecosystem resilience under accelerating environmental changes. Although numerous studies have explored floristic composition and species diversity along elevational gradients, no study to date has simultaneously assessed how topography (especially slope aspect), soil properties, and climate jointly influence tree and shrub communities. Moreover, there is limited understanding of how these factors shape vegetation structure and regeneration patterns across broad elevation bands. Additionally, limited studies have incorporated multivariate ordination and variance partitioning to identify the dominant environmental drivers of community composition across an elevation gradient (Ram and Chawla, 2024; Sharma et al., 2018). To address these knowledge gaps, the objectives of this study are to: 1). Investigate the effect of topography (slope aspect and elevation) and bioclimatic variables on soil properties and woody vegetation communities (floristic composition and diversity, forest structure and regeneration patterns), and 2). quantify the relative contribution of abiotic factors on community composition in the protected forests of the Western Himalayan region. Given that topographic features such as slope aspect and elevation drive environmental heterogeneity among forest sites, we hypothesized that (1) soil properties and associated woody vegetation communities differ along elevational gradients; such that (2) local plant species composition will vary with specific forest communities along these gradients, and therefore, (3) topographically mediated soil properties and bioclimatic factors might shape community composition in the region. Eventually, we discuss our findings in the context of existing scientific literature to provide evidence-based recommendations for sustainable forest management strategies for the Western Himalayan forest ecosystems.

2. Material and methods

2.1. Study site

The present study was conducted in the protected forests of Sirmour district, Himachal Pradesh, located between 30° 22′30"–31° 01′20" N and 77°01′12"–77°49′40" E (Fig. 1). The district exhibits a significant altitudinal gradient, ranging from 337 m a.s.l. to 3514 m a.s.l., with Churdhar peak marking the highest point in the region. The climate varies from hot and dry at lower elevations to moderate in middle elevations and very cold at higher elevations (Table S1). Summer temperatures (May-June) range between 15 and 42°C, while winter temperatures (November-February) vary from 0 to 21°C. The average annual rainfall in the district ranges from 1,014 mm to 1,547 mm, with an average of 1,250 mm (District Survey Report, 2016). Snowfall is observed at elevations above 1800 m. The predominant geological formations in the area include sandstone, shale, limestone, and schist (Rawat et al., 2010), and soil types range from deep alluvial sandy loam at lower elevations to clayey loam at higher elevations (District Survey Report, 2016). The total geographical area of Sirmaur district is 2,825 km^2, of which 1415.88 km^2 is designated as total forest cover, accounting for approximately 50.12% of the district's total area. This forest cover is categorized into three classes based on canopy density: Very Dense Forest (canopy density >70%; 238.40 sq km), Moderately Dense Forest (canopy density 40-70%; 646.70 sq km), and Open Forest (canopy density 10-40%; 530.78 sq km) (FSI, 2023). The study area can be altitudinally divided into subtropical Sal forest, subtropical Pine forest, lower temperate mixed forest, upper temperate mixed forest (Champion and Seth, 1968; Saxena and Singh, 1984) (Fig. 1, see details of the dominant vegetation and associated species in Table S2). We expected low levels of anthropogenic disturbance since the study sites are located inside protected areas.

2.2. Vegetation analysis

Nine elevational zones with contrasting aspects (north and south) and two replicates were selected for this study, altogether forming thirty-six forest stands representing diverse forest types (Fig. 1, Table 1). A total of 360 plots (10 plots × 9 elevation zones × 2 slope aspects × 2 replicates) measuring 0.1 ha (31.62 m × 31.62 m) each were sampled during 2017-2018. A minimum distance of 150 m between plots was maintained to ensure spatial independence. Plots were established following a systematic design along elevational transects, with random placement within each elevation × aspect combination. Sampling was conducted across two vegetation layers i.e., adult trees and shrub layers, and three life cycle stages of tree species i.e., adult trees (Circumference at breast height, CBH >30 cm), saplings (10-30 cm CBH), seedlings (CBH <10 cm) (Saxena and Singh, 1984). Within each 0.1 ha plot, shrub species and tree saplings were sampled within five sub-plots of 5 m × 5 m, and tree seedlings within five sub-plots of 1 m × 1 m (Curtis and McIntosh, 1950) altogether forming 1800 sub-plots (360 plots × 5 sub-plots). Tree and shrub species were identified using the Glossary of Forest Flora provided by the Sirmour district Forest Department at Forest Division, Nahan, and Rajgarh (Kaur and Sharma, 2004). CBH was used for determination of tree basal area, which was later converted to DBH (Diameter at breast height). The data were quantitatively analyzed for stem density, frequency, and abundance following (Curtis and

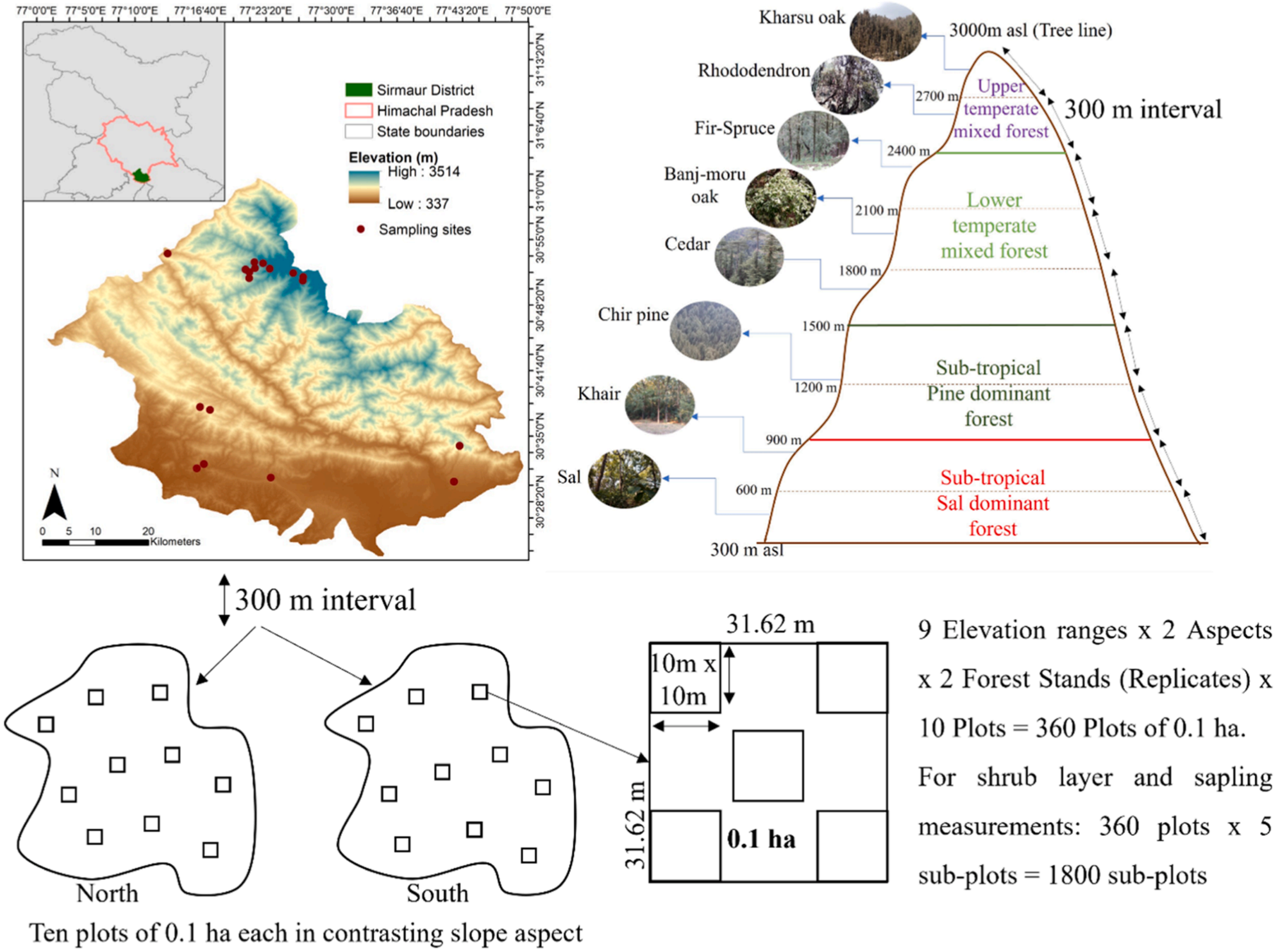


Fig. 1. Location of 18 sampling sites (red dots,18×2 replicates = 36 forest stands) in Sirmour district, Himachal Pradesh, India across an elevation range of 337-3514 m (upper left). Schematic representation of major forest types across elevation zones at 300 m intervals, showing dominant tree species: *Shorea robusta* (Sal), *Acacia catechu* (Khair), *Pinus roxburghii* (Chir pine), *Cedrus deodara* (Cedar), *Quercus leucotrichophora* (Banj oak), *Picea smithiana–Abies pindrow* (Fir-Spruce), *Rhododendron arboreum*, and *Quercus semecarpifolia* (Kharsu oak) at the treeline (upper right). Within each elevation zone, each forest stand consisted of a ten 0.1 ha plot (31.62 m × 31.62 m) for north and south aspect for tree sampling (bottom left) which was further subdivided into five 10 m × 10 m subplots used for shrubs and saplings, while seedlings were recorded within 1 m × 1 m quadrats (bottom right).

McIntosh, 1950). The Importance Value Index (IVI) was calculated as the sum of relative density, relative frequency, and relative dominance to assess the ecological significance of each species. Relative density represents the proportion of individuals of a species relative to all individuals; relative frequency indicates the proportion of plots containing that species; and relative dominance reflects the proportion of basal area contributed by that species. IVI values range from 0 to 300, with higher values indicating greater ecological importance. The Shannon-Wiener diversity index (H′) (Shannon and Weaver, 1949), species evenness (SE) (Pielou, 1966), and species richness (SR) (Margalef, 1973) were calculated. The regeneration pattern of tree species was analyzed based on the presence of number of seedlings, saplings, and adults of each species (Khan et al., 1987).

2.3. *Soil sampling and analysis*

Soil samples were collected in three replicates from 0-10 cm, 10-20 cm, and 20-30 cm soil depths from each forest stand to analyze variations in physical and chemical properties. Soils were sampled using a soil corer of 5 cm inner diameter and were packed in airtight zip bags and transported to the laboratory. Soil samples were air-dried and sieved through 2 mm and 0.5 mm sieves for further analysis. Soil moisture content (MC) was determined gravimetrically on a wet basis by oven drying 10 g of fresh soil at 105°C for 48 hours or until constant weight was achieved (Misra, 1968). Soil bulk density (BD) was determined from undisturbed core segments as dry soil mass per unit volume (Ingram and Anderson, 1993). The Bouyoucos hydrometer method was followed for particle size analysis using 10% Calgon's solution (sodium hexametaphosphate) (Okalebo et al., 2002). Organic carbon (OC) was measured using dichromate oxidation of an air-dried sample of 1 g followed by titration with $FeSO_4$ based on the modified Walkley and Black method (Walkley and Black, 1934). Total nitrogen (TN) was estimated by digesting the soil sample with concentrated H_2SO_4 and K_2SO_4:$CuSO_4$ catalyst, and analyzing the digest using a Micro-Kjeldahl apparatus (KELPLUS Distyl-EMBA) (Jackson, 1973). Available potassium (AK) was extracted using the neutral normal ammonium acetate method (Merwin and Peech, 1951) and was quantified using a flame photometer. Available phosphorous (AP) was estimated colorimetrically using Bray reagent (0.025N HCl in 0.03N NH_4F) in a 1N sulphuric acid system (Bray and Kurtz, 1945).

2.4. *Environmental data*

A total of 31 environmental variables were utilized to explore their relationship with species composition and diversity, serving as explanatory factors. These variables included physiographic and climatic data

Table 1
Details of the nine forest types along elevation gradient sampled in the study site. (Code as per classification by Champion & Seth 1968).

Community Group	Elevation range (m)	Forest type	Code	Dominant vegetation and associated species
Sub-tropical Sal dominant	300-600	Moist Siwalik Sal forest	3C/C2a	*Shorea robusta, Mallotus philippensis, Terminalia tomentosa, Lantana camara*
	600-900	Dry Siwalik Sal forest	5B/C1a	*S. robusta, Lannea grandis, Murraya koenigii*
Sub-tropical Pine dominant	900-1200	Siwalik chir pine forest	9/C1a	*Pinus roxburghii, Pyrus pashia, Acacia catechu, Adhatoda vasica*
	1200-1500	Himalayan chir pine forest	9/C1b	*P. roxburghii, Cedrus deodara, Ziziphus mauritiana*
Lower temperate mixed forest	1500-1800	Moist Deodar forest	12/C1c	*C. deodara, Quercus floribunda, Neolitsea pallens, P. roxburghii, Sarcococca saligna*
	1800-2100	Ban-oak forest	12/C1a	*Q. leucotrichophora Q. floribunda, P. wallichiana, C. deodara, Berberis aristata*
	2100-2400	Western mixed coniferous forest	12/C1d	*Q. floribunda, Q. leucotrichophora, P. wallichiana, C. deodara, Picea smithiana, B.aristata*
Upper temperate mixed forest	2400-2700	West Himalayan upper oak /fir forest	12/C2b	*Abies pindrow, P. smithiana, Q. semecarpifolia, Rhododendron arboreum, Rosa macrophylla*
	2700-3000	Kharsu oak forest	12/C2a	*Q. semecarpifolia, P. smithiana, Cotonoeaster bacillaris*

(Table S1). Physiographic factors, including altitude and coordinates for each site, were determined using a Global Positioning System (GPS-Garmin). Bioclimatic variables were obtained for each site from the global high-resolution ($\sim$1 km^2) database at www.worldclim.org. We extracted 19 bioclimatic variables representing long-term climatic averages for the baseline period 1970-2000 at ~1 km spatial resolution, Bio1 (Annual Mean Temperature), Bio2 (Mean Diurnal Range, calculated as the mean of monthly (max temp - min temp)), Bio3 (Isothermality (Bio2/Bio7), representing the seasonality of temperature), Bio4 (Temperature Seasonality, calculated as standard deviation ×100), Bio5 (Max Temperature of Warmest Month), Bio6 (Min Temperature of Coldest Month), Bio7 (Temperature Annual Range (Bio5 - Bio6)), Bio8 (Mean Temperature of Wettest Quarter), Bio9 (Mean Temperature of Driest Quarter), Bio10 (Mean Temperature of Warmest Quarter), Bio11 (Mean Temperature of Coldest Quarter), Bio12 (Annual Precipitation), Bio13 (Precipitation of Wettest Month), Bio14 (Precipitation of Driest Month), Bio15 (Precipitation Seasonality, expressed as Coefficient of Variation), Bio16 (Precipitation of Wettest Quarter), Bio17 (Precipitation of Driest Quarter), Bio18 (Precipitation of Warmest Quarter), and Bio19 (Precipitation of Coldest Quarter). These variables capture key aspects of temperature variability and moisture availability that influence vegetation distribution in mountain ecosystems. Correlation analysis was performed to examine relationships among all environmental variables. To address potential collinearity, a multi-collinearity test was conducted. The variance inflation factor (VIF), which measures the proportion of variance in one predictor explained by other predictors in the model, was calculated for each variable (Zuur et al., 2010). A VIF value of 1 indicates no collinearity, with higher values suggesting increasing multicollinearity. Variables with VIF values below 5 were considered to have low collinearity (Johnston et al., 2018).

2.5. *Data analysis*

All statistical analyses were conducted using R version 4.5.0 (R Core Team, 2020). Data matrices of species IVI and the corresponding variables were compiled using Microsoft Excel 2019 and R statistical software. Soil data normality was assessed using Shapiro-Wilk's test and homogeneity of variance was tested using Levene's test in the car package. Non-metric multidimensional scaling (NMDS) was performed to visualize the floristic associations among the sites using Bray-Curtis dissimilarities (Minchin, 1987) with the *metaMDS* function from the vegan package. Significant differences in species composition were determined through Permutational Multivariate Analysis of Variance (PERMANOVA) using the *adonis* function in the vegan package (Clarke, 1993). Species vegetation parameters, diversity indices and soil parameters were determined using different functions in the vegan package and then regressed along elevation using the ggplot2 package. Two-way ANOVA was used to test the effects of elevation and aspect on vegetation structure, diversity indices, and soil properties. Additionally, Principal Component Analysis (PCA) was used to analyze correlations among soil properties and environmental factors using the factoextra and imputeTS packages. Redundancy Analysis (RDA) was performed to examine species–environment relationships and to explain variation in species composition using Hellinger-transformed abundance data as the response variable and selected environmental predictors as explanatory variables. Multicollinearity among predictors was checked using variance inflation factors (VIF) from the *car* package. Permutation tests for the RDA models and variance partitioning were conducted with 99,999 permutations using the *permutest* function from vegan package. Finally, variance partitioning was conducted to quantify the relative importance of the environmental factors that shape the regeneration potential in the region, thus identifying the important factors that affect the regeneration pattern using the *varpart* function in the vegan package.

3. Results

3.1. *Community composition, structure and diversity*

A total of 3486 individuals were recorded across 36 forest stands representing 47 tree species and 34 shrub species. NMDS based on Bray–Curtis dissimilarity revealed four distinct clusters namely, Sub-tropical Sal forests, Sub-tropical Pine forests, lower temperate mixed forests, and upper temperate mixed forests along the elevational gradient, with minimal overlap among groups indicating strong species turnover (stress = 0.02, Fig. 2). Sub-tropical Sal and Pine forests formed tight clusters at lower elevations (E1–E4), while lower temperate mixed forests (E5–E7) occupied intermediate positions, bridging the compositional shift toward upper temperate mixed forests (E8–E9). PERMANOVA showed significant compositional differences among elevation zones ($F = 55.63$, $p < 0.001$).

The tree layer was dominated by *Shorea robusta* at lower elevations, while between 900–1500 m, *Pinus roxburghii* became the principal tree species. At mid-elevations (~1600–1900 m) *Cedrus deodara* replaced *P. roxburghii* on north-facing slopes, with Pine persisting on drier south-facing aspects. In lower temperate mixed forests, oak–conifer assemblages (*Quercus floribunda, Q. leucotrichophora*) dominated, shifting to *Q. semecarpifolia* with *Rhododendron arboreum* at >2700 m (Table S2). Tree density and basal area increased significantly with elevation (tree density: $R^2 = 0.68$, $F = 74.51$, $p < 0.001$; basal area: $R^2 = 0.71$, $F = 86.34$, $p < 0.001$), peaking in upper temperate forests (>2400 m: ~1128 ind ha^{-1} and ~68 m^2 ha^{-1}) (Figs. 3, S1, Table S4). Two-way ANOVA revealed that tree species richness ($F = 28.99$, $p < 0.001$) and evenness ($F = 32.31$, $p < 0.001$) increased significantly with elevation, whereas aspect showed no significant effect (richness: $F = 0.89$, $p = 0.35$; evenness: $F = 1.24$, $p = 0.27$). However, aspect effects were significant for tree structural attributes, with north-facing slopes supporting higher

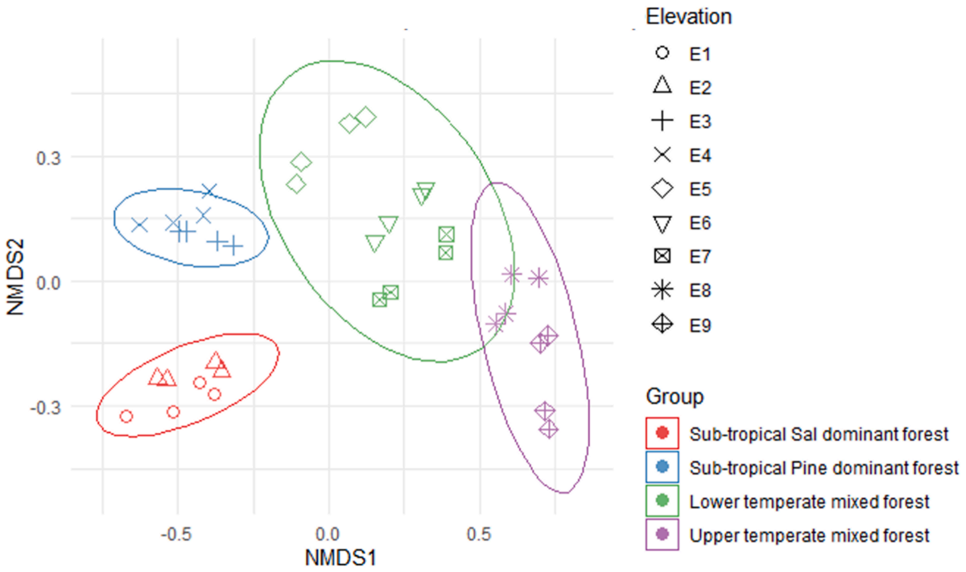


Fig. 2. Non-metric multidimensional scaling (NMDS) depicting four distinct plant community groups. Plots located on different elevation zones were represented based on Bray-Curtis dissimilarity (stress 0.02). Permutational Multivariate Analysis of Variance (PERMANOVA) indicates significant variation among sites ($F = 55.63$, $p < 0.001$). Abbreviations: E1: 300-600 m, E2: 600-900 m, E3: 900-1200 m, E4: 1200-1500 m, E5: 1500-1800 m, E6: 1800-2100 m, E7: 2100-2400 m, E8: 2400-2700 m, E9: 2700-3000 m.

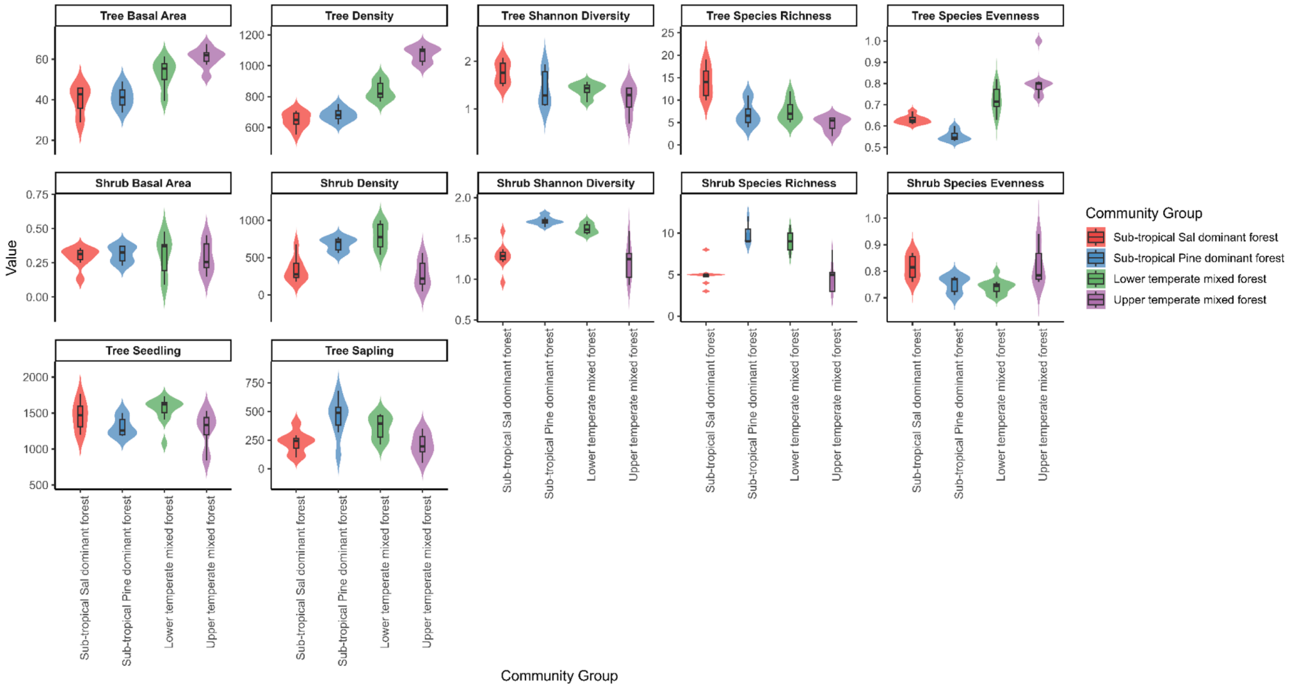


Fig. 3. Variation in tree and shrub structural and diversity attributes across forest community groups in Sirmaur district, Himachal Pradesh. Violin plots represent variability of values with embedded boxplots showing medians and interquartile ranges. Attributes include tree basal area (m^2 ha^{-1}), density (ind ha^{-1}), Shannon diversity, species richness, species evenness, seedling and sapling density (ind ha^{-1}), and corresponding shrub attributes.

tree density ($F = 8.26$, $p < 0.01$) and basal area ($F = 10.59$, $p < 0.01$). Tree seedling density was higher on north-facing slopes ($F = 5.82$, $p < 0.05$), while sapling density showed no significant aspect effect but exhibited a mid-elevation peak. Tree seedling density was highest around 400 m, whereas sapling density peaked around mid-elevations (~1200-1500 m) before declining in upper temperate forests (Fig. S1).

The shrub layer in subtropical forests included *Lantana camara, Murraya koenigii*, and *Carissa spinarum*; mid-elevations were characterized by *Adhatoda vasica* and *Ziziphus mauritiana*, while temperate forests were dominated by *Berberis aristata, Boenninghausenia albiflora*, and *Sarcococca saligna*. At >2400 m, *Rosa macrophylla, Cotoneaster bacillaris*, and *Prinsepia utilis* prevailed, with *Zanthoxylum alatum* restricted to the highest sites (Table S3). significant elevational responses ($p < 0.001$) but were not influenced by aspect. Elevation strongly influenced shrub density ($F = 41.72$, $p < 0.001$) and basal area ($F = 9.51$, $p < 0.001$), with maximum values observed in lower temperate forests. Shrub diversity (Shannon index: $F = 35.24$, $p < 0.001$) and richness ($F = 29.87$, $p < 0.001$) similarly exhibited significant elevational responses but were not influenced by aspect (diversity: $F = 1.02$, $p = 0.32$; richness: $F = 0.78$, $p = 0.38$).

3.2. Soil physical and chemical properties

Soil MC increased significantly with elevation ($F = 46.81, p < 0.001$) and was higher on north-facing slopes ($F = 10.01, p < 0.01$). The highest values were observed in upper temperate forests (~38.2%), while the lowest values were recorded in Sal forests (7.5–11.9%) (Fig. 4, S2, Table S4). Conversely, BD was higher on south-facing slopes ($F = 4.52, p < 0.05$) and increased with elevation ($F = 211.03, p < 0.001$). Soil texture ranged from sandy loam to loam. Soil pH was recorded acidic to slightly acidic but did not vary significantly with elevation ($F = 2.14, p = 0.11$) or aspect ($F = 0.89, p = 0.35$). OC increased with elevation ($F = 84.85, p < 0.001$), reaching maximum in upper temperate forests (~3.5%). TN did not vary with elevation ($F = 2.43, p = 0.09$) but was higher on north-facing slopes ($F = 8.56, p < 0.01$). AK increased significantly with elevation ($F = 87.7, p < 0.001$) and aspect ($F = 6.09, p < 0.05$) and exhibited a significant elevation × aspect interaction ($F = 4.00, p < 0.05$). AP showed no effects of elevation ($F = 1.78, p = 0.15$) or aspect ($F = 0.92, p = 0.34$) but showed a significant elevation × aspect interaction ($F = 7.14, p < 0.01$), with between-aspect differences emerging at upper temperate mixed forests (Fig. S2).

3.3. Influence of environment on community composition and soil properties

The first two axes of the PCA biplot explained 62.4% of the total variation (PC1 = 42.3%, PC2 = 20.1%) (Fig. 5). Upper temperate mixed forests were strongly associated with higher altitude, tree density, basal area, OC, MC, and AK, indicating that soil fertility and topographic factors are major determinants at higher elevations. Sub-tropical Pine forests were strongly associated with dense shrub understorey. In contrast, sub-tropical Sal forests grouped closely with climatic variables such as mean diurnal temperature range (bio02), temperature seasonality (bio04), minimum temperature of the coldest month (bio06), annual precipitation (bio12), and precipitation of the wettest quarter (bio16), together with tree species richness (SR) and Shannon diversity (H′), indicating that temperature and precipitation variability play a dominant role in shaping these low-elevation communities. Correlation analysis further confirmed strong positive associations among OC, TN, altitude, and MC, and negative relationships between sand content and climatic variables (Fig. S3). RDA constrained by soil and climatic variables explained 59% of the variance ($R^2_{adj.} = 0.59, p < 0.001$; Fig. 6a). Sub-tropical Sal forests aligned with high sand content and strong climatic influences (bio02, bio04, bio12, bio16). Lower temperate mixed forests correlated with higher soil OC, BD, silt, and AK, while upper temperate forests were strongly linked to MC. Variance partitioning (Fig. 6b) showed soil and topography as dominant drivers, explaining the largest pure fractions of community variation, while climate had comparatively weaker independent effects, indicating that its influence is largely modified by interactions with other factors. Overall, soil nutrients and topography jointly govern species turnover along the elevation gradient, whereas climate primarily modulates subtropical forest composition.

4. Discussion

This study demonstrated significant variation in species composition, vegetation structure, and soil properties across the Western Himalayan forests. This study reveals significant elevational shifts in forest community composition, species diversity, and structural and soil attributes driven by the combined effects of topography, climate, and edaphic conditions. The identification of four distinct forest community types i.e., sub-tropical Sal dominated, sub-tropical Pine-dominated, lower temperate mixed, and upper temperate mixed forests underscores the combined influence of elevation, climate, and soil as key ecological filters governing community assembly in montane ecosystems (Rawal et al., 2025; Thakur et al., 2022).

Tree basal area and density increased significantly with altitude, peaking in the upper temperate mixed forests, suggesting that despite

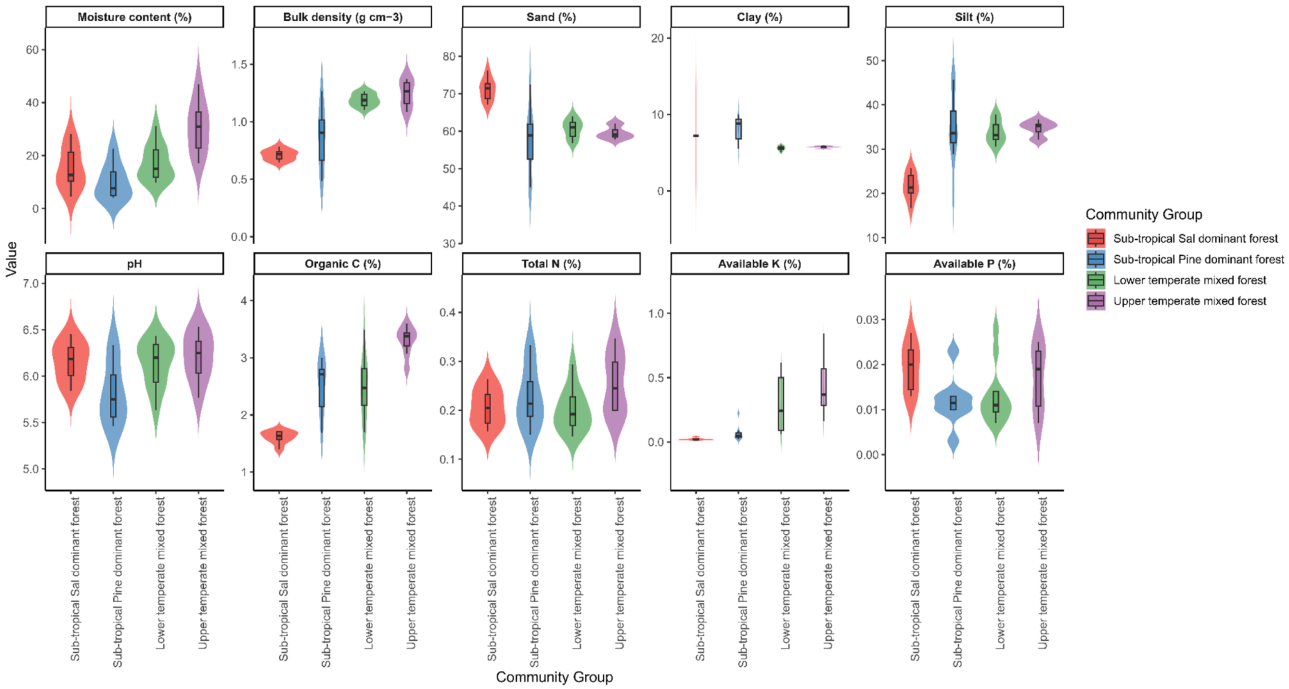


Fig. 4. Variation in soil physicochemical properties across four forest community groups in Sirmaur district, Himachal Pradesh. Violin plots illustrate the distribution and variability of values with embedded boxplots showing medians and interquartile ranges. Measured attributes include soil moisture content (%), bulk density (g cm^{-3}), sand (%), clay (%), and silt (%) fractions, soil pH (unitless), organic carbon (%), total nitrogen (%), available potassium (%), and available phosphorus (%). Community groups are: Sub-tropical *Sal* dominant forest (red), Sub-tropical *Pine* dominant forest (blue), Lower temperate mixed forest (green), and Upper temperate mixed forest (purple).

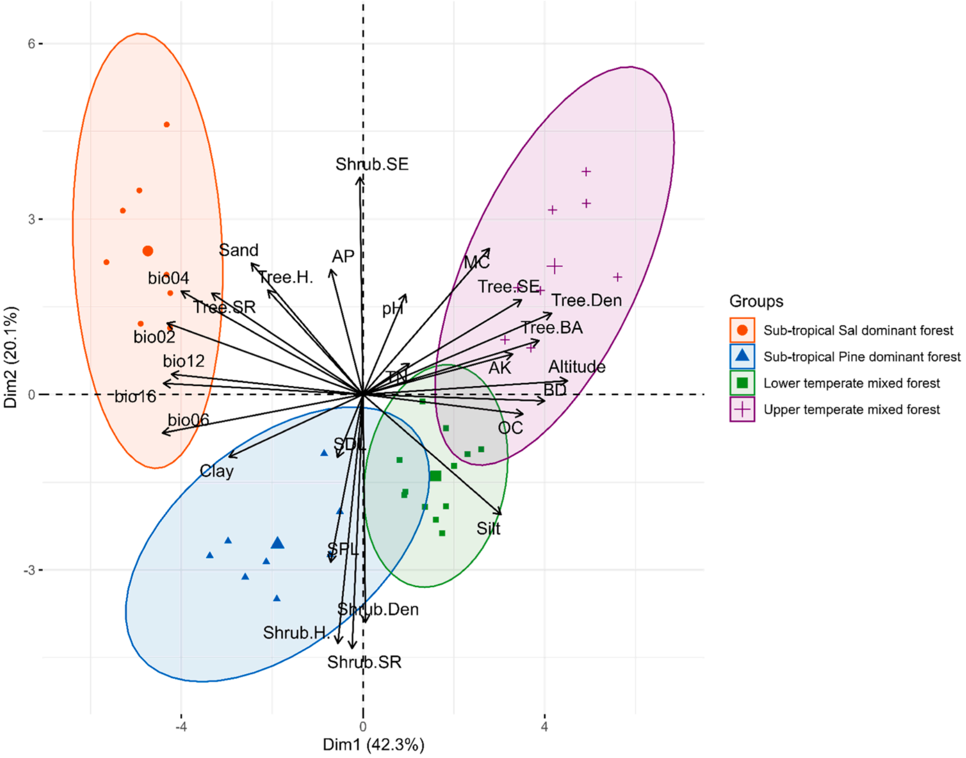
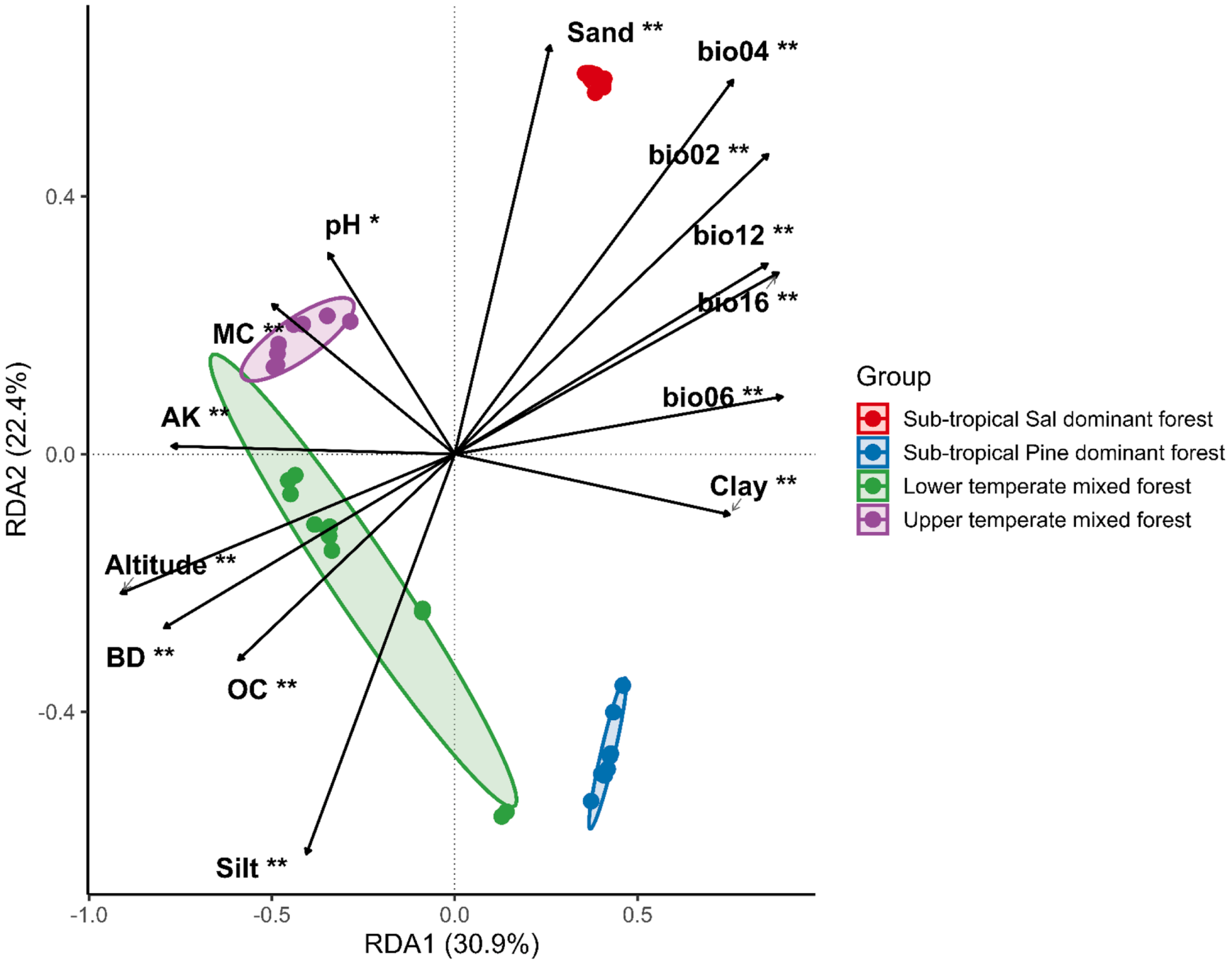


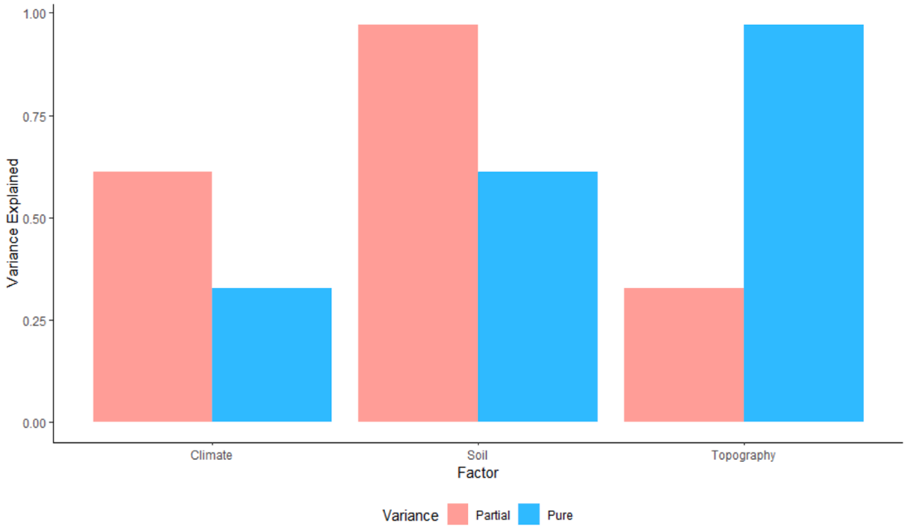
Fig. 5. Principal Component Analysis (PCA) biplot showing the relationship between vegetation attributes, environmental variables, and forest community groups in Sirmaur district, Himachal Pradesh. Arrows represent environmental and vegetation variables, where the length and direction indicate their relative contribution to community differentiation. Symbols denote forest types: Sub-tropical *Sal* dominant forest (red circles), Sub-tropical *Pine* dominant forest (blue triangles), Lower temperate mixed forest (green squares), and Upper temperate mixed forest (purple crosses). Shaded ellipses represent 95% confidence intervals around each community group. Abbreviations: Tree.BA: tree basal area (m^2 ha^{-1}), Tree.Den: tree density (ind ha^{-1}), Tree.SE: tree species evenness. Tree.H.: Tree Shannon Weiner Diversity Index, Tree.SR: Tree Species Richness, SDL: Tree Seedling Density (ind ha^{-1}), SPL: Tree Sapling Density (ind ha^{-1}), Shrub. Den: shrub density (ind ha^{-1}), Shrub.SE: shrub species evenness. Shrub.H.: Shrub Shannon Weiner Diversity Index, Shrub.SR: Shrub Species Richness. Soil variables include pH, Silt (%), Clay (%), Sand (%), OC (soil organic carbon, %), BD (bulk density, g cm^{-3}), TN (total nitrogen, %), AK (available potassium, %), AP (available phosphorous, %), MC (soil moisture, %), and Altitude (Elevation, m). Bioclimatic predictors are bio02 (mean diurnal temperature range,°C), bio04 (temperature seasonality), bio06 (minimum temperature of the coldest month,°C), bio12 (annual precipitation, mm), and bio16 (precipitation of the wettest quarter, mm).

lower diversity, trees in these stands accumulate greater biomass under less disturbed conditions (Yadav et al., 2025). Although Sal forests are known to attain high basal area in the Nepal Terai and parts of Uttarakhand, Sal stands in the western Himalayan region occur near the species' north-western climatic limit and are subject to higher seasonality and long-term anthropogenic disturbance (Sharma et al., 2018; Timilsina et al., 2007). Consequently, Sal forests in Sirmour are characterized by lower mean tree diameter and reduced cumulative basal area compared to relatively undisturbed temperate oak–conifer forests at higher elevations. In contrast, tree SR and H′ were highest in the sub-tropical Sal-dominated forests and declined towards the temperate forests. This pattern reflects the well-established species pools and favorable climatic conditions in warmer, lower elevation forests that promote recruitment and coexistence (Negi et al., 2025). However, shrub attributes followed a different pattern, with shrub density, H′ and SR exhibiting a mid-elevation peak consistent with the hump-shaped diversity-elevation hypothesis (Fraser et al., 2015). Such patterns are generally associated with optimal climatic conditions and resource availability at mid-elevations, which facilitate species coexistence by reducing environmental stress (Bastianelli et al., 2017; Thakur et al., 2022). Climatic gradients further explained the contrasting responses of the tree and shrub layers. Low-elevation Sal-dominated forests were strongly associated with climatic variables (bio02, bio04, bio06, bio12, bio16), indicating that both thermal and monsoonal regimes govern tree diversity and productivity at lower elevations (Mishra et al., 2021). In contrast, mid- and high-elevation communities aligned more closely with edaphic and topographic variables, including soil MC, OC, and AK, suggesting that as temperature and precipitation constraints intensify with elevation, soil water retention and nutrient availability become the dominant controls on shrub diversity and composition (Singh and Verma, 2025). At higher elevations, denser tree canopies limited light penetration to the shrub layer, while lower temperatures and shorter growing seasons constrained overall diversity (Thakur et al., 2022; Yadav et al., 2025). However, at lower elevations, invasive species such as *Lantana camara* (~50%) reduced shrub density and basal area by outcompeting native species for space and resources, particularly on south-facing slopes (Hansda et al., 2024; Kumar et al., 2021). This climatic-edaphic partitioning highlights a vertical ecological shift, from climate-driven control of tree communities in the lower belt to microclimate-mediated regulation of shrub assemblages at mid-elevations, while higher elevations are increasingly governed by edaphic factors, where greater soil moisture and nutrient accumulation enhance tree density and basal area (Sharma et al., 2018; Singh and Verma, 2018).

Patterns in regeneration revealed topographically mediated responses, highlighting how microclimatic variation regulates forest renewal across the Himalayan gradient. North-facing slopes, being cooler and moist, supported higher seedling densities, while the warmer, drier south-facing slopes favored light-demanding species such as *Pinus roxburghii*. Although the aspect-related differences were not statistically significant, the observed contrasts are consistent with differential solar radiation and soil moisture regimes that shape local regeneration strategies and species assemblages (Måren et al., 2015; Yang et al., 2020). At lower elevations, *Shorea robusta*-dominated stands showed high seedling



(a)



(b)

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Fig. 6. Redundancy Analysis (RDA) and Variance Partitioning of Forest Communities along Environmental Gradients. *(a)* RDA biplot showing the influence of climatic, soil, and topographic variables on forest community structure across four forest types: Sub-tropical Sal dominant forest (red), Sub-tropical Pine dominant forest (blue), Lower temperate mixed forest (green), and Upper temperate mixed forest (purple). Significant environmental variables are represented as vectors, with the direction and length indicating the strength and gradient of influence. Ellipses represent 95% confidence intervals for community groupings. Abbreviations: pH, Silt (%), Clay (%), Sand (%), OC (soil organic carbon, %), BD (bulk density, g cm^{-3}), AK (available potassium, %) and MC (soil moisture, %). Altitude is elevation (m). Bioclimatic predictors are bio02 (mean diurnal temperature range,°C), bio04 (temperature seasonality), bio06 (minimum temperature of the coldest month,°C), bio12 (annual precipitation, mm), and bio16 (precipitation of the wettest quarter, mm). *(b)* Variance partitioning diagram showing the relative contributions of climate, soil, and topography to explaining community variation. Pink bars indicate partial variance explained, while blue bars represent pure variance uniquely attributable to each factor.

abundance but low sapling density, indicating strong recruitment potential but poor transition to later stages (Saxena and Singh, 1984; Timilsina et al., 2025). This could be due to the presence of *L. camara* at lower elevation sites, which suppresses native seedlings through competition for resources. In contrast, mid-elevation mixed pine-oak forests (*Pinus roxburghii, Quercus leucotrichophora*) supported greater seedling survival and sapling establishment. These conditions likely represent optimal combinations of light, moisture, and nutrients for regeneration (Malik and Bhatt, 2016; Pant and Samant, 2012; Verma and Garkoti, 2019). At higher elevations, broadleaved-conifer stands with dense tree layers created protective microhabitats that reduced evaporative stress and facilitated seedling survival under low-temperature conditions. The increased soil moisture and organic matter in these forests further enhanced regeneration potential, although reduced light penetration due to dense canopy limited sapling establishment (Singh, 2021; Singh and Verma, 2025). Collectively, these findings demonstrate that regeneration is not uniformly governed by climate or elevation alone but emerges from the joint effects of canopy structure, soil moisture, nutrient availability, aspect-driven microclimates, and species-specific competitive interactions.

There is increasing evidence that soil moisture plays a crucial role in determining the composition of vegetation communities in mountainous landscapes (Fartyal et al., 2024; Zhou et al., 2025). In this study, soil MC emerged as a significant driver of species composition across sites. Higher elevation sites exhibited greater soil MC, likely due to denser canopy cover and multi-layering, which reduces evaporation and enhances moisture retention. In contrast, lower elevation sites, with lower tree density and basal area, created a sparse canopy that allowed greater light penetration, increasing evaporation and reducing moisture content (Lenk et al., 2024; Saxena and Singh, 1984). The study also found that MC, OC and soil nutrients, particularly TN and AK were greatest at higher elevations, especially in the upper temperate mixed forests. This is likely due to the lower decomposition rates in cooler, higher elevation sites, where litter accumulates and increases soil organic matter (Singh and Kashyap, 2006; Tashi et al., 2016; Wang et al., 2023). Increased organic matter improves moisture retention and cation exchange capacity, which in turn reduces leaching losses and enhances nutrient availability, particularly AK (Sanjeewani et el., 2024), although phosphorus concentrations were lower at these sites. While most nutrients showed elevation-related trends, AK and AP exhibited a significant elevation × aspect interaction, indicating that their distribution was not uniform along the gradient. Specifically, north-facing slopes at higher elevations contained greater AK concentrations, likely due to higher organic matter accumulation and reduced leaching, whereas south-facing slopes showed relatively higher AP at lower elevations, possibly driven by faster decomposition and mineralization under warmer, drier conditions (Pandey et al., 2007; Pandey et al., 2025). This interaction underscores how aspect modifies elevation-driven nutrient dynamics by influencing microclimate and organic matter turnover. The soil pH was slightly acidic throughout the study sites, which is favorable for nutrient availability to plants. In slightly acidic conditions, nitrogen and potassium remain readily available, whereas phosphorus availability is often constrained due to fixation by iron and aluminium oxides (Mitsuta et al., 2025). This pH-mediated phosphorus limitation likely explains the low available phosphorus observed at higher elevations despite greater organic matter inputs. Together, interactions among soil moisture, pH, organic matter accumulation, and nutrient cycling may impose phosphorus limitation at higher elevations, favoring species adapted to low-phosphorus environments and contributing to shifts in community composition (Lambers et al., 2022). Overall, this study demonstrates that soil MC and nutrient availability are key edaphic constraints for species distribution, and that these are further modified by elevation, aspect and canopy structure.

4.1. *Implications for forest management under future global change scenarios*

Montane forests are fragile ecosystems, highly vulnerable to climate change and global warming (Pauli and Halloy, 2019). Forests with multi-layered canopies and nutrient-rich forest floors provide better ecological stability and buffering capacity against climatic stress (Frenne et al., 2021). Establishing baseline data on floristic composition, diversity, and regeneration potential is therefore essential for adaptive forest management (Prada et al., 2017). Our results indicate that management interventions in the Western Himalaya must be explicitly elevation- and aspect-specific. Low-elevation Sal forests track bioclimatic variability, as seasonal temperature and precipitation regulate canopy dynamics, soil moisture availability, and drought stress, directly influencing seedling establishment and survival (Mishra et al., 2021). Higher temperature seasonality and diurnal temperature range can exacerbate moisture stress, making these forests particularly vulnerable under future warming. Management in Sal forests should therefore prioritize reducing anthropogenic pressure and controlling invasive species, particularly *Lantana camara*, which suppresses native regeneration and reduces stand structural integrity (Kumar et al., 2021). In mid-elevation Pine forests, regeneration constraints are strongly linked to forest floor conditions rather than climate alone. Accumulation of pine needles limits light penetration and nutrient cycling, indicating that periodic needle removal or controlled fuel management may facilitate native species establishment (Manral et al., 2020). At higher elevations, upper temperate mixed forests were structured primarily by edaphic controls, including soil moisture, organic carbon, and nutrient availability, rather than direct climatic forcing. These forests are especially sensitive to soil disturbance and erosion, particularly on steep slopes. These findings highlight the need to incorporate both climatic and soil–topographic variables into predictive vegetation models to enhance resilience under future climate scenarios (Bertrand et al., 2012; Franklin et al., 2020).

5. Conclusion

This study demonstrates that topography and soil properties are the dominant drivers of species composition and diversity in Western Himalayan forests, with climate exerting a secondary but reinforcing influence, particularly in subtropical zones. Tree density and basal area peaked at higher elevations, while understory components (seedlings, saplings, shrubs) showed maximum values at mid- to low elevations, reflecting differential responses to resource heterogeneity along the elevational gradient. Elevational increases in soil OC, TN, MC, and AK further reinforced compositional shifts, underscoring the role of edaphic properties in sustaining temperate forest communities. Multivariate analyses (PCA and RDA) revealed strong coupling of community composition with elevation, aspect, and soil nutrients, while variance partitioning confirmed that soil and topography explained the largest pure fractions of variation, with climate shaping species composition mainly through interactions with these edaphic and topographic factors. These findings highlight that species turnover across the Himalayan elevational gradient is not governed by single drivers but by the synergistic effects of resource gradients and microclimatic heterogeneity. This study underscores the need to explicitly incorporate both spatial and temporal heterogeneity across resource gradients, considering both abiotic and biotic factors, to better understand species-environment relationships at local and regional scales. Conservation should prioritize north-facing, high-elevation slopes that function as climate refugia due to higher biomass and soil nutrient stocks. Management must be elevation-specific, including invasive species control in subtropical Sal forests, pine needle management in mid-elevation Pine forests, and erosion control in upper temperate forests. Finally, herbaceous and shrub layers should be incorporated into monitoring and modeling frameworks, as they stabilize soils, facilitate regeneration, and improve predictions of forest responses to climate change across the Western Himalaya.

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CRediT authorship contribution statement

Shipra Singh: Writing – original draft, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Abhishek K. Verma:** Writing – review & editing, Visualization, Methodology, Formal analysis, Data curation, Conceptualization. **Rajendra Kumar Joshi:** Writing – review & editing. **Florian Hofhansl:** Writing – review & editing, Visualization, Supervision.

Declaration of competing interest

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

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.tfp.2026.101194.

Data availability

Data will be made available on request.

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