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Shipra Singh (singhs@iiasa.ac.at)
International Institute for Applied Systems Analysis

Abhishek Verma
Forest Research Institute

Florian Hofhansl
International Institute for Applied Systems Analysis

Research Article

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Posted Date: October 20th, 2023

DOI: https://doi.org/10.21203/rs.3.rs-3462205/v1

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Additional Declarations: No competing interests reported.
Topographical heterogeneity governs species distribution and regeneration potential by mediating soil attributes in Western Himalayan forests

Shipra Singh¹,²*, Abhishek K. Verma²,³ and Florian Hofhansl¹

¹International Institute for Applied Systems Analysis, Schlossplatz 1, A-2361 Laxenburg, Austria.

²School of Environmental Sciences, Jawaharlal Nehru University, New Delhi, India.

³Forest Ecology and Climate Change Division, Forest Research Institute, Dehradun, Uttarakhand-248006, India.

Corresponding author: Shipra Singh (singhs@iiasa.ac.at)

Acknowledgement

SS is thankful to Ambuj Mishra, School of Environmental Sciences, JNU for his support in field survey and sampling. SS and AKV are extremely thankful to Forest Guard, Late Ambadutta Sharma, Himachal Pradesh Forest Division. We are extremely thankful to residents of the reserve forest for their help and support throughout the field survey. We acknowledge the financial support from University Grants Commission (UGC) (Grant number: 3787/NET-DEC 2018), New Delhi, India.
Abstract

The present study is an attempt to understand variation in species composition and diversity and soil properties along topographic gradients in Western Himalayan reserve forests (400-3000m asl). To analyze changes in floristic composition, diversity, and regeneration status, we measured woody vegetation in forest plots at different altitudinal levels and contrasting aspects (North and south). Trees (diameter at breast height (DBH)>10cm) and saplings (3-10cm DBH) were sampled in 10m×10m plots, shrubs were sampled in 5m×5m plots and seedlings (0-3cm DBH) were sampled in 1m×1m plots. To study variation in soil properties, samples were collected from each forest stand in five replicates from layers of 0-10cm, 10-20cm, and 20-30cm in soil depths. Canonical Correspondence Analysis (CCA) was applied to identify important factors that govern species distribution. Variance partitioning was conducted to quantify the relative contribution of elevation, slope aspect, vegetation attributes, and soil properties on regeneration potential of tree species. We found that environmental filtering shapes local species composition and associated edaphic factors in the region. Species richness and diversity were found to decrease with elevation. Soil properties (Organic Carbon, pH, and texture) and associated vegetation parameters did not vary significantly between the aspects. CCA confirmed that species composition was positively related to moisture content and available phosphorous at higher elevations, while reduced weathering rates and bulk density at lower elevations might have caused relatively lower nutrient turnover rates. Our study concludes that topographical variation and increased sum of soil nutrients are highly favorable for growth and development of plant species.

Keywords: Diversity; Elevation; Forest structure; Montane ecosystem; Slope aspect.
Introduction

Topographical features, such as slope angle, aspect, and elevation (Singh, 2018) affect species diversity, ecosystem structure and processes, resource availability, and energy partitioning in forest ecosystems (Jucker et al., 2018; Méndez-Toribio et al., 2016) through the modification of the surrounding environment (Ali et al., 2019; Jucker et al., 2018). In Montane Forest ecosystems, the slope aspect and topographical position are the most influential drivers of temperature changes (Geml 2019) and soil water content variability (Wang et al. 2011). North-facing slopes are characterized by relatively moist conditions and cooler temperatures, whereas south-facing slopes are comparatively warmer and drier (Holland and Steyn 1975). However, this relationship is inverted in the northern and southern hemispheres, such that the northern hemisphere exhibits a cooler climate at north-facing slopes while the same applies to south-facing slopes in the southern hemisphere (Budyko, 1969). Resulting differences in solar radiation, soil water content, and temperatures between the two different aspects strongly affect the vegetation's structure and composition (Guo et al. 2017; Jucker et al. 2018). Furthermore, the asymmetry in environmental drivers between northern and southern aspects was shown to affect crucial ecosystem processes such as organic matter decomposition, which in turn determines local resource availability of water and nutrients (Sidari et al. 2008; Fortunel et al. 2018; Muscarella et al. 2020). The slope aspect further governs the input of solar energy at the landscape level forming distinct microclimatic conditions (Goran et al., 2012; Jucker et al., 2018), which trigger differences in temperature, moisture, humidity, and evaporation (Chadwick and Asner 2016; Jasińska et al. 2019), and thus affect soil edaphic properties and vegetation dynamics (Eisenlohr et al. 2013; Uriarte et al. 2018; Yang et al. 2020). Due to the linkage of elevation and slope aspect to multiple environmental variables, topography has been proposed as the single most important factor responsible for determining spatial patterns of biodiversity (Singh, 2018; Tiwari et al., 2020; Yang et al., 2020).
Within a micro-climatic condition, forest attributes such as species composition and diversity along with edaphic properties affect the regeneration pattern in montane forest ecosystems (Rodrigues et al. 2020). Forest stands having increased soil moisture and optimum light availability tend to regenerate rapidly (Verma and Garkoti, 2019). Topographical heterogeneity creates variations in soil nutrient availability, pH, and soil texture that ultimately affects regeneration pattern in any region (Pinho et al. 2018; Tiwari et al. 2020) via mediating their effect on species composition and richness (Laughlin et al. 2015). In addition, temperature variability with increasing elevation plays an important role in understanding seedling survival rates, providing clues for climate change effects (Dobrowski et al. 2015; Shive et al. 2018; Verma and Garkoti 2019). Thus, regeneration potential could be considered an important indicator to analyze shift in vegetation composition and diversity with changing climate (Woodall et al. 2018). Regeneration of species on gentle slope tends to be comparatively higher as compared to steeper slope (Finegan and Delgado 2000; Estrada-Villegas et al. 2020). The gradual development of an individual from seedling to mature individual faces increased environmental harshness with increasing elevation (Yan et al. 2015). Additionally, it has also been found that saplings are more prone to environmental harshness with increasing elevation (Liang and Wei 2020). With increasing topographical heterogeneity, distinct regeneration niche leads to species stabilization in different ecosystems (Dobrowski et al. 2015; Uriarte et al. 2018).

Mountain regions are considered an important habitat for endemic species and natural forest vegetation, which typically provides important ecosystem services, such as carbon sequestration, nutrient cycling, climate regulation, and timber production (Ai et al. 2017). In addition, montane forest ecosystems provide natural laboratory conditions to understand the important biotic and abiotic factors shaping species composition and biodiversity locally as well as globally (Raz et al. 2009). These differences vary greatly depending on the scale of
observation (Jarzyna & Jetz, 2018) and the underlying environmental factors governing species composition at the landscape-scale (Hofhansl et al. 2021). Regional studies investigating biodiversity, species composition, and plant community structure along altitudinal gradients, have documented soil physicochemical properties as drivers of vegetation structure in Central Himalayan regions (Kharkwal et al. 2005; Sharma et al. 2010; Gairola et al. 2012; Tiwari et al. 2020) but are comparatively missing in Western Himalayan forests. Therefore, we state that there is currently a lack of knowledge about the effect of contrasting slope aspects on vegetation composition at varying elevations, which would be required to develop sustainable management strategies for Montane Forest ecosystems in the Western Himalaya. The objective of this study was 1). To investigate the effect of topography (slope aspect and elevation) on soil properties (soil texture and chemistry) and woody vegetation characteristics (floristic composition and diversity, forest structure and regeneration pattern) and 2). To quantify the relative contribution of topography and soil properties on regeneration potential in the protected forests of the Western Himalayan region. Due to the fact 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 characteristics differ along elevational gradients; such that (2) local plant species composition varies with specific forest habitat types located along environmental gradients of the study region and therefore, (3) the impact of topographically mediated species composition and associated soil properties might affect regeneration potential of species. Eventually, we discuss our findings in light of the scientific literature with the goal to develop sustainable forest management recommendations for the Western Himalayan Forest ecosystems.
Methods

Study site

The study was conducted in protected forests located between 30° 22’30”–31° 01’20” N, and 77°01´12”–77°49´40” E in Sirmour district, Himachal Pradesh (Fig. 1). The altitudinal variation of Sirmour district ranges between 400 m a.s.l. and 3630 m a.s.l., with Churdhar peak being the highest point of the district. The climate of the district is sub-tropical to temperate depending upon the elevation. Climate varies from hot and dry (up to 1,800 m) to moderate (1,800-2,500 m) and cold to very cold at higher elevations (2,500-3,630 m). The temperature in the summer season (May-June) ranges between 15 to 42 °C, while in the winter season (November-February), it varies from 0 to 21 °C. The region has an average annual rainfall of 1,014-1,547 mm with an average of 1,250 mm (District Survey Report, 2016) (Fig. S1). The region also experiences snowfall above the altitude 1800 m. The rocks found in the area consist of sandstone, shale, limestone, and schist (Rawat et al. 2010). Soil type varies from deep alluvial sandy loam at lower elevation to clayey loam at higher elevations (District Survey Report, 2016).

Site selection

The different forest types in the study region are classified under 3C/C2a- Moist Shiwalik Sal Forest, 9C1- Himalayan Sub-tropical Pine Forest, Group 12 C1- Lower Western Himalayan moist-temperate forest, C2- Upper West Himalayan moist temperate forest, and Group 12- DSI oak scrub (Champion and Seth, 1968). Five different elevational zones (E1:400–1000 m, E2:1000–1500 m, E3:1500–2000 m, E4:2000–2500 m, and E5:2500–3000 m asl) with contrasting aspects, north and south, altogether forming ten forest stands representing diverse forest types were chosen for the study. We expect low levels of anthropogenic disturbances since the study sites are located inside protected areas.
Vegetation analysis

Physiographic factors i.e., altitude and coordinates across different forest types were determined by Global Positioning System (GPS-Garmin). Sampling was conducted in two layers of the vegetation 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). A total of 200 plots (20 plots × 5 elevation zones × 2 slope aspect) measuring 10 m × 10 m each were sampled between September 2016 and April 2017. Shrub species and tree saplings were sampled within sub-plots of 5 m × 5 m, and tree seedlings within sub-plots of 1 m × 1 m (Curtis and McIntosh 1950). Tree and shrub species were identified with the Glossary of forest flora provided by the Sirmour district Forest Department at Forest Division, Nahan, and Rajgarh. CBH was used for determination of tree basal area, which was later converted to the DBH (Diameter at breast height). The data were quantitatively analyzed for stem density, frequency, and abundance following (Curtis and McIntosh 1950). Shannon-Wiener Diversity index (H’) (Shannon and Weaver 1949), Species evenness (SE) (Pielou 1966), and species richness (SR) (Margalef, 1973) were calculated. Density-diameter distribution curve (population structure) for each site along with the dominant tree species was analyzed by plotting the graph against the number of individuals in different DBH classes i.e., 0-10; 10-20; 20-30; 30-40; 40-50; 50-60; 60-70; 70-80; and 80-90 cm respectively. 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).

Soil sampling and analysis

From each of the ten forest stands, soil samples were collected in five replicates from layers of 0-10 cm, 10-20 cm, and 20-30 cm in soil depth 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 brought to the laboratory. Soil samples were air-dried for 48
hours and sieved through a 2 mm and 0.5 mm sieve 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 Mishra (1968). Soil bulk density (BD) was determined from the undisturbed core segments as dry soil mass per unit volume (Ingram and Anderson 1993). The Bouyoucos hydrometer method of silt and clay measurement was followed for analysis of particle size using 10% Calgon’s solution (sodium hexametaphosphate) (Okalebo et al., 2002). Organic carbon (C) of the soil sample was measured with dichromate oxidation using an air-dried sample of 1 g and titrating with FeSO₄ based on modified Walkley and Black method(Verma et al. 2021) Total Nitrogen (N) was estimated by digesting 3 g soil sample with concentrated H₂SO₄ and K₂SO₄:CuSO₄ catalyst, and further analyzed using Micro-Kjeldahl apparatus (KELPLUS Distyl-EMBA) (Jackson, 1973). Available Potassium (K) was extracted following neutral normal ammonium acetate method (Morwin and Peach, 1951) and was determined using the flame photometer. Available Phosphorous (P) was estimated colorimetrically using Bray reagent (0.025N HCl in 0.03N NH₄F) in 1N sulphuric acid system (Bray and Kurtz, 1945).

Statistical analysis

Data matrices of species’ IVI and the corresponding variables were prepared in Microsoft Excel-2019. Soil data normality was assessed based on Shapiro–Wilk’s test and homogeneity of variance was tested by Levene’s test. Non-metric multidimensional scaling (NMDS) was performed to visualize the floristic associations among the sites by using Bray–Curtis dissimilarities (Minchin 1987) using the metaMDS function of the vegan package. Significant differences in species composition were determined through permutational multivariate analysis of variance (PERMANOVA) by using the adonis function of the vegan package (Clarke, 1993). Species vegetation parameters and diversity indices were determined using different functions of the vegan package and visualized using ggplot2 package. β diversity
variation along the elevation gradient and between contrasting slope aspect was analysed using the quantitative Sorensen (Bray–Curtis) distance measure (Yang et al. 2020). The analysis was done using betadiver function of the vegan package. Comparison of vegetation structure and diversity along elevation, contrasting slope aspect, and their interaction were analyzed using two-way ANOVA for the study sites, and the differences were reported significant at $P<0.05$. Soil values were regressed along elevation using ggplot2 function. Soil values were visualized using box plot for contrasting slope aspect and independent t-test was applied to calculate the difference of means between north and south aspect. Further, Principal Component Analysis (PCA) was used to analyze correlation among vegetation parameters and soil properties using factoextra and imputeTS packages. Additionally, Canonical Correspondence Analysis (CCA) was used to investigate significant relationships between tree species distribution and associated environmental variables among study sites. After CCA, the Monte Carlo test was used to evaluate the effect of explanatory variables obtained on the vegetation composition using cca function. In the end, variance decomposition analysis was done to quantify the relative importance of the environmental factors that shape the regeneration potential in the region thus confirming the important factors that affect the regeneration pattern using varpart function of the vegan package. All statistical analyses were conducted using R version 3.5.0 (R Core Team, 2018).
Results

Floristic composition and species diversity

A total of 3486 individuals belonging to 47 tree species and 19 shrub species were found in the study sites (Fig. S2 and S3). Non-metric multidimensional scaling (NMDS) produced a two-dimensional plot of species composition along an elevational gradient (Fig. 2) and between contrasting slope aspect (Fig. S4). We found a stress value of 0.03 indicating a greater reliable ordination. NMDS showed species composition based on elevation gradient were strongly separated in ordination space with least overlap, however, species from the E3 site (mid-elevation zone) formed a connecting bridge with the adjacent elevation zone (Higher, E4). Permutational Analysis of Variance showed significant compositional differences among the elevation zones (F=5.72, P<0.001). However, species composition did not significant differences between the north- and south-facing slopes (F=1.02, P<0.419) (Fig. S4). Tree Species Richness (SR) and Shannon-Weiner Diversity index (H') were found decreasing with increasing elevation (Fig. 3). The values for SR and H' were found maximum for E1 (400-1000 m) sites and northern aspect. Whereas for shrub layer, NMDS showed a stress value of 0.15 (Fig. 4). The plot showed species at E1 and E2 sites were closely associated whereas species at E3, E4, and E5 sites were clumped together. Overall, we found significant differences among species composition with increasing elevation (F=6.29, P<0.001). Based on slope aspect variation, NMDS plot showed no significant variation (Fig. S5). Shrub SR and H' first decreased with elevation and then increased after 2000 m asl. The values for diversity indices were greater for the northern aspect except SR which was found greater for southern aspect in lower elevation (Fig. 5). β diversity was found significantly (P<0.05) higher on higher elevation (Fig. S6) and northern aspect. For the tree layer, it was found significantly higher (P<0.05) for E3 sites indicating increase in vegetative heterogeneity with increasing elevation (Fig. S6). β diversity was found higher on southern aspect as compared to northern aspect for both the tree
and shrub layer, however, the differences were not found significant. The diversity indices were found significantly varying with increasing elevation for both tree and shrub layer (Table S1).

**Vegetation structure and regeneration pattern**

For the tree layer, Tree density (F=13.41, P<0.001) and basal area (F= 22.14, P<0.001) were found decreasing with elevation and then increased after 2000m (E3) significantly. The least values for both density and basal area were found for E3 sites. Shrub density (F= 41.72, P<0.001) and basal area (F= 9.51, P<0.001) were found decreasing significantly with elevation (Fig. 6). Both total basal area as well as stem density were higher in northern aspect than in southern aspect, but the differences were not significant. A density-diameter curve was drawn to understand the distribution of individuals in different DBH class for each site (Fig. 7) and the dominant tree species (Fig. S7). Greater number of seedlings and saplings than adults indicated an inverted-J shaped curve for E1N, E1S, E3N, E3S, E4N and E4S sites whereas E2N, E2S, E5N and E5S represented a bell-shaped curve. Species-wise population structure showed inverted-J shaped for species restricted to lower elevation (E1) like *Shorea robusta* and *Mallotus philippensis*. Similarly, species at higher elevation (E5) such as *Quercus semecarpifolia*, *Q. floribunda*, *Abies pindrow* showed bell-shaped pattern. A total of 7480 individuals of seedlings and 8180 individuals of saplings were observed in the study sites (Fig. 8). Taken together, maximum regeneration was observed for lower elevation (E1) which decreased significantly with increasing elevation (F=3.89, P=0.008). Overall, the number of seedling counts were maximum in north aspect irrespective of elevation change however sapling counts were higher for south aspect in lower elevation (E1, 400-1000m) and south aspect for higher elevation sites (E4, 2000-2500 m and E5, 2500-3000 m) (Fig. 8).

Moisture content (MC) was found significantly increasing with elevation (R²=0.63, P<0.001) (Fig. 9). Between the contrasting slope aspect, MC was found to be significantly
different (P<0.05) being greater for northern aspect. The values for MC were found increasing
with increasing depth (Table S2). Similarly, bulk density was also found increasing with soil
depth and the values were found to be significantly greater for southern aspect than northern
aspect (P<0.05). Texture of the soil varied from sandy loam to loam irrespective of aspect,
elevation, and depth. Soil pH was found to be acidic to slightly acidic throughout the study site.
Soil OC decreased with increasing depth and the values were found to increase with elevation
significantly (R^2=0.53, P<0.001). Similarly, Total N, Available K, and Available P decreased
with increasing soil depth. Available P and Available K were found significantly varying with
elevation. All the soil nutrients (N, P, K) and OC showed greater values in the north aspect as
compared to south. PCA plot explained around 49% of variation in vegetation and soil
properties among sites (Fig. 10). PCA clearly showed two spectra of variation among the sites.
The first PC axis reflected increased soil pH and BD. Whereas the second spectra of variation
showed increased diversity (H' and SR), seedling, and sapling count at lower elevations on one
hand and increased MC, organic C, and soil nutrient (N,P,K) at higher elevations on the other
hand. Constrained correspondence analysis (CCA) revealed the interrelationship of species
assemblage, study sites, and environmental variables (Fig. 11), such that environmental
heterogeneity caused distinct clusters of floristic composition at different elevations, which in
turn significantly (P<0.05) affected MC, AP, Texture and BD. The CCA plot furthermore
indicated that elevation significantly affected species composition via increased MC and AP at
higher elevation sites and by decreased soil BD at lower elevation sites. The eigenvalues were
0.92 (CCA axis 1) and 0.81 (CCA axis 2) whereas, the proportion of cumulative variance
explained for CCA1 and CCA2 were 70.23 and 87.91% respectively. The total inertia was 3.45
while the explanatory variables accounted for 82% variation. The Monte Carlo test showed
significant variation after permutations (F-ratio: 3.41, P<0.001). Further, the effect of
topographical heterogeneity (elevation and slope aspect), associated vegetation attributes and
soil properties on regeneration potential were visualised using venn diagram. The explanatory variables used for the analysis were grouped into four classes: Elevation, Aspect, Edaphic factors (Soil texture, pH, BD and OC) and Vegetation attributes (Density, Basal Area and species richness). Variation partitioning tests (partial CCA) were conducted for all 15 possible classes (Table S3). Overall variation in regeneration pattern explained by the associated environmental factors was 94%. Maximum variation was explained by soil properties (41.12%) followed by elevation (39.18%), vegetation attributes (37.59%) and aspect (18.33%) (Fig. 12), which reflected the number of variables in a particular category. The value of fractions with shared variance were not very high. Hence it was found that the variance partitioning among factors explaining regeneration potential revealed a significant relation to environmental and topographical variables.
Discussion

We found striking variation in soil properties and associated vegetation characteristics between inventory plots located in Western Himalayan forests. In accordance with foregoing studies our analysis identified topography as the most important factor affecting taxonomic species composition along orographic gradients (Måren et al., 2015; Méndez-Toribio et al., 2016). However, we furthermore showed that variation in soil properties (MC, BD, AP, and texture) was the underlying factor driving these relationships, such that there are distinct clusters in taxonomic species composition associated with specific forest habitats across the landscape.

Environmental filtering shapes local species composition and diversity

Species composition significantly differed among the elevation zones based on NMDS, such that species composition at lower elevation (E1 and E2) was found to be completely different from that at higher elevation (E4 and E5), while the mid-elevation zone (E3) created an ecotone with the adjacent community (E4). Distinct cluster formation across the elevation zones might be due to the creation of patchy microhabitats based on resource availability and competition in a heterogeneous environment (Guo et al. 2017). Thus, the distribution of species and their co-existence are strongly under environmental control having different microhabitats irrespective of their life histories (Douda et al. 2012). For instance, *S. robusta* and *M. phillipensis* were restricted to lower elevations (E1) whereas *A. pindrow* and *Q. semecarpifolia* dominated the higher elevation sites (E5). Therefore, the observed strong differences in species composition are probably due to different ecological adaptation of species surviving in different environmental conditions (Yang et al. 2020). This separation of species composition in the region supports the Champion and Seth (1968) forest classification which classified forest vegetation based on climate variability. Species diversity is expected to increase with
increasing elevation with a peak at the mid-elevation zone. This was not possible in our study since *P. roxburghii* tend to form nearly mono-dominant stand in the mid-elevation sites (E2 and E3) which contributed to observed reduction in diversity indices in these sites. It doesn’t allow other species to proliferate in its vicinity because of its capacity to immobilise the soil nutrients which makes it unavailable to other species (Singh et al. 1994). Additionally, it forms thick needle-like leaf layer on forest floor that hinders the growth of other species. Therefore, competition exclusion might be another phenomenon responsible for the paucity of tree species diversity in these sites. Since according to the species-area hypothesis, species diversity should increase with the number of forest plots observed within a study region, we would expect a decrease in similarity of plant species composition with geographic distance among forest sites. Indeed, it was shown that geographic distance led to a reduction in floristic dispersion among forest plots (Prada et al. 2017) with increasing elevation and change in aspect. Thus, we found distinct species composition associated with certain forest habitat types varying across the study region.

(Måren et al. 2015) in his study on variation in species composition in semi-arid trans-Himalayan region based on slope aspect found high density of tree species in north aspect and few species were restricted to the north aspect only. The present study did not find aspect to play significant role in governing species composition and structure, however the values for tree density and basal area were found greater for northern aspect as compared to south. Maximum tree density and basal area were reported for higher elevation and northern aspect sites. Sharma & Baduni (2000) also reported the highest tree density at an elevation of 2875m in their studies covering an elevation gradient of 2600 m to 2875 m. Lower atmospheric pressure, higher atmospheric precipitation, and humidity might be the reason for increased density at a higher elevation (Sharma et al. 2010). (Singh 1998) reported highest human population density in 1000–2000 m elevation zone in the Indian Himalayan region. On the contrary, lowest tree
density values were found for this range in the present study which could certainly be due to increased number of household residences in lower elevation zone which are dependent on the forest resources for their survival and livelihood. For instance, species such as *Q. leucotrichophora* is one of the most important species supporting human livelihood in such regions (Rawal et al., 2012). This suggested natural and anthropogenic disturbance factors such as lopping, deadwood counts, etc. to be equally important in governing species composition and diversity. Another study conducted at three sites of sub-alpine forests revealed that density decreased with increasing elevation (Gairola et al. 2012). We here observed the same trend of decreasing total basal area and density of shrub species with increasing elevation. This was specifically due to contribution of maximum basal area at lower elevation by *Lantana camara* (~50%) which is an invasive species. *Lantana camara* was found to take advantage of scattered canopy cover on south aspect and it doesn’t allow other species to grow in its periphery. Therefore, due to competition for resources and space, invasive shrub species grow well in lower elevation zone leading to lower tree density as compared to higher elevation (Kumar et al. 2021). We found shrub density and basal area to be higher at lower elevations, unlike tree layer. This might be due to scattered tree canopy at lower elevations allowing more light penetration such that the understorey species can proliferate well.

**Topographical heterogeneity and vegetation structure drives edaphic factors**

There is increasing amounts of evidence that soil moisture plays an important role in governing the composition of vegetation communities in mountainous landscapes (Kutiel and Lavee 1999; Panthi M et al. 2007). Differences in soil MC played an important role in controlling species composition across the sites. The higher elevational site (E4 and E5) has greater soil MC which might be due to dense canopy and multi-layering at higher altitudinal forest whereas lower density and basal area at lower elevation creates sparse canopy cover which enhances light penetration resulting in higher evaporation rate and lower moisture content (Saxena and
The study suggested increased amount of soil nutrient (N and K) along with OC and MC to be greater in higher elevation sites. The complex structure of the vegetation in the study region results from the interaction of edaphic factors and associated forest attributes. The successional changes occurring in an ecosystem with time and their development process bring about changes in edaphic properties whereas selective absorption of macro- and micro-nutrients by different species alters the process of feedback mechanism by them (Singh, 2018, 2021). PCA plot showed tree basal area and soil total nitrogen were strongly correlated along with soil OC. Generally, the increase in OC with increasing elevation is due to an increased amount of litter accumulation on the forest floor and due to lower temperatures, there is a very slow rate of decomposition (Singh & Kashyap, 2006) and lower turnover of nutrients and thus selects for species with a conservative resource-use strategy characterized by slow growth and high biomass (Quesada et al., 2012). Also, increase in soil nitrogen and available potassium with increasing basal area might be the result of increased tree growth which in turn leads to higher nutrient returns via litterfall (Verma and Garkoti 2019). A possible explanation for this might be that presence of organic matter due to reduced decomposition rate at higher elevation leads to slow turnover of plant materials that significantly improves the retention of potassium in the soil (Sharma et al. 2006) but this impacted the phosphorus concentration which was lower in higher elevation sites. Aspect significantly affected moisture content, bulk density, phosphorous, and potassium in the present study however, other soil parameters were not affected confirming relatively low role of aspect in creating differences in soil parameters. The study site showed slightly acidic pH throughout which is recommended for nutrient availability to the plants in the forest (Paudel and Sah 2003). Thus, the study suggested soil moisture content and nutrient availability are the important edaphic constraints for species distribution which are significantly influenced by topographical variation. CCA also confirmed that the sites at higher elevations had higher AP and MC content which might be due to slower cycling.
of nutrients in response to reduced decomposition at low temperatures while reduced weathering rates at lower elevation might have caused relatively lower nutrient turnover rates. However, over any large region, distribution of species is supposed to be governed by two or more environmental factors, not a single factor (Sagar et al. 2008).

Topographical heterogeneity and associated edaphic properties regulate regeneration pattern

Density diameter curve suggested high density of species in lower DBH class whereas absence of old-growth individuals in higher DBH class indicating natural succession of young forests as opposed to mature forest stands (Singh & Singh, 1986). However, higher elevation sites (E5) followed bell-shaped pattern indicating mature forest stands. However, species-wise (for Pinus roxburhii, Q. leucotrichophora and Q. semicarpifolia) population structure showed slight discontinuity in number of individuals with increasing DBH class. This was mainly due to different levels of environmental harshness to be responsible for governing population structure. The seedling density varied nearly three-fold and sapling density varied nearly two-fold amongst the study sites. The values fit the values reported by previous studies from other regions located in the Himalayas (Pant and Samant 2012; Pala et al. 2013; Malik and Bhatt 2016). Seedling and sapling density decreased with increasing elevation while the opposite was found for matured tree individuals. This might be due to the lower survival rates of species in lower elevation sites along with low soil TN which increases with increasing basal area. This suggests that lower elevation sites are characterized by late-successional forest stands with low stand density but higher recruitment rates. A higher number of saplings indicate an increased survival rate and low mortality rate (Uriarte et al. 2018). Increased seedling density at lower elevation sites could be also due to increased amount of light penetration to the ground layer creating favourable conditions for regeneration, unlike higher elevation sites which form closed canopy due to increased density and basal area (Singh 1998). Also, reduced seedling density in E2 (1000-1500 m) sites might be due to mono-specific nature of P. roxburghii that forms
thick needle-like leaf layer on forest floor obstructing the growth of seedlings in the area. It also holds the capacity to immobilise soil nutrients which makes it unavailable to other species seedlings (Saikia et al. 2009). Therefore, there occurs an increased rate of competition for the survival of new seedlings in such sites. This suggests vegetation attributes and soil nutrient availability along with topography play a major role in governing the regeneration potential in such regions (Terakunpisut et al. 2007; Gairola et al. 2012). Furthermore, these changes cause differences in the overall productivity of the region (Hall et al., 2006).

Implications for forest management under future scenarios

Montane forests are very fragile ecosystems and are highly affected by variation in climatic changes and global warming scenarios (Barradas et al. 2011). A forest having multi-layered canopy with significant canopy index and depth, as well as forest floor rich in organic matter and nutrients has a greater protective value compared to a forest with lesser layers and a lower canopy index (Kumar et al. 2013). Without adequate baseline data on floristic composition and diversity and factors determining regeneration potential are fundamental for management of natural regions (Prada et al. 2017). Variation in soil properties adds another dimension to changes in species diversity and species distribution pattern. The aforementioned parameters are therefore liable for creating variations in ecosystem functioning at local level (within stand differences) as well as landscape-level (between stand differences), thereby producing spatial heterogeneity (Timilsina et al. 2007). Studies conducted to date suggest that more emphasis should be given to the northern aspect for conservation as well as restoration purposes due to its favourable properties for plant growth(Sharma et al. 2010). However, a similar assessment of management implementations should be considered for the southern aspect. After a reconnaissance survey, one should adopt different strategies for the conservation of vegetation in different habitat types. In moist Shiwalik Sal forest, reduced density, and basal area due to increased dominance of *L. camara* should be managed using mechanical uprooting
and chemical control methods whereas, in the pine forest, pine leaves that form the forest floor further inhibiting regeneration and habitation of other species should be collected and removed periodically. The soils at higher altitudes (Himalayan moist temperate forests) with steeper slopes having scattered canopy tend to get eroded easily. Programs should be launched to cover those areas with native shrub species as well as fast-growing and light-demanding species to reduce the chances of erosion and maintain overall soil properties at both aspects. Therefore, it is recommended that plantation of species should be considered for both aspects to increase biodiversity and a sustainable management of Himalayan forests. Also, predictive models of vegetation changes suggest climate be the most important factor exerting strong effect on variation in species composition and diversity (Heikkinen et al. 2006). However, several studies, in line with this study suggest plant composition and diversity to be largely affected by edaphic properties, such as soil pH, elevation, slope aspect, and, soil nutrients (Bertrand et al. 2012). Therefore, evaluation of edaphic parameters and topographic features such as slope aspect and elevation could benefit projections of next-generation vegetation models significantly (Franklin et al., 2020)

Conclusions

The study suggests that among topographic factors, elevation rather than slope aspect is important in governing differences in species composition among study sites in Western Himalayan Montane forests. Tree density and basal area were found maximum at higher elevation sites while seedling and sapling density along with shrub density and basal area were maximum at lower elevation sites. This was basically due to increased light penetration for understorey and regenerating species due to scattered canopy at lower elevation sites. Variation in soil properties adds another dimension to changes in species diversity and distribution pattern. Soil nutrient (TN, AP and AK) along with OC and moisture content significantly
increased with increasing elevation. Therefore, the study concludes that topographical variation
and an increased sum of OC, TN, and available K contents of the soil, are highly favorable for
the growth and development of plant species. Population structure was found to expand at
lower elevation sites (E1) which indicates rapid growth in population. However, higher
elevation sites (E5) followed bell-shaped pattern indicating mature forest stands. There is a
growing need for incorporation of the herbaceous layers that form a significant part of the forest
understory and thus should allow to improve predictions based on observations of the
overstory, which might lead to uncertainties related to changes in species composition under
future scenarios. The study also strongly argues integration of spatial and temporal
heterogeneity across resource gradient at both local and regional scales to analyze the species-
environment relationships considering several abiotic as well as biotic factors.
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Statements & Declarations

Funding

University Grants Commission (UGC) (Grant number: 3787/NET-DEC 2018), New Delhi, India.

Competing Interests

The authors declare no competing interests among themselves.

Author contributions

Fig. 1. Location of the selected sites in Sirmour district (Study Area), Himachal Pradesh, Indian Himalaya. The different symbols represent different elevation ranges. ●: 500-1000 m asl, ■: 1001-1500 m asl, ▲: 1501-2000 m asl, ○: 2001-2500 m asl, ●: 2501-3000 m asl.
Fig. 2. Non-metric multidimensional scaling (NMDS) for tree layer. Plots located on different elevation zones were represented based on Bray-Curtis dissimilarity (stress 0.03). Permutational analysis of Variance indicates significant variation among sites (F=5.72, \( p<0.001 \)). Species abbreviations are mentioned in Fig. S1.
Fig. 3. Line plots showing variation in tree Density (ind ha$^{-1}$), Basal Area (m$^2$ ha$^{-1}$), Species Richness, Shannon diversity and Species Evenness with increasing elevation and contrasting slope aspect: North (red) and South (blue).
Fig. 4. Non-metric multidimensional scaling (NMDS) for the shrub layer. Plots located on different elevation zones were represented based on Bray-Curtis dissimilarity (stress 0.15). Permutational analysis of Variance indicates significant variation among sites (F=6.29, p<0.001). Species abbreviations are mentioned in Fig. S2.
Fig. 5. Line plots showing variation in shrub Density (ind ha$^{-1}$), Basal Area (m$^2$ ha$^{-1}$), Species Richness, Shannon diversity and Species Evenness with increasing elevation and contrasting slope aspect: North (red) and South (blue).
Fig. 6. Line plots showing variation in Density (ind ha$^{-1}$) and Basal Area (m$^2$ ha$^{-1}$) for trees (upper panel) and shrubs (lower panel) with increasing elevation and contrasting slope aspect: North (red) and South (blue).
Fig. 7. Population structure of tree species for all the sites: E1N (400-1000 m asl northern aspect), E1S (400-1000 m asl southern aspect), E2N (1001-1500 m asl northern aspect), E2S (1001-1500 m asl southern aspect), E3N (1501-2000 m asl northern aspect), E3S (1501-2000 m asl southern aspect), E4N (2001-2500 m asl northern aspect), E4S (2001-2500 m asl southern aspect), E5N (2501-3000 m asl northern aspect) and E5S (2501-3000 m asl southern aspect) where x-axis represents DBH Class (Diameter at Breast Height) and y-axis represents number of individuals.
Fig. 8. Regeneration status (seedlings and saplings, no. of individuals ha$^{-1}$) of tree species with increasing elevation for contrasting slope aspect: North (red) and South (blue).
Fig. 9. Linear regression analysis of soil properties along increasing elevation
[Moisture Content (MC %), Bulk Density (BD g cm$^{-3}$), pH (unitless),
Texture-Sand, Silt and Clay (%), Organic Carbon (OC %), Total Nitrogen
(TN %), Available Potassium (AK %), Available Phosphorous (AP %)].
Right panel: Box plot with t-test showing variation in soil properties with varying slope aspect:
North (blue) and South (yellow). The limits of boxes indicate the first and third quartiles, and
the horizontal line within boxes corresponds to the median. The upper whisker extends from
the third quartile to the highest value within $1.5 \times$ IQR (interquartile range) of the third quartile.
The lower whisker extends from the first quartile to the lowest value within $1.5 \times$ IQR of the
first quartile.
Fig 10. Principal Component Analysis of vegetation attributes and soil parameters among sites.

Abbreviations: Density (Den, individuals ha\(^{-1}\)), Basal Area (BA, m\(^2\) ha\(^{-1}\)), Seedling and Sapling (individuals ha\(^{-1}\)), Shannon-Weiner Diversity (H', unitless), Species Richness (SR, unitless), Species Evenness (SE, unitless), Moisture Content (MC %), Bulk Density (BD g cm\(^{-3}\)), pH (unitless), Texture-Ratio of Sand, Silt and Clay (%), Organic Carbon (OC %), Total Nitrogen (TN %), Available Potassium (AK %), Available Phosphorous (AP %).
Fig. 11. CCA ordination diagram of tree species (red) among the study sites (black) to analyze the major gradients among the combination of explanatory variables. The length of vectors in the ordination diagram represents the strength of the correlation, while the angle between two vectors shows the degree of correlation among variables with each axis. Species abbreviations are mentioned in Figure S2.
Fig. 12. A Venn diagram showing the partitioning of variation according to four groups of independent variables, Elevation, Vegetation (Density, Basal area and Species Richness), Soil properties (Moisture content, Texture and soil nutrients) and Slope aspect. The rectangle corresponds to the total variation in the dependent (species regeneration) data. Each area of overlap of the four ellipses is representative of the intersection of the four groups in terms of their explained variation. The area of the rectangle (total variation) that the four ellipses do not cover represents the unexplained variation (residuals) (refer to Table S2 for negative adjusted R-square values of each class).
Supplementary Files

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