

# Topographical heterogeneity governs species distribution and regeneration potential by mediating soil attributes in Western Himalayan forests

Shipra Singh (✉ [singhs@iiasa.ac.at](mailto: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

**Keywords:** Diversity, Elevation, Forest structure, Montane ecosystem, Slope aspect

**Posted Date:** October 20th, 2023

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

**License:**  This work is licensed under a Creative Commons Attribution 4.0 International License.

[Read Full License](#)

**Additional Declarations:** No competing interests reported.

---

1 **Topographical heterogeneity governs species distribution and regeneration potential by**  
2 **mediating soil attributes in Western Himalayan forests**

3 Shipra Singh<sup>1,2\*</sup>, Abhishek K. Verma<sup>2,3</sup> and Florian Hofhansl<sup>1</sup>

4 <sup>1</sup>International Institute for Applied Systems Analysis, Schlossplatz 1, A-2361 Laxenburg,  
5 Austria.

6 <sup>2</sup>School of Environmental Sciences, Jawaharlal Nehru University, New Delhi, India.

7 <sup>3</sup>Forest Ecology and Climate Change Division, Forest Research Institute, Dehradun,  
8 Uttarakhand-248006, India.

9 Corresponding author: Shipra Singh ([singhs@iiasa.ac.at](mailto:singhs@iiasa.ac.at))

10

11 **Acknowledgement**

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

18 **Abstract**

19 The present study is an attempt to understand variation in species composition  
20 and diversity and soil properties along topographic gradients in Western Himalayan reserve  
21 forests (400-3000m asl). To analyze changes in floristic composition, diversity, and  
22 regeneration status, we measured woody vegetation in forest plots at different altitudinal levels  
23 and contrasting aspects (North and south). Trees (diameter at breast height (DBH)>10cm) and  
24 saplings (3-10cm DBH) were sampled in 10m×10m plots, shrubs were sampled in 5m×5m  
25 plots and seedlings (0-3cm DBH) were sampled in 1m×1m plots. To study variation in soil  
26 properties, samples were collected from each forest stand in five replicates from layers of 0-  
27 10cm, 10-20cm, and 20-30cm in soil depths. Canonical Correspondence Analysis (CCA) was  
28 applied to identify important factors that govern species distribution. Variance partitioning was  
29 conducted to quantify the relative contribution of elevation, slope aspect, vegetation attributes,  
30 and soil properties on regeneration potential of tree species. We found that environmental  
31 filtering shapes local species composition and associated edaphic factors in the region. Species  
32 richness and diversity were found to decrease with elevation. Soil properties (Organic Carbon,  
33 pH, and texture) and associated vegetation parameters did not vary significantly between the  
34 aspects. CCA confirmed that species composition was positively related to moisture content  
35 and available phosphorous at higher elevations, while reduced weathering rates and bulk  
36 density at lower elevations might have caused relatively lower nutrient turnover rates. Our  
37 study concludes that topographical variation and increased sum of soil nutrients are highly  
38 favorable for growth and development of plant species.

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

## 40 **Introduction**

41           Topographical features, such as slope angle, aspect, and elevation (Singh, 2018) affect  
42 species diversity, ecosystem structure and processes, resource availability, and energy  
43 partitioning in forest ecosystems (Jucker et al., 2018; Méndez-Toribio et al., 2016) through the  
44 modification of the surrounding environment (Ali et al., 2019; Jucker et al., 2018). In Montane  
45 Forest ecosystems, the slope aspect and topographical position are the most influential drivers  
46 of temperature changes (Geml 2019) and soil water content variability (Wang et al. 2011).  
47 North-facing slopes are characterized by relatively moist conditions and cooler temperatures,  
48 whereas south-facing slopes are comparatively warmer and drier (Holland and Steyn 1975).  
49 However, this relationship is inverted in the northern and southern hemispheres, such that the  
50 northern hemisphere exhibits a cooler climate at north-facing slopes while the same applies to  
51 south-facing slopes in the southern hemisphere (Budyko, 1969). Resulting differences in solar  
52 radiation, soil water content, and temperatures between the two different aspects strongly affect  
53 the vegetation's structure and composition (Guo et al. 2017; Jucker et al. 2018). Furthermore,  
54 the asymmetry in environmental drivers between northern and southern aspects was shown to  
55 affect crucial ecosystem processes such as organic matter decomposition, which in turn  
56 determines local resource availability of water and nutrients (Sidari et al. 2008; Fortunel et al.  
57 2018; Muscarella et al. 2020). The slope aspect further governs the input of solar energy at the  
58 landscape level forming distinct microclimatic conditions (Goran et al., 2012; Jucker et al.,  
59 2018), which trigger differences in temperature, moisture, humidity, and evaporation  
60 (Chadwick and Asner 2016; Jasińska et al. 2019), and thus affect soil edaphic properties and  
61 vegetation dynamics (Eisenlohr et al. 2013; Uriarte et al. 2018; Yang et al. 2020). Due to the  
62 linkage of elevation and slope aspect to multiple environmental variables, topography has been  
63 proposed as the single most important factor responsible for determining spatial patterns of  
64 biodiversity (Singh, 2018; Tiwari et al., 2020; Yang et al., 2020).

65           Within a micro-climatic condition, forest attributes such as species composition and  
66 diversity along with edaphic properties affect the regeneration pattern in montane forest  
67 ecosystems (Rodrigues et al. 2020). Forest stands having increased soil moisture and optimum  
68 light availability tend to regenerate rapidly (Verma and Garkoti, 2019). Topographical  
69 heterogeneity creates variations in soil nutrient availability, pH, and soil texture that ultimately  
70 affects regeneration pattern in any region (Pinho et al. 2018; Tiwari et al. 2020) via mediating  
71 their effect on species composition and richness (Laughlin et al. 2015). In addition, temperature  
72 variability with increasing elevation plays an important role in understanding seedling survival  
73 rates, providing clues for climate change effects (Dobrowski et al. 2015; Shive et al. 2018;  
74 Verma and Garkoti 2019). Thus, regeneration potential could be considered an important  
75 indicator to analyze shift in vegetation composition and diversity with changing climate  
76 (Woodall et al. 2018). Regeneration of species on gentle slope tends to be comparatively higher  
77 as compared to steeper slope (Finegan and Delgado 2000; Estrada-Villegas et al. 2020). The  
78 gradual development of an individual from seedling to mature individual faces increased  
79 environmental harshness with increasing elevation (Yan et al. 2015). Additionally, it has also  
80 been found that saplings are more prone to environmental harshness with increasing elevation  
81 (Liang and Wei 2020). With increasing topographical heterogeneity, distinct regeneration  
82 niche leads to species stabilization in different ecosystems (Dobrowski et al. 2015; Uriarte et  
83 al. 2018).

84           Mountain regions are considered an important habitat for endemic species and natural  
85 forest vegetation, which typically provides important ecosystem services, such as carbon  
86 sequestration, nutrient cycling, climate regulation, and timber production (Ai et al. 2017). In  
87 addition, montane forest ecosystems provide natural laboratory conditions to understand the  
88 important biotic and abiotic factors shaping species composition and biodiversity locally as  
89 well as globally (Raz et al. 2009). These differences vary greatly depending on the scale of

90 observation (Jarzyna & Jetz, 2018) and the underlying environmental factors governing species  
91 composition at the landscape-scale (Hofhansl et al. 2021). Regional studies investigating  
92 biodiversity, species composition, and plant community structure along altitudinal gradients,  
93 have documented soil physicochemical properties as drivers of vegetation structure in Central  
94 Himalayan regions (Kharkwal et al. 2005; Sharma et al. 2010; Gairola et al. 2012; Tiwari et al.  
95 2020) but are comparatively missing in Western Himalayan forests. Therefore, we state that  
96 there is currently a lack of knowledge about the effect of contrasting slope aspects on vegetation  
97 composition at varying elevations, which would be required to develop sustainable  
98 management strategies for Montane Forest ecosystems in the Western Himalaya. The objective  
99 of this study was 1). To investigate the effect of topography (slope aspect and elevation) on  
100 soil properties (soil texture and chemistry) and woody vegetation characteristics (floristic  
101 composition and diversity, forest structure and regeneration pattern) and 2). To quantify the  
102 relative contribution of topography and soil properties on regeneration potential in the  
103 protected forests of the Western Himalayan region. Due to the fact that topographic features  
104 such as slope aspect and elevation drive environmental heterogeneity among forest sites, we  
105 hypothesized that (1) soil properties and associated woody vegetation characteristics differ  
106 along elevational gradients; such that (2) local plant species composition varies with specific  
107 forest habitat types located along environmental gradients of the study region and therefore,  
108 (3) the impact of topographically mediated species composition and associated soil properties  
109 might affect regeneration potential of species. Eventually, we discuss our findings in light of  
110 the scientific literature with the goal to develop sustainable forest management  
111 recommendations for the Western Himalayan Forest ecosystems.

## 112 **Methods**

### 113 Study site

114 The study was conducted in protected forests located between 30° 22'30"–31° 01'20"  
115 N, and 77°01'12"–77°49'40" E in Sirmour district, Himachal Pradesh (Fig. 1). The altitudinal  
116 variation of Sirmour district ranges between 400 m a.s.l. and 3630 m a.s.l., with Churdhar peak  
117 being the highest point of the district. The climate of the district is sub-tropical to temperate  
118 depending upon the elevation. Climate varies from hot and dry (up to 1,800 m) to moderate  
119 (1,800-2,500 m) and cold to very cold at higher elevations (2,500-3,630 m). The temperature  
120 in the summer season (May-June) ranges between 15 to 42 °C, while in the winter season  
121 (November-February), it varies from 0 to 21 °C. The region has an average annual rainfall of  
122 1,014-1,547 mm with an average of 1,250 mm (District Survey Report, 2016) (Fig. S1). The  
123 region also experiences snowfall above the altitude 1800 m. The rocks found in the area consist  
124 of sandstone, shale, limestone, and schist (Rawat et al. 2010). Soil type varies from deep  
125 alluvial sandy loam at lower elevation to clayey loam at higher elevations (District Survey  
126 Report, 2016).

### 127 Site selection

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

136 Vegetation analysis

137            Physiographic factors i.e., altitude and coordinates across different forest types were  
138 determined by Global Positioning System (GPS-Garmin). Sampling was conducted in two  
139 layers of the vegetation i.e., adult trees and shrub layers, and three life cycle stages of tree  
140 species i.e., adult trees (Circumference at breast height, CBH >30 cm), saplings (10-30 cm  
141 CBH), seedlings (CBH <10 cm) (Saxena and Singh 1984). A total of 200 plots (20 plots × 5  
142 elevation zones × 2 slope aspect) measuring 10 m × 10 m each were sampled between  
143 September 2016 and April 2017. Shrub species and tree saplings were sampled within sub-  
144 plots of 5 m × 5 m, and tree seedlings within sub-plots of 1 m × 1 m (Curtis and McIntosh  
145 1950). Tree and shrub species were identified with the Glossary of forest flora provided by the  
146 Sirmour district Forest Department at Forest Division, Nahan, and Rajgarh. CBH was used for  
147 determination of tree basal area, which was later converted to the DBH (Diameter at breast  
148 height). The data were quantitatively analyzed for stem density, frequency, and abundance  
149 following (Curtis and McIntosh 1950). Shannon-Wiener Diversity index (H') (Shannon and  
150 Weaver 1949), Species evenness (SE) (Pielou 1966), and species richness (SR) (Margalef,  
151 1973) were calculated. Density-diameter distribution curve (population structure) for each site  
152 along with the dominant tree species was analyzed by plotting the graph against the number of  
153 individuals in different DBH classes i.e., 0-10; 10-20; 20-30; 30-40; 40-50; 50-60; 60-70; 70-  
154 80; and 80-90 cm respectively. The regeneration pattern of tree species was analyzed based on  
155 the presence of number of seedlings, saplings, and adults of each species (Khan et al., 1987).

156 Soil sampling and analysis

157            From each of the ten forest stands, soil samples were collected in five replicates from  
158 layers of 0-10 cm, 10-20 cm, and 20-30 cm in soil depth to analyze variations in physical and  
159 chemical properties. Soils were sampled using a soil corer of 5 cm inner diameter and were  
160 packed in airtight zip bags and brought to the laboratory. Soil samples were air-dried for 48

161 hours and sieved through a 2 mm and 0.5 mm sieve for further analysis. Soil moisture content  
162 (MC) was determined gravimetrically on a wet basis by oven drying 10 g of fresh soil at 105 °C  
163 for 48 hours Mishra (1968). Soil bulk density (BD) was determined from the undisturbed core  
164 segments as dry soil mass per unit volume (Ingram and Anderson 1993). The Bouyoucos  
165 hydrometer method of silt and clay measurement was followed for analysis of particle size  
166 using 10% Calgon's solution (sodium hexametaphosphate) (Okalebo et al., 2002). Organic  
167 carbon (C) of the soil sample was measured with dichromate oxidation using an air-dried  
168 sample of 1 g and titrating with FeSO<sub>4</sub> based on modified Walkley and Black method (Verma  
169 et al. 2021) Total Nitrogen (N) was estimated by digesting 3 g soil sample with concentrated  
170 H<sub>2</sub>SO<sub>4</sub> and K<sub>2</sub>SO<sub>4</sub>:CuSO<sub>4</sub> catalyst, and further analyzed using Micro-Kjeldahl apparatus  
171 (KELPLUS Distyl-EMBA) (Jackson, 1973). Available Potassium (K) was extracted following  
172 neutral normal ammonium acetate method (Morwin and Peach, 1951) and was determined  
173 using the flame photometer. Available Phosphorous (P) was estimated colorimetrically using  
174 Bray reagent (0.025N HCl in 0.03N NH<sub>4</sub>F) in 1N sulphuric acid system (Bray and Kurtz,  
175 1945).

#### 176 Statistical analysis

177 Data matrices of species' IVI and the corresponding variables were prepared in Microsoft  
178 Excel-2019. Soil data normality was assessed based on Shapiro–Wilk's test and homogeneity  
179 of variance was tested by Levene's test. Non-metric multidimensional scaling (NMDS) was  
180 performed to visualize the floristic associations among the sites by using Bray–Curtis  
181 dissimilarities (Minchin 1987) using the metaMDS function of the vegan package. Significant  
182 differences in species composition were determined through permutational multivariate  
183 analysis of variance (PERMANOVA) by using the adonis function of the vegan package  
184 (Clarke, 1993). Species vegetation parameters and diversity indices were determined using  
185 different functions of the vegan package and visualized using ggplot2 package.  $\beta$  diversity

186 variation along the elevation gradient and between contrasting slope aspect was analysed using  
187 the quantitative Sorensen (Bray–Curtis) distance measure (Yang et al. 2020). The analysis was  
188 done using betadiver function of the vegan package. Comparison of vegetation structure and  
189 diversity along elevation, contrasting slope aspect, and their interaction were analyzed using  
190 two-way ANOVA for the study sites, and the differences were reported significant at  $P < 0.05$ .  
191 Soil values were regressed along elevation using ggplot2 function. Soil values were visualized  
192 using box plot for contrasting slope aspect and independent t-test was applied to calculate the  
193 difference of means between north and south aspect. Further, Principal Component Analysis  
194 (PCA) was used to analyze correlation among vegetation parameters and soil properties using  
195 factoextra and imputeTS packages. Additionally, Canonical Correspondence Analysis (CCA)  
196 was used to investigate significant relationships between tree species distribution and  
197 associated environmental variables among study sites. After CCA, the Monte Carlo test was  
198 used to evaluate the effect of explanatory variables obtained on the vegetation composition  
199 using cca function. In the end, variance decomposition analysis was done to quantify the  
200 relative importance of the environmental factors that shape the regeneration potential in the  
201 region thus confirming the important factors that affect the regeneration pattern using varpart  
202 function of the vegan package. All statistical analyses were conducted using R version 3.5.0 (R  
203 Core Team, 2018).

204

## 205 **Results**

### 206 Floristic composition and species diversity

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

230 and shrub layer, however, the differences were not found significant. The diversity indices were  
231 found significantly varying with increasing elevation for both tree and shrub layer (Table S1).

### 232 Vegetation structure and regeneration pattern

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

252 Moisture content (MC) was found significantly increasing with elevation ( $R^2=0.63$ ,  
253  $P<0.001$ ) (Fig. 9). Between the contrasting slope aspect, MC was found to be significantly

254 different ( $P < 0.05$ ) being greater for northern aspect. The values for MC were found increasing  
255 with increasing depth (Table S2). Similarly, bulk density was also found increasing with soil  
256 depth and the values were found to be significantly greater for southern aspect than northern  
257 aspect ( $P < 0.05$ ). Texture of the soil varied from sandy loam to loam irrespective of aspect,  
258 elevation, and depth. Soil pH was found to be acidic to slightly acidic throughout the study site.  
259 Soil OC decreased with increasing depth and the values were found to increase with elevation  
260 significantly ( $R^2 = 0.53$ ,  $P < 0.001$ ). Similarly, Total N, Available K, and Available P decreased  
261 with increasing soil depth. Available P and Available K were found significantly varying with  
262 elevation. All the soil nutrients (N, P, K) and OC showed greater values in the north aspect as  
263 compared to south. PCA plot explained around 49% of variation in vegetation and soil  
264 properties among sites (Fig. 10). PCA clearly showed two spectra of variation among the sites.  
265 The first PC axis reflected increased soil pH and BD. Whereas the second spectra of variation  
266 showed increased diversity ( $H'$  and SR), seedling, and sapling count at lower elevations on one  
267 hand and increased MC, organic C, and soil nutrient (N,P,K) at higher elevations on the other  
268 hand. Constrained correspondence analysis (CCA) revealed the interrelationship of species  
269 assemblage, study sites, and environmental variables (Fig. 11), such that environmental  
270 heterogeneity caused distinct clusters of floristic composition at different elevations, which in  
271 turn significantly ( $P < 0.05$ ) affected MC, AP, Texture and BD. The CCA plot furthermore  
272 indicated that elevation significantly affected species composition via increased MC and AP at  
273 higher elevation sites and by decreased soil BD at lower elevation sites. The eigenvalues were  
274 0.92 (CCA axis 1) and 0.81 (CCA axis 2) whereas, the proportion of cumulative variance  
275 explained for CCA1 and CCA2 were 70.23 and 87.91% respectively. The total inertia was 3.45  
276 while the explanatory variables accounted for 82% variation. The Monte Carlo test showed  
277 significant variation after permutations (F-ratio: 3.41,  $P < 0.001$ ). Further, the effect of  
278 topographical heterogeneity (elevation and slope aspect), associated vegetation attributes and

279 soil properties on regeneration potential were visualised using venn diagram. The explanatory  
280 variables used for the analysis were grouped into four classes: Elevation, Aspect, Edaphic  
281 factors (Soil texture, pH, BD and OC) and Vegetation attributes (Density, Basal Area and  
282 species richness). Variation partitioning tests (partial CCA) were conducted for all 15 possible  
283 classes (Table S3). Overall variation in regeneration pattern explained by the associated  
284 environmental factors was 94%. Maximum variation was explained by soil properties (41.12%)  
285 followed by elevation (39.18%), vegetation attributes (37.59%) and aspect (18.33%) (Fig. 12),  
286 which reflected the number of variables in a particular category. The value of fractions with  
287 shared variance were not very high. Hence it was found that the variance partitioning among  
288 factors explaining regeneration potential revealed a significant relation to environmental and  
289 topographical variables.

## 290 **Discussion**

291 We found striking variation in soil properties and associated vegetation characteristics  
292 between inventory plots located in Western Himalayan forests. In accordance with foregoing  
293 studies our analysis identified topography as the most important factor affecting taxonomic  
294 species composition along orographic gradients (Måren et al., 2015; Méndez-Toribio et al.,  
295 2016). However, we furthermore showed that variation in soil properties (MC, BD, AP, and  
296 texture) was the underlying factor driving these relationships, such that there are distinct  
297 clusters in taxonomic species composition associated with specific forest habitats across the  
298 landscape.

### 299 Environmental filtering shapes local species composition and diversity

300 Species composition significantly differed among the elevation zones based on NMDS, such  
301 that species composition at lower elevation (E1 and E2) was found to be completely different  
302 from that at higher elevation (E4 and E5), while the mid-elevation zone (E3) created an ecotone  
303 with the adjacent community (E4). Distinct cluster formation across the elevation zones might  
304 be due to the creation of patchy microhabitats based on resource availability and competition  
305 in a heterogeneous environment (Guo et al. 2017). Thus, the distribution of species and their  
306 co-existence are strongly under environmental control having different microhabitats  
307 irrespective of their life histories (Douda et al. 2012). For instance, *S. robusta* and *M.*  
308 *phillipensis* were restricted to lower elevations (E1) whereas *A. pindrow* and *Q. semecarpifolia*  
309 dominated the higher elevation sites (E5). Therefore, the observed strong differences in species  
310 composition are probably due to different ecological adaptation of species surviving in different  
311 environmental conditions (Yang et al. 2020). This separation of species composition in the  
312 region supports the Champion and Seth (1968) forest classification which classified forest  
313 vegetation based on climate variability. Species diversity is expected to increase with

314 increasing elevation with a peak at the mid-elevation zone. This was not possible in our study  
315 since *P. roxburghii* tend to form nearly mono-dominant stand in the mid-elevation sites (E2 and  
316 E3) which contributed to observed reduction in diversity indices in these sites. It doesn't allow  
317 other species to proliferate in its vicinity because of its capacity to immobilise the soil nutrients  
318 which makes it unavailable to other species (Singh et al. 1994). Additionally, it forms thick  
319 needle-like leaf layer on forest floor that hinders the growth of other species. Therefore,  
320 competition exclusion might be another phenomenon responsible for the paucity of tree species  
321 diversity in these sites. Since according to the species-area hypothesis, species diversity should  
322 increase with the number of forest plots observed within a study region, we would expect a  
323 decrease in similarity of plant species composition with geographic distance among forest sites.  
324 Indeed, it was shown that geographic distance led to a reduction in floristic dispersion among  
325 forest plots (Prada et al. 2017) with increasing elevation and change in aspect. Thus, we found  
326 distinct species composition associated with certain forest habitat types varying across the  
327 study region.

328 (Måren et al. 2015) in his study on variation in species composition in semi-arid trans  
329 Himalayan region based on slope aspect found high density of tree species in north aspect and  
330 few species were restricted to the north aspect only. The present study did not find aspect to  
331 play significant role in governing species composition and structure, however the values for  
332 tree density and basal area were found greater for northern aspect as compared to south.  
333 Maximum tree density and basal area were reported for higher elevation and northern aspect  
334 sites. Sharma & Baduni (2000) also reported the highest tree density at an elevation of 2875m in  
335 their studies covering an elevation gradient of 2600 m to 2875 m. Lower atmospheric pressure,  
336 higher atmospheric precipitation, and humidity might be the reason for increased density at a  
337 higher elevation (Sharma et al. 2010). (Singh 1998) reported highest human population density  
338 in 1000–2000 m elevation zone in the Indian Himalayan region. On the contrary, lowest tree

339 density values were found for this range in the present study which could certainly be due to  
340 increased number of household residences in lower elevation zone which are dependent on the  
341 forest resources for their survival and livelihood. For instance, species such as *Q.*  
342 *leucotrichophora* is one of the most important species supporting human livelihood in such  
343 regions (Rawal et al., 2012). This suggested natural and anthropogenic disturbance factors such  
344 as lopping, deadwood counts, etc. to be equally important in governing species composition  
345 and diversity. Another study conducted at three sites of sub-alpine forests revealed that density  
346 decreased with increasing elevation (Gairola et al. 2012). We here observed the same trend of  
347 decreasing total basal area and density of shrub species with increasing elevation. This was  
348 specifically due to contribution of maximum basal area at lower elevation by *Lantana camara*  
349 (~50%) which is an invasive species. *Lantana camara* was found to take advantage of scattered  
350 canopy cover on south aspect and it doesn't allow other species to grow in its periphery.  
351 Therefore, due to competition for resources and space, invasive shrub species grow well in  
352 lower elevation zone leading to lower tree density as compared to higher elevation (Kumar et  
353 al. 2021). We found shrub density and basal area to be higher at lower elevations, unlike tree  
354 layer. This might be due to scattered tree canopy at lower elevations allowing more light  
355 penetration such that the understorey species can proliferate well.

#### 356 Topographical heterogeneity and vegetation structure drives edaphic factors

357 There is increasing amounts of evidence that soil moisture plays an important role in governing  
358 the composition of vegetation communities in mountainous landscapes (Kutiel and Lavee  
359 1999; Panthi M et al. 2007). Differences in soil MC played an important role in controlling  
360 species composition across the sites. The higher elevational site (E4 and E5) has greater soil  
361 MC which might be due to dense canopy and multi-layering at higher altitudinal forest whereas  
362 lower density and basal area at lower elevation creates sparse canopy cover which enhances  
363 light penetration resulting in higher evaporation rate and lower moisture content (Saxena and

364 Singh 1984). The study suggested increased amount of soil nutrient (N and K) along with OC  
365 and MC to be greater in higher elevation sites. The complex structure of the vegetation in the  
366 study region results from the interaction of edaphic factors and associated forest attributes. The  
367 successional changes occurring in an ecosystem with time and their development process bring  
368 about changes in edaphic properties whereas selective absorption of macro- and micro-  
369 nutrients by different species alters the process of feedback mechanism by them (Singh, 2018,  
370 2021). PCA plot showed tree basal area and soil total nitrogen were strongly correlated along  
371 with soil OC. Generally, the increase in OC with increasing elevation is due to an increased  
372 amount of litter accumulation on the forest floor and due to lower temperatures, there is a very  
373 slow rate of decomposition (Singh & Kashyap, 2006) and lower turnover of nutrients and thus  
374 selects for species with a conservative resource-use strategy characterized by slow growth and  
375 high biomass (Quesada et al., 2012). Also, increase in soil nitrogen and available potassium  
376 with increasing basal area might be the result of increased tree growth which in turn leads to  
377 higher nutrient returns via litterfall (Verma and Garkoti 2019). A possible explanation for this  
378 might be that presence of organic matter due to reduced decomposition rate at higher elevation  
379 leads to slow turnover of plant materials that significantly improves the retention of potassium  
380 in the soil (Sharma et al. 2006) but this impacted the phosphorus concentration which was  
381 lower in higher elevation sites. Aspect significantly affected moisture content, bulk density,  
382 phosphorous, and potassium in the present study however, other soil parameters were not  
383 affected confirming relatively low role of aspect in creating differences in soil parameters. The  
384 study site showed slightly acidic pH throughout which is recommended for nutrient availability  
385 to the plants in the forest (Paudel and Sah 2003). Thus, the study suggested soil moisture  
386 content and nutrient availability are the important edaphic constraints for species distribution  
387 which are significantly influenced by topographical variation. CCA also confirmed that the  
388 sites at higher elevations had higher AP and MC content which might be due to slower cycling

389 of nutrients in response to reduced decomposition at low temperatures while reduced  
390 weathering rates at lower elevation might have caused relatively lower nutrient turnover rates.  
391 However, over any large region, distribution of species is supposed to be governed by two or  
392 more environmental factors, not a single factor (Sagar et al. 2008).

### 393 Topographical heterogeneity and associated edaphic properties regulate regeneration pattern

394 Density diameter curve suggested high density of species in lower DBH class whereas  
395 absence of old-growth individuals in higher DBH class indicating natural succession of young  
396 forests as opposed to mature forest stands (Singh & Singh, 1986). However, higher elevation sites  
397 (E5) followed bell-shaped pattern indicating mature forest stands. However, species-wise (for  
398 *Pinus roxburhii*, *Q. leucotrichophora* and *Q. semicarpifolia*) population structure showed  
399 slight discontinuity in number of individuals with increasing DBH class. This was mainly due  
400 to different levels of environmental harshness to be responsible for governing population  
401 structure. The seedling density varied nearly three-fold and sapling density varied nearly two-  
402 fold amongst the study sites. The values fit the values reported by previous studies from other  
403 regions located in the Himalayas (Pant and Samant 2012; Pala et al. 2013; Malik and Bhatt  
404 2016). Seedling and sapling density decreased with increasing elevation while the opposite was  
405 found for matured tree individuals. This might be due to the lower survival rates of species in  
406 lower elevation sites along with low soil TN which increases with increasing basal area. This  
407 suggests that lower elevation sites are characterized by late-successional forest stands with low  
408 stand density but higher recruitment rates. A higher number of saplings indicate an increased  
409 survival rate and low mortality rate (Uriarte et al. 2018). Increased seedling density at lower  
410 elevation sites could be also due to increased amount of light penetration to the ground layer  
411 creating favourable conditions for regeneration, unlike higher elevation sites which form closed  
412 canopy due to increased density and basal area (Singh 1998). Also, reduced seedling density  
413 in E2 (1000-1500 m) sites might be due to mono-specific nature of *P. roxburghii* that forms

414 thick needle-like leaf layer on forest floor obstructing the growth of seedlings in the area. It  
415 also holds the capacity to immobilise soil nutrients which makes it unavailable to other species  
416 seedlings (Saikia et al. 2009). Therefore, there occurs an increased rate of competition for the  
417 survival of new seedlings in such sites. This suggests vegetation attributes and soil nutrient  
418 availability along with topography play a major role in governing the regeneration potential in  
419 such regions (Terakunpisut et al. 2007; Gairola et al. 2012). Furthermore, these changes cause  
420 differences in the overall productivity of the region (Hall et al., 2006).

#### 421 Implications for forest management under future scenarios

422 Montane forests are very fragile ecosystems and are highly affected by variation in  
423 climatic changes and global warming scenarios (Barradas et al. 2011). A forest having multi-  
424 layered canopy with significant canopy index and depth, as well as forest floor rich in organic  
425 matter and nutrients has a greater protective value compared to a forest with lesser layers and  
426 a lower canopy index (Kumar et al. 2013). Without adequate baseline data on floristic  
427 composition and diversity and factors determining regeneration potential are fundamental for  
428 management of natural regions (Prada et al. 2017). Variation in soil properties adds another  
429 dimension to changes in species diversity and species distribution pattern. The aforementioned  
430 parameters are therefore liable for creating variations in ecosystem functioning at local level  
431 (within stand differences) as well as landscape-level (between stand differences), thereby  
432 producing spatial heterogeneity (Timilsina et al. 2007). Studies conducted to date suggest that  
433 more emphasis should be given to the northern aspect for conservation as well as restoration  
434 purposes due to its favourable properties for plant growth (Sharma et al. 2010). However, a  
435 similar assessment of management implementations should be considered for the southern  
436 aspect. After a reconnaissance survey, one should adopt different strategies for the conservation  
437 of vegetation in different habitat types. In moist Shiwalik Sal forest, reduced density, and basal  
438 area due to increased dominance of *L. camara* should be managed using mechanical uprooting

439 and chemical control methods whereas, in the pine forest, pine leaves that form the forest floor  
440 further inhibiting regeneration and habitation of other species should be collected and removed  
441 periodically. The soils at higher altitudes (Himalayan moist temperate forests) with steeper  
442 slopes having scattered canopy tend to get eroded easily. Programs should be launched to cover  
443 those areas with native shrub species as well as fast-growing and light-demanding species to  
444 reduce the chances of erosion and maintain overall soil properties at both aspects. Therefore, it  
445 is recommended that plantation of species should be considered for both aspects to increase  
446 biodiversity and a sustainable management of Himalayan forests. Also, predictive models of  
447 vegetation changes suggest climate be the most important factor exerting strong effect on  
448 variation in species composition and diversity (Heikkinen et al. 2006). However, several  
449 studies, in line with this study suggest plant composition and diversity to be largely affected  
450 by edaphic properties, such as soil pH, elevation, slope aspect, and, soil nutrients (Bertrand et  
451 al. 2012). Therefore, evaluation of edaphic parameters and topographic features such as slope  
452 aspect and elevation could benefit projections of next-generation vegetation models  
453 significantly (Franklin et al., 2020)

## 454 **Conclusions**

455 The study suggests that among topographic factors, elevation rather than slope aspect is  
456 important in governing differences in species composition among study sites in Western  
457 Himalayan Montane forests. Tree density and basal area were found maximum at higher  
458 elevation sites while seedling and sapling density along with shrub density and basal area were  
459 maximum at lower elevation sites. This was basically due to increased light penetration for  
460 understory and regenerating species due to scattered canopy at lower elevation sites. Variation  
461 in soil properties adds another dimension to changes in species diversity and distribution  
462 pattern. Soil nutrient (TN, AP and AK) along with OC and moisture content significantly

463 increased with increasing elevation. Therefore, the study concludes that topographical variation  
464 and an increased sum of OC, TN, and available K contents of the soil, are highly favorable for  
465 the growth and development of plant species. Population structure was found to expand at  
466 lower elevation sites (E1) which indicates rapid growth in population. However, higher  
467 elevation sites (E5) followed bell-shaped pattern indicating mature forest stands. There is a  
468 growing need for incorporation of the herbaceous layers that form a significant part of the forest  
469 understory and thus should allow to improve predictions based on observations of the  
470 overstory, which might lead to uncertainties related to changes in species composition under  
471 future scenarios. The study also strongly argues integration of spatial and temporal  
472 heterogeneity across resource gradient at both local and regional scales to analyze the species-  
473 environment relationships considering several abiotic as well as biotic factors.

474 **References**

- 475 Ai Z, He L, Xin Q, Yang T, Liu G, Xue S (2017) Slope aspect affects the non-structural  
476 carbohydrates and C:N:P stoichiometry of *Artemisia sacrorum* on the Loess Plateau in  
477 China. *Catena (Amst)* 152:9–17. <https://doi.org/10.1016/j.catena.2016.12.024>
- 478 Alberto Quesada C, Paz C, Oblitas Mendoza E, Lawrence Phillips O, Saiz G, Lloyd J (2020)  
479 Variations in soil chemical and physical properties explain basin-wide Amazon forest soil  
480 carbon concentrations. *SOIL* 6:53–88. <https://doi.org/10.5194/soil-6-53-2020>
- 481 Ali A, Lin SL, He JK, Kong FM, Yu JH, Jiang HS (2019) Elucidating space, climate, edaphic,  
482 and biodiversity effects on aboveground biomass in tropical forests. *Land Degrad Dev*  
483 30:918–927. <https://doi.org/10.1002/ldr.3278>
- 484 Barradas VL, Cervantes-Perez J, Ramos-Palacios R, Puchet-Anyul C, Vazquez-Rodriguez P,  
485 Granados-Ramirez R (2011) Meso-scale climate change in the central mountain region of  
486 veracruz state, mexico. In: *Tropical Montane Cloud Forests: Science for Conservation and*  
487 *Management*. Cambridge University Press, pp 549–556
- 488 Bertrand R, Perez V, Gégout JC (2012) Disregarding the edaphic dimension in species  
489 distribution models leads to the omission of crucial spatial information under climate  
490 change: The case of *Quercus pubescens* in France. *Glob Chang Biol* 18:2648–2660.  
491 <https://doi.org/10.1111/j.1365-2486.2012.02679.x>
- 492 Bray RH, Kurtz LT (1945) bray1945. *Soil Sci* 39–45
- 493 Budyko MI (1969) The effect of solar radiation variations on the climate of the Earth. *Tellus*  
494 A: Dynamic Meteorology and Oceanography 21:611.  
495 <https://doi.org/10.3402/tellusa.v21i5.10109>
- 496 Chadwick KD, Asner GP (2016) Tropical soil nutrient distributions determined by biotic and  
497 hillslope processes. *Biogeochemistry* 127:273–289. [https://doi.org/10.1007/s10533-015-](https://doi.org/10.1007/s10533-015-0179-z)  
498 [0179-z](https://doi.org/10.1007/s10533-015-0179-z)
- 499 Champion H, Seth S (1968) A revised survey of the forest types of India.
- 500

501 CLARKE KR (1993) Non-parametric multivariate analyses of changes in community  
502 structure. *Australian Journal of Ecology* 18:117–143. [https://doi.org/10.1111/j.1442-](https://doi.org/10.1111/j.1442-9993.1993.tb00438.x)  
503 [9993.1993.tb00438.x](https://doi.org/10.1111/j.1442-9993.1993.tb00438.x)

504 Curtis JT, McIntosh RP (1950) The Interrelations of Certain Analytic and Synthetic  
505 Phytosociological Characters THE INTERRELATIONS OF CERTAIN ANALYTIC  
506 AND SYNTHETIC PHYTOSOCIOLOGICAL CHARACTERS’

507 District Survey Report DISTRICT SURVEY REPORT Distt. Survey Report of District  
508 Sirmour

509 Dobrowski SZ, Swanson AK, Abatzoglou JT, Holden ZA, Safford HD, Schwartz MK, Gavin  
510 DG (2015) Forest structure and species traits mediate projected recruitment declines in  
511 western US tree species. *Global Ecology and Biogeography* 24:917–927.  
512 <https://doi.org/10.1111/geb.12302>

513 Douda J, Doudová-Kochánková J, Boublík K, Drašnarová A (2012) Plant species coexistence  
514 at local scale in temperate swamp forest: Test of habitat heterogeneity hypothesis.  
515 *Oecologia* 169:523–534. <https://doi.org/10.1007/s00442-011-2211-x>

516 Eisenlohr P V., Alves LF, Bernacci LC, Padgurschi MCG, Torres RB, Prata EMB, dos Santos  
517 FAM, Assis MA, Ramos E, Rochelle ALC, Martins FR, Campos MCR, Pedroni F,  
518 Sanchez M, Pereira LS, Vieira SA, Gomes JAMA, Tamashiro JY, Scaranello MAS, Caron  
519 CJ, Joly CA (2013) Disturbances, elevation, topography and spatial proximity drive  
520 vegetation patterns along an altitudinal gradient of a top biodiversity hotspot. *Biodivers*  
521 *Conserv* 22:2767–2783. <https://doi.org/10.1007/s10531-013-0553-x>

522 Estrada-Villegas S, Bailón M, Hall JS, Schnitzer SA, Turner BL, Caughlin T, van Breugel M  
523 (2020) Edaphic factors and initial conditions influence successional trajectories of early  
524 regenerating tropical dry forests. *Journal of Ecology* 108:160–174.  
525 <https://doi.org/10.1111/1365-2745.13263>

526 Finegan B, Delgado D (2000) Structural and floristic heterogeneity in a 30-year-old Costa  
527 Rican rain forest restored on pasture through natural secondary succession. *Restor Ecol*  
528 8:380–393. <https://doi.org/10.1046/j.1526-100X.2000.80053.x>

529 Fortunel C, Lasky JR, Uriarte M, Valencia R, Wright SJ, Garwood NC, Kraft NJB (2018)  
530 Topography and neighborhood crowding can interact to shape species growth and

531 distribution in a diverse Amazonian forest. *Ecology* 99:2272–2283.  
532 <https://doi.org/10.1002/ecy.2441>

533 Franklin O, et. al, et. al (2020) Organizing principles for vegetation dynamics *Nature Plants*

534 Gairola S, Sharma CM, Ghildiyal SK, Suyal S (2012) Chemical properties of soils in relation  
535 to forest composition in moist temperate valley slopes of Garhwal Himalaya, India.  
536 *Environmentalist* 32:512–523. <https://doi.org/10.1007/s10669-012-9420-7>

537 Geml J (2019) Soil fungal communities reflect aspect-driven environmental structuring and  
538 vegetation types in a Pannonian forest landscape. *Fungal Ecol* 39:63–79.  
539 <https://doi.org/10.1016/j.funeco.2018.12.005>

540 Goran O, Agren I, Andersson FO *Terrestrial Ecosystem Ecology Principles and Applications*

541 Guo Y, Wang B, Mallik AU, Huang F, Xiang W, Ding T, Wen S, Lu S, Li D, He Y, Li X  
542 (2017) Topographic species–habitat associations of tree species in a heterogeneous  
543 tropical karst seasonal rain forest, China. *Journal of Plant Ecology* 10:450–460.  
544 <https://doi.org/10.1093/jpe/rtw057>

545 Hall RJ, Raulier F, Price DT, Arsenault E, Bernier PY, Case BS, Guo X Integrating remote  
546 sensing and climate data with process-based models to map forest productivity within  
547 west-central Alberta’s boreal forest: *Ecoleap-West 1*

548 Heikkinen RK, Luoto M, Araújo MB, Virkkala R, Thuiller W, Sykes MT (2006) Methods and  
549 uncertainties in bioclimatic envelope modelling under climate change. *Prog Phys Geogr*  
550 30:751–777

551 Hofhansl F, Chacón-Madrigal E, Brännström Å, Dieckmann U, Franklin O (2021) Mechanisms  
552 driving plant functional trait variation in a tropical forest. *Ecol Evol* 11:3856–3870.  
553 <https://doi.org/10.1002/ece3.7256>

554 Holland PG, Steyn DG (1975) Vegetational Responses to Latitudinal Variations in Slope Angle  
555 and Aspect

556 Ingram JSI, Anderson JM (1993) *Tropical soil biology and fertility : a handbook of methods.*  
557 CAB International

558 Jarzyna MA, Jetz W (2018) Taxonomic and functional diversity change is scale dependent. *Nat*  
559 *Commun* 9. <https://doi.org/10.1038/s41467-018-04889-z>

560 Jasińska J, Sewerniak P, Markiewicz M (2019) Links between slope aspect and rate of litter  
561 decomposition on inland dunes. *Catena* (Amst) 172:501–508.  
562 <https://doi.org/10.1016/j.catena.2018.09.025>

563 Jucker T, Bongalov B, Burslem DFRP, Nilus R, Dalponte M, Lewis SL, Phillips OL, Qie L,  
564 Coomes DA (2018) Topography shapes the structure, composition and function of tropical  
565 forest landscapes. *Ecol Lett* 21:989–1000

566 Kharkwal G, Mehrotra P, Rawat YS, Pangtey YPS (2005) Phytodiversity and growth form in  
567 relation to altitudinal gradient in the Central Himalayan (Kumaun) region of India

568 Kumar M, Kumar S, Verma AK, Joshi RK, Garkoti SC (2021) Invasion of *Lantana camara* and  
569 *Ageratina adenophora* alters the soil physico-chemical characteristics and microbial  
570 biomass of chir pine forests in the central Himalaya, India. *Catena* (Amst) 207.  
571 <https://doi.org/10.1016/j.catena.2021.105624>

572 Kumar M, Singh H, Bhat JA, Rajwar GS (2013) Altitudinal Variation in Species Composition  
573 and Soil Properties of Banj Oak and Chir Pine Dominated Forests. *Journal of Forest and  
574 Environmental Science* 29:29–37. <https://doi.org/10.7747/jfs.2013.29.1.29>

575 Kutiel P, Lavee H (1999) Effect of slope aspect on soil and vegetation properties along an  
576 aridity transect. *Isr J Plant Sci* 47:169–178.  
577 <https://doi.org/10.1080/07929978.1999.10676770>

578 Latif Khan M, Rai JPN, Tripathi RS (1987) Population structure of some tree species in  
579 disturbed and protected subtropical forests of north-east India Monitoring and Mapping  
580 of Forest Communities with special reference to Invasive Plant Species using Airborne  
581 Visible/Infrared Imaging Spectrometer-Next Generation (AVIRIS-NG) and Sentinel-1  
582 SAR images View project Urban hazard-risk-resilience assessment View project

583 Laughlin DC, Joshi C, Richardson SJ, Peltzer DA, Mason NWH, Wardle DA (2015)  
584 Quantifying multimodal trait distributions improves trait-based predictions of species  
585 abundances and functional diversity. *Journal of Vegetation Science* 26:46–57.  
586 <https://doi.org/10.1111/jvs.12219>

587 Liang W, Wei X (2020) Factors promoting the natural regeneration of *Larix principis-  
588 rupprechtii* plantation in the Lvliang Mountains of central China. *PeerJ* 2020.  
589 <https://doi.org/10.7717/peerj.9339>

- 590 Malik ZA, Bhatt AB (2016) Regeneration status of tree species and survival of their seedlings  
591 in Kedarnath Wildlife Sanctuary and its adjoining areas in Western Himalaya, India. *Trop*  
592 *Ecol* 57:677–690
- 593 Måren IE, Karki S, Prajapati C, Yadav RK, Shrestha BB (2015) Facing north or south: Does  
594 slope aspect impact forest stand characteristics and soil properties in a semiarid trans-  
595 Himalayan valley? *J Arid Environ* 121:112–123.  
596 <https://doi.org/10.1016/j.jaridenv.2015.06.004>
- 597 Margalef Margalef\_1973
- 598 Méndez-Toribio M, Meave JA, Zermeño-Hernández I, Ibarra-Manríquez G (2016a) Effects of  
599 slope aspect and topographic position on environmental variables, disturbance regime and  
600 tree community attributes in a seasonal tropical dry forest. *Journal of Vegetation Science*  
601 27:1094–1103. <https://doi.org/10.1111/jvs.12455>
- 602 Méndez-Toribio M, Meave JA, Zermeño-Hernández I, Ibarra-Manríquez G (2016b) Effects of  
603 slope aspect and topographic position on environmental variables, disturbance regime and  
604 tree community attributes in a seasonal tropical dry forest. *Journal of Vegetation Science*  
605 27:1094–1103. <https://doi.org/10.1111/jvs.12455>
- 606 Minchin PR (1987) An evaluation of the relative robustness of techniques for ecological  
607 ordination
- 608 Mishra R (1968) *Ecology Workbook*. Scientific Publishers, India
- 609 Muscarella R, Kolyaie S, Morton DC, Zimmerman JK, Uriarte M (2020) Effects of topography  
610 on tropical forest structure depend on climate context. *Journal of Ecology* 108:145–159.  
611 <https://doi.org/10.1111/1365-2745.13261>
- 612 Pala NA, Negi AK, Gokhale Y, Todaria NP (2013) Tree Regeneration Status of Sacred and  
613 Protected Landscapes in Garhwal Himalaya, India. *Journal of Sustainable Forestry*  
614 32:230–246. <https://doi.org/10.1080/10549811.2013.762492>
- 615 Pant S, Samant SS (2012) Diversity and regeneration status of tree species in Khokhan Wildlife  
616 Sanctuary, north-western Himalaya. *Trop Ecol* 53:317–331
- 617 Panthi M P, Chaudhary R P, Vetaas O R (2007) *Himalayan Journal of Sciences*

- 618 Paudel S, Sah JP (2003) Physiochemical characteristics of soil in tropical sal (*Shorea robusta*  
619 Gaertn.) forests in eastern Nepal
- 620 Pielou EC (1966) The Measurement of Diversity in Different Types of Biological Colledions
- 621 Pinho BX, de Melo FPL, Arroyo-Rodríguez V, Pierce S, Lohbeck M, Tabarelli M (2018) Soil-  
622 mediated filtering organizes tree assemblages in regenerating tropical forests. *Journal of*  
623 *Ecology* 106:137–147. <https://doi.org/10.1111/1365-2745.12843>
- 624 Prada CM, Morris A, Andersen KM, Turner BL, Caballero P, Dalling JW (2017) Soils and  
625 rainfall drive landscape-scale changes in the diversity and functional composition of tree  
626 communities in premontane tropical forest. *Journal of Vegetation Science* 28:859–870.  
627 <https://doi.org/10.1111/jvs.12540>
- 628 Rawal RS, Gairola S, Dhar U (2012) Effects of disturbance intensities on vegetation patterns  
629 in oak forests of Kumaun, west Himalaya. *J Mt Sci* 9:157–165.  
630 <https://doi.org/10.1007/s11629-012-2029-y>
- 631 Rawat TPS, Joshi GB, Basu B, Absar N (2010) Occurrence of Proterozoic Black Shale-hosted  
632 Uranium Mineralisation in Tal Group, Sirmour District, Himachal Pradesh
- 633 Raz S, Retzkin S, Pavliček T, Hoffman A, Kimchi H, Zehavi D, Beiles A, Nevo E (2009)  
634 Scorpion biodiversity and interslope divergence at “Evolution Canyon”, Lower Nahal  
635 Oren Microsite, Mt. Carmel, Israel. *PLoS One* 4.  
636 <https://doi.org/10.1371/journal.pone.0005214>
- 637 Robert Okalebo, Gathua KW, Woomer PL (2002) LABORATORY METHODS OF SOIL  
638 AND PLANT ANALYSIS: A Working Manual The Second Edition The Sustainable  
639 Agriculture Centre for Research Extension and Development in Africa
- 640 Rodrigues AC, Villa PM, Ali A, Ferreira-Júnior W, Neri AV (2020) Fine-scale habitat  
641 differentiation shapes the composition, structure and aboveground biomass but not species  
642 richness of a tropical Atlantic forest. *J For Res (Harbin)* 31:1599–1611.  
643 <https://doi.org/10.1007/s11676-019-00994-x>
- 644 Sagar R, Raghubanshi AS, Singh JS (2008) Comparison of community composition and  
645 species diversity of understory and overstorey tree species in a dry tropical forest of  
646 northern India. *J Environ Manage* 88:1037–1046.  
647 <https://doi.org/10.1016/j.jenvman.2007.05.013>

648 Saikia MK, Kalita J, Saikia PK (2009) Ecology and conservation needs of nymphalid  
649 butterflies in disturbed tropical forest of Eastern Himalayan biodiversity hotspot, Assam,  
650 India

651 Saxena AK, Singh JS (1984) Tree Population Structure of Certain Himalayan Forest  
652 Associations and Implications concerning Their Future Composition

653 Shannon CE, Weaver W (1949) THE MATHEMATICAL THEORY OF COMMUNICATION

654 Sharma B, Mukhopadhyay S, Sawhney J (2006) Distribution of potassium fractions in relation  
655 to landforms in a Himalayan catena. Arch Agron Soil Sci 52:469–476.  
656 <https://doi.org/10.1080/03650340600743717>

657 Sharma CM, Baduni NP (2000) Effect of aspect on the structure of some natural stands of  
658 *Abies pindrow* in Himalayan moist temperate forest

659 Sharma CM, Gairola S, Ghildiyal SK, Suyal S (2010) b). Physical properties of soils in relation  
660 to forest composition in moist temperate valley slopes of the Central Western Himalaya.  
661 J Forest Sci 26:117–129. <https://doi.org/10.1007/s10669-012-9420-7>

662 Shive KL, Preisler HK, Welch KR, Safford HD, Butz RJ, O’Hara KL, Stephens SL (2018)  
663 From the stand scale to the landscape scale: predicting the spatial patterns of forest  
664 regeneration after disturbance. Ecological Applications 28:1626–1639.  
665 <https://doi.org/10.1002/eap.1756>

666 Sidari M, Ronzello G, Vecchio G, Muscolo A (2008) Influence of slope aspects on soil  
667 chemical and biochemical properties in a *Pinus laricio* forest ecosystem of Aspromonte  
668 (Southern Italy). Eur J Soil Biol 44:364–372. <https://doi.org/10.1016/j.ejsobi.2008.05.001>

669 Singh JS, Kashyap AK (2006) Dynamics of viable nitrifier community, N-mineralization and  
670 nitrification in seasonally dry tropical forests and savanna. Microbiol Res 161:169–179.  
671 <https://doi.org/10.1016/j.micres.2005.07.009>

672 Singh S Understanding the role of slope aspect in shaping the vegetation attributes and soil  
673 properties in Montane ecosystems

674 Singh S (2021) Low- to Moderate-Level Forest Disturbance Effects on Plant Functional Traits  
675 and Associated Soil Microbial Diversity in Western Himalaya. Frontiers in Forests and  
676 Global Change 4. <https://doi.org/10.3389/ffgc.2021.710658>

- 677 Singh SP (1998) Chronic disturbance, a principal cause of environmental degradation in  
678 developing countries. *Environ Conserv* 25:1–2
- 679 Singh SP, Adhikari BS, Zobel DB (1994) Biomass, Productivity, Leaf Longevity, and Forest  
680 Structure in the Central Himalaya
- 681 Singh SP, Singh JS (1986) Structure and function of the Central Himalayan oak forests
- 682 Terakunpisut J, Gajaseni - N, Ruankawe \* -N (2007) CARBON SEQUESTRATION  
683 POTENTIAL IN ABOVEGROUND BIOMASS OF THONG PHA PHUM NATIONAL  
684 FOREST, THAILAND
- 685 Timilsina N, Ross MS, Heinen JT (2007) A community analysis of sal (*Shorea robusta*) forests  
686 in the western Terai of Nepal. *For Ecol Manage* 241:223–234.  
687 <https://doi.org/10.1016/j.foreco.2007.01.012>
- 688 Tiwari OP, Sharma CM, Rana YS (2020) Influence of altitude and slope-aspect on diversity,  
689 regeneration and structure of some moist temperate forests of Garhwal Himalaya. *Trop*  
690 *Ecol* 61:278–289. <https://doi.org/10.1007/s42965-020-00088-4>
- 691 Uriarte M, Muscarella R, Zimmerman JK (2018) Environmental heterogeneity and biotic  
692 interactions mediate climate impacts on tropical forest regeneration. *Glob Chang Biol*  
693 24:e692–e704. <https://doi.org/10.1111/gcb.14000>
- 694 Verma AK, Garkoti SC (2019) Population structure, soil characteristics and carbon stock of  
695 the regenerating banj oak forests in Almora, Central Himalaya. *Forest Sci Technol*  
696 15:117–127. <https://doi.org/10.1080/21580103.2019.1620135>
- 697 Verma AK, Garkoti SC, Singh S, Kumar S, Kumar M (2021) Fine root production and nutrient  
698 dynamics in relation to stand characteristics of chir pine mixed banj oak forests in central  
699 Himalaya. *Flora: Morphology, Distribution, Functional Ecology of Plants* 279.  
700 <https://doi.org/10.1016/j.flora.2021.151808>
- 701 Wang L, Wei S, Horton R, Shao M (2011) Effects of vegetation and slope aspect on water  
702 budget in the hill and gully region of the Loess Plateau of China. *Catena (Amst)* 87:90–  
703 100. <https://doi.org/10.1016/j.catena.2011.05.010>
- 704 Woodall CW, Westfall JA, D’Amato AW, Foster JR, Walters BF (2018) Decadal changes in  
705 tree range stability across forests of the eastern U.S. *For Ecol Manage* 429:503–510.  
706 <https://doi.org/10.1016/j.foreco.2018.07.049>

707 Yan WY, Shaker A, El-Ashmawy N (2015) Urban land cover classification using airborne  
708 LiDAR data: A review. *Remote Sens Environ* 158:295–310

709 Yang J, El-Kassaby YA, Guan W (2020) The effect of slope aspect on vegetation attributes in  
710 a mountainous dry valley, Southwest China. *Sci Rep* 10. [https://doi.org/10.1038/s41598-](https://doi.org/10.1038/s41598-020-73496-0)  
711 [020-73496-0](https://doi.org/10.1038/s41598-020-73496-0)

712 Champion\_and\_seth\_1968\_A\_Revised\_Survey\_of\_the\_Forest\_Types\_of

713 R Core Team (2018) *R A Language and Environment for Statistical Computing*. R Foundation  
714 for Statistical Computing, Vienna. - References - Scientific Research Publishing.  
715 [https://www.scirp.org/\(S\(lz5mqp453edsnp55rrgjt55\)\)/reference/ReferencesPapers.aspx](https://www.scirp.org/(S(lz5mqp453edsnp55rrgjt55))/reference/ReferencesPapers.aspx?ReferenceID=2342186)  
716 [?ReferenceID=2342186](https://www.scirp.org/(S(lz5mqp453edsnp55rrgjt55))/reference/ReferencesPapers.aspx?ReferenceID=2342186). Accessed 26 Dec 2022b

717

718

719 **Statements & Declarations**

720 **Funding**

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

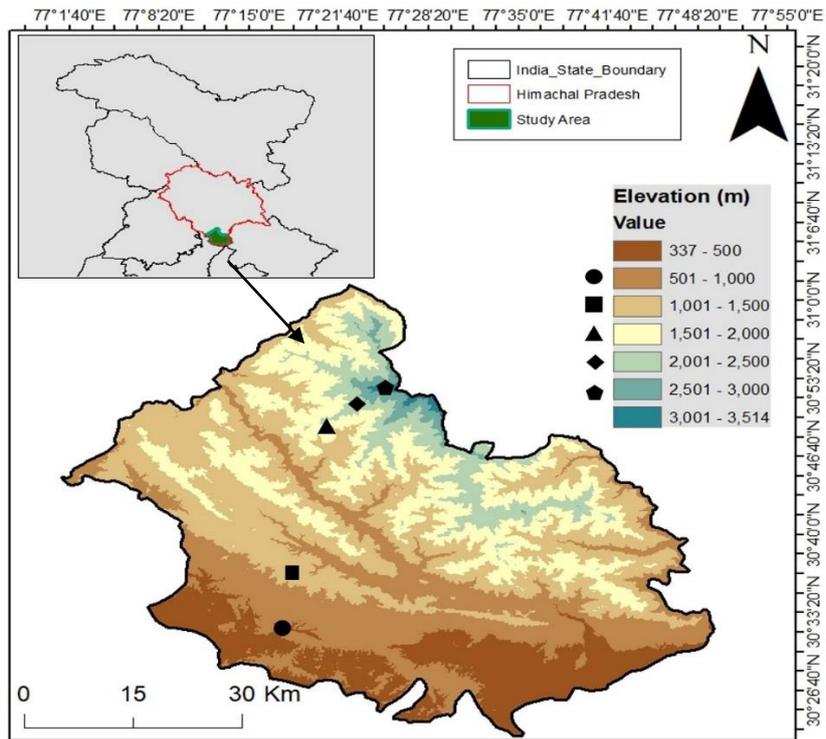
723 **Competing Interests**

724 The authors declare no competing interests among themselves.

725 **Author contributions**

726 SS: Designing, Sampling, Data Collection and Analysis, Writing Draft of Manuscript, and  
727 Literature Survey; AKV: Statistical Analysis, Writing and Reviewing Draft of the Manuscript,  
728 and Finalization; FH: Reviewing, Finalizing, and Supervision.

729

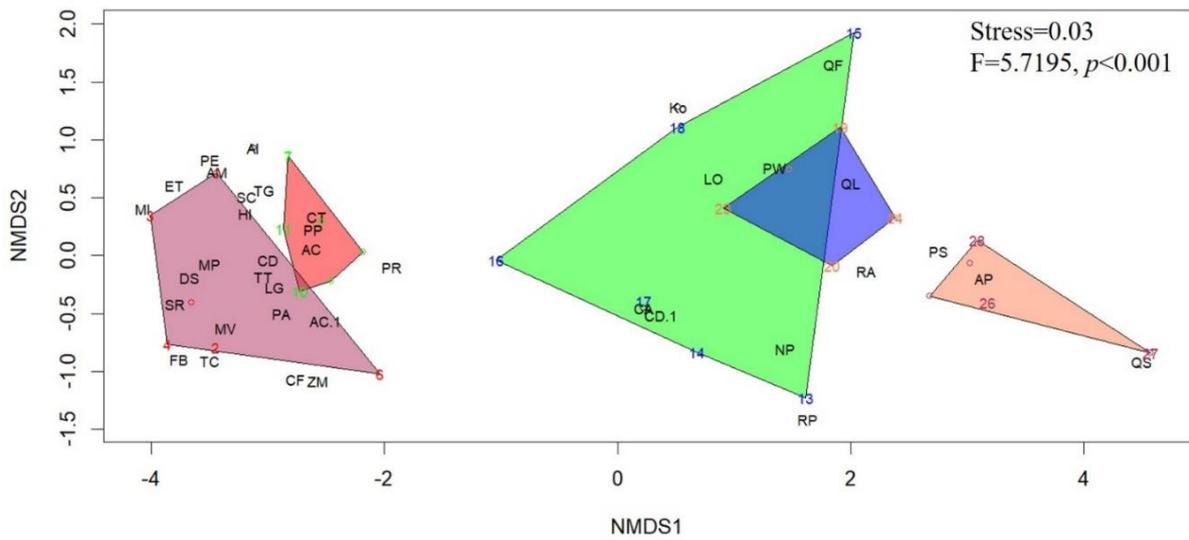


730

731 **Fig. 1.** Location of the selected sites in Sirmour district (Study Area), Himachal Pradesh, Indian  
 732 Himalaya. The different symbols represent different elevation ranges. ● :500-1000 m asl, ■ :1001-  
 733 1500 m asl, ▲ :1501-2000 m asl, ◆ :2001-2500 m asl, ◆ :2501-3000 m asl.

734

735



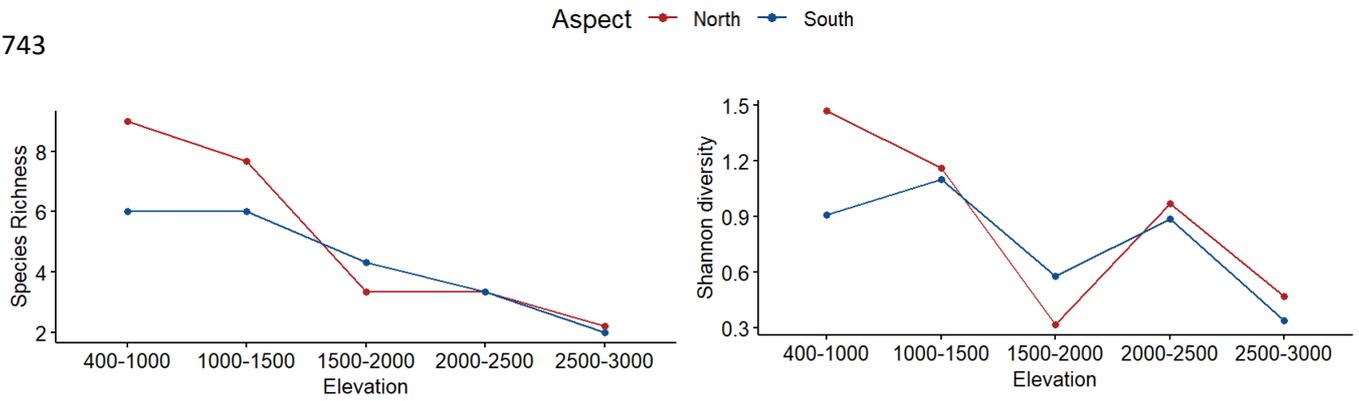
736

737 **Fig. 2.** Non-metric multidimensional scaling (NMDS) for tree layer. Plots located on different  
738 elevation zones were represented based on Bray-Curtis dissimilarity (stress 0.03).  
739 Permutational analysis of Variance indicates significant variation among sites ( $F=5.72$ ,  
740  $p<0.001$ ). Species abbreviations are mentioned in Fig. S1.

741

742

743



744

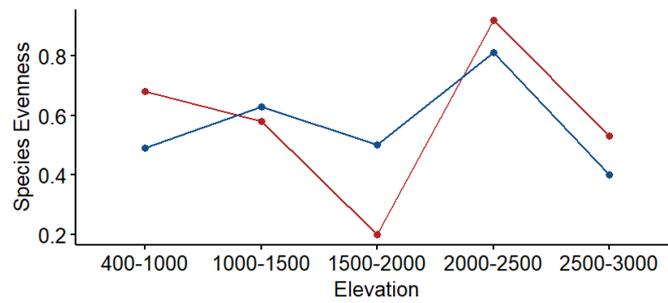
750

751

752

753

754



755

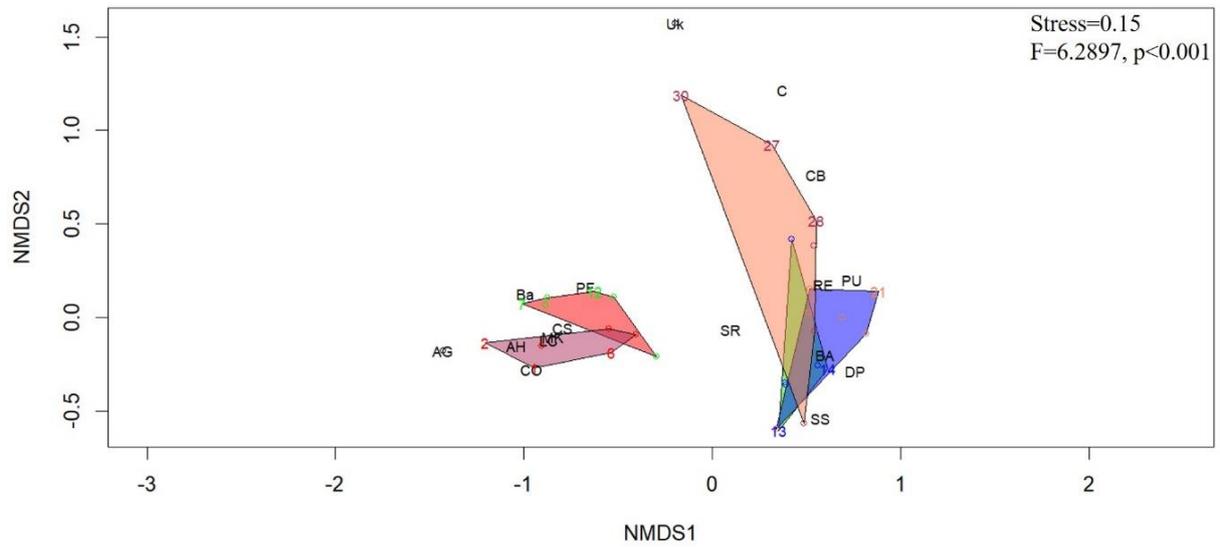
756

757

758

**Fig. 3.** Line plots showing variation in tree Density ( $\text{ind ha}^{-1}$ ), Basal Area ( $\text{m}^2 \text{ha}^{-1}$ ), Species Richness, Shannon diversity and Species Evenness with increasing elevation and contrasting slope aspect: North (red) and South (blue).

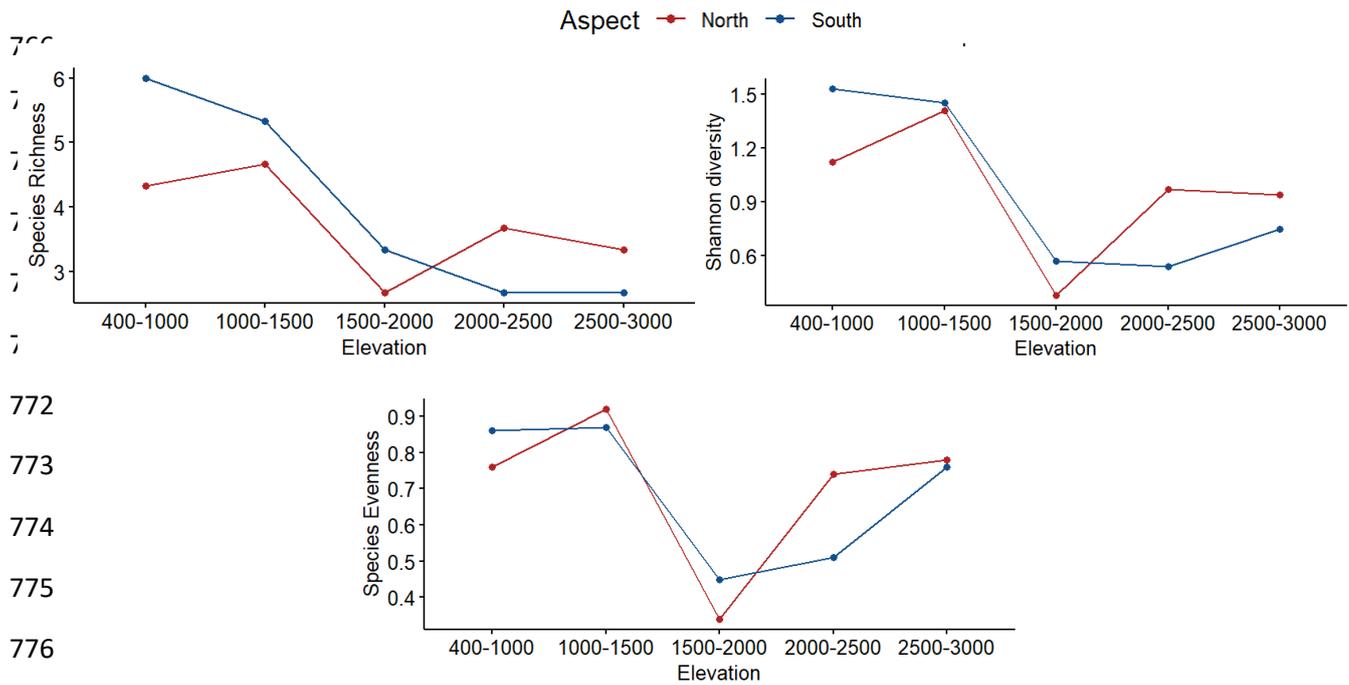
759



760

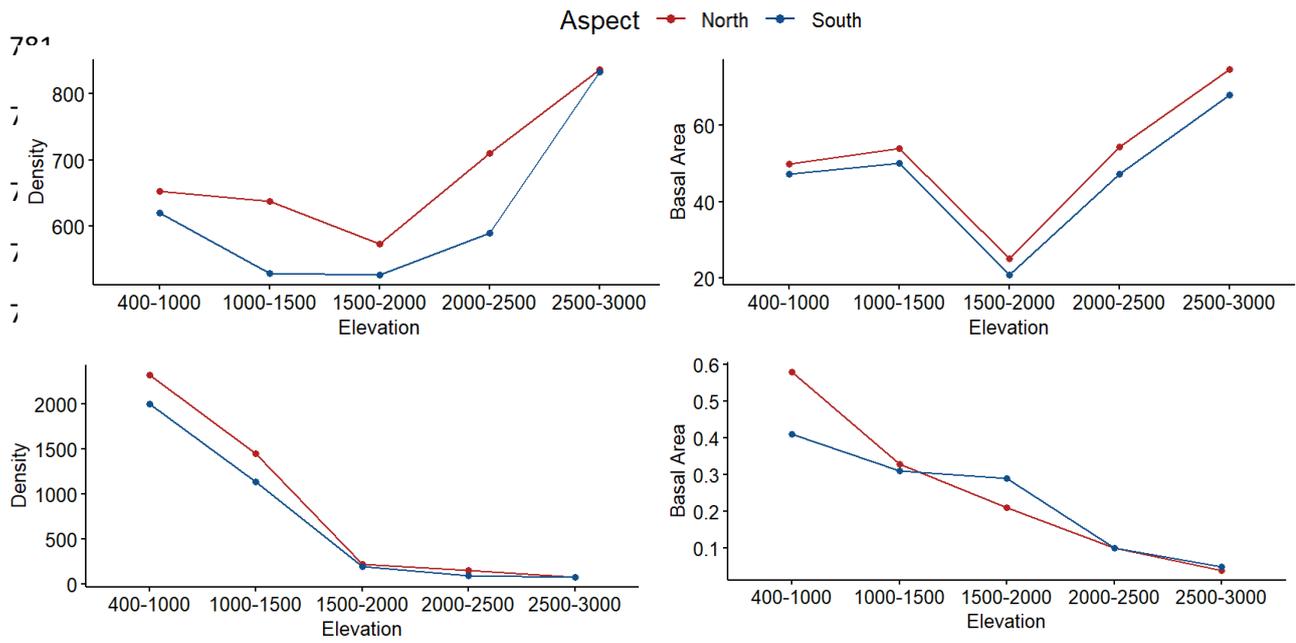
761 **Fig. 4.** Non-metric multidimensional scaling (NMDS) for the shrub layer. Plots located on  
762 different elevation zones were represented based on Bray-Curtis dissimilarity (stress 0.15).  
763 Permutational analysis of Variance indicates significant variation among sites ( $F=6.29$ ,  
764  $p<0.001$ ). Species abbreviations are mentioned in Fig. S2.

765



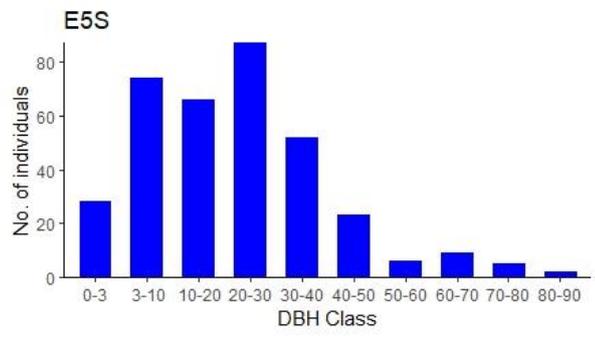
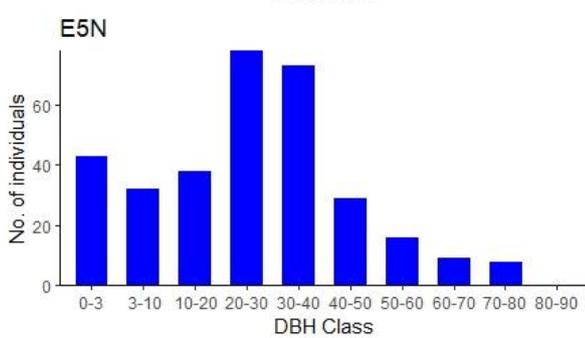
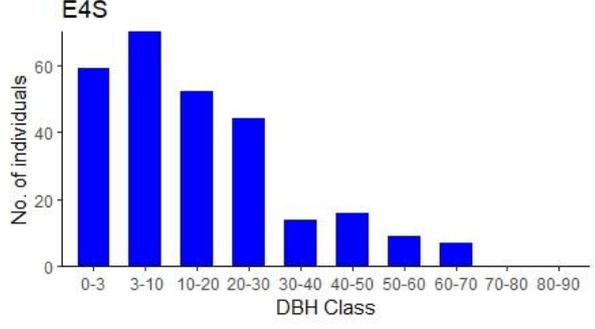
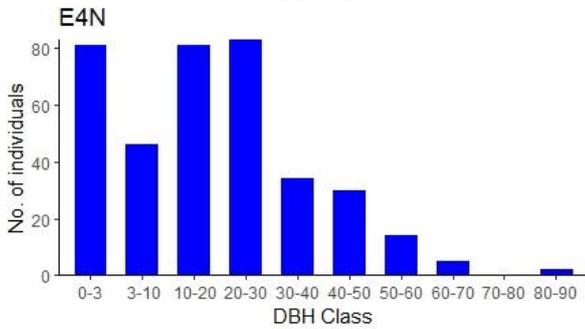
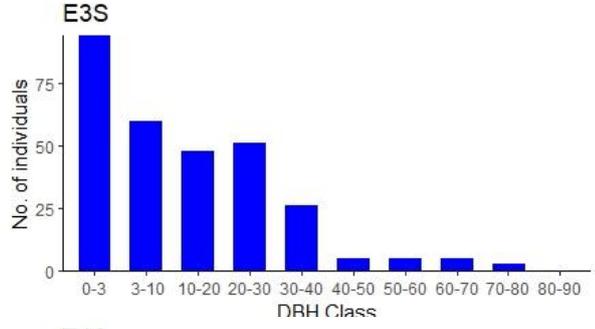
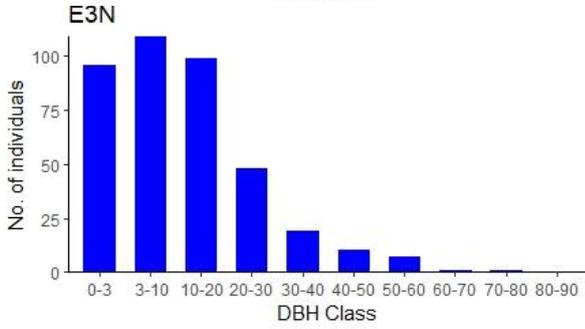
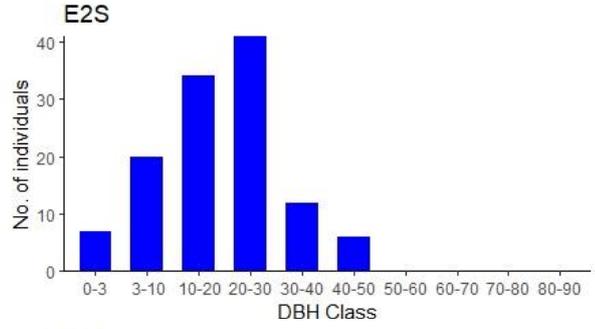
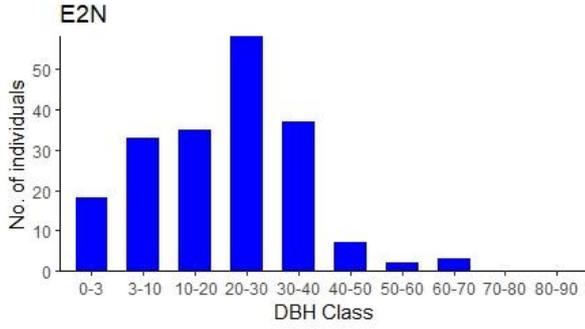
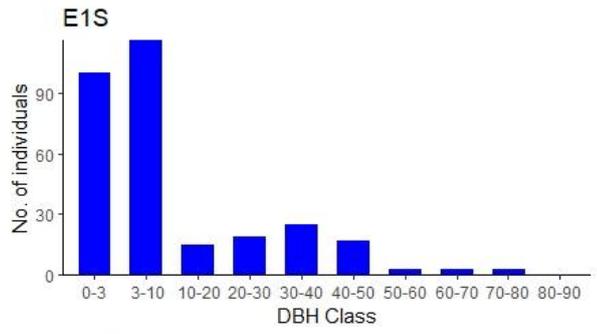
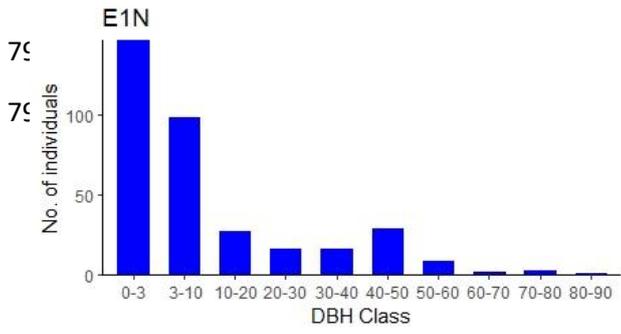
777 **Fig. 5.** Line plots showing variation in shrub Density (ind ha<sup>-1</sup>), Basal Area (m<sup>2</sup> ha<sup>-1</sup>), Species  
 778 Richness, Shannon diversity and Species Evenness with increasing elevation and contrasting  
 779 slope aspect: North (red) and South (blue).

780



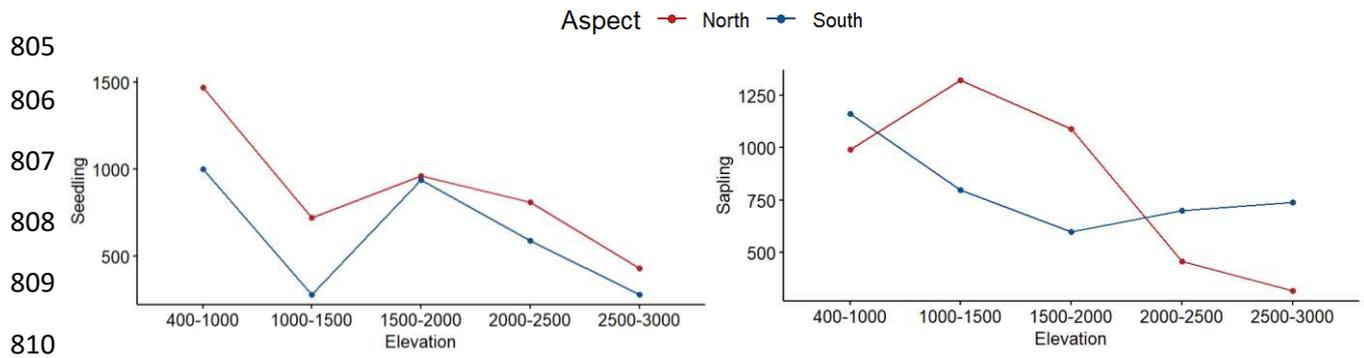
791 **Fig. 6.** Line plots showing variation in Density (ind ha<sup>-1</sup>) and Basal Area (m<sup>2</sup> ha<sup>-1</sup>) for trees  
 792 (upper panel) and shrubs (lower panel) with increasing elevation and contrasting slope aspect:  
 793 North (red) and South (blue).

794



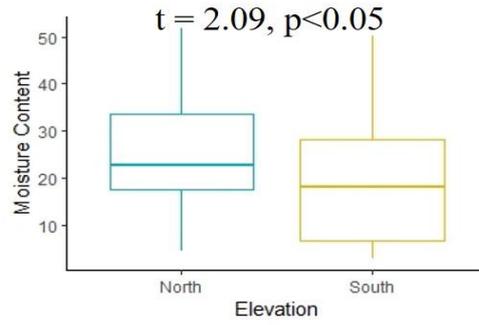
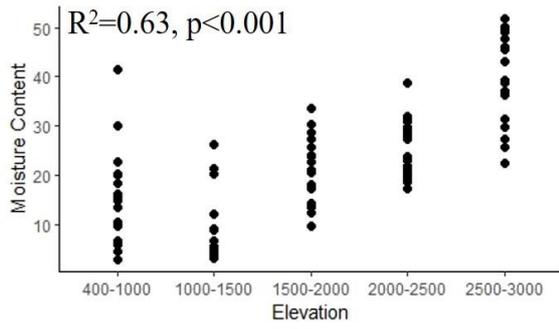
797 **Fig. 7.** Population structure of tree species for all the sites: E1N (400-1000 m asl northern  
798 aspect), E1S (400-1000 m asl southern aspect), E2N (1001-1500 m asl northern aspect), E2S  
799 (1001-1500 m asl southern aspect), E3N (1501-2000 m asl northern aspect), E3S (1501-2000  
800 m asl southern aspect), E4N (2001-2500 m asl northern aspect), E4S (2001-2500 m asl southern  
801 aspect), E5N (2501-3000 m asl northern aspect) and E5S (2501-3000 m asl southern aspect)  
802 where x-axis represents DBH Class (Diameter at Breast Height) and y-axis represents number  
803 of individuals.

804

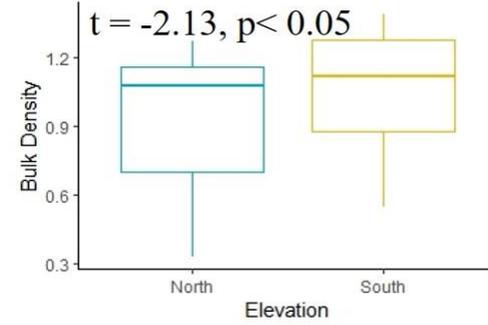
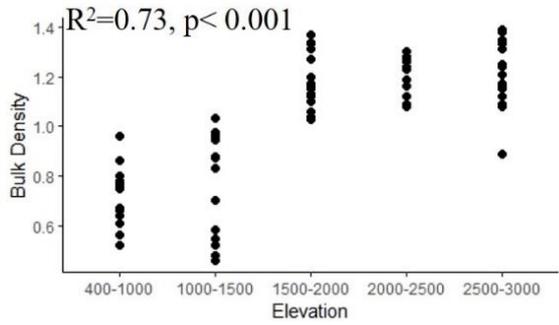


811 **Fig. 8.** Regeneration status (seedlings and saplings, no. of individuals ha<sup>-1</sup>) of tree species with  
 812 increasing elevation for contrasting slope aspect: North (red) and South (blue).

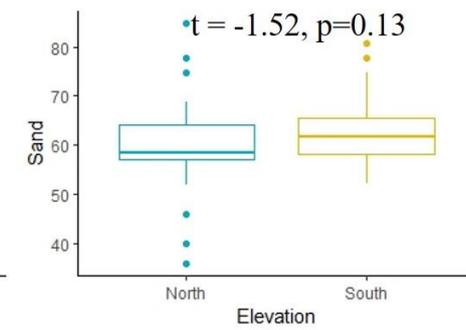
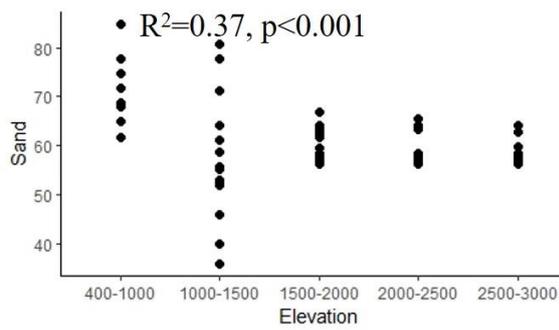
813



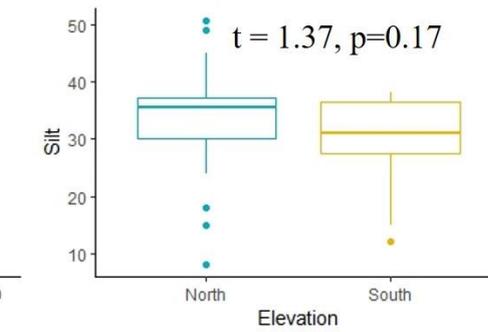
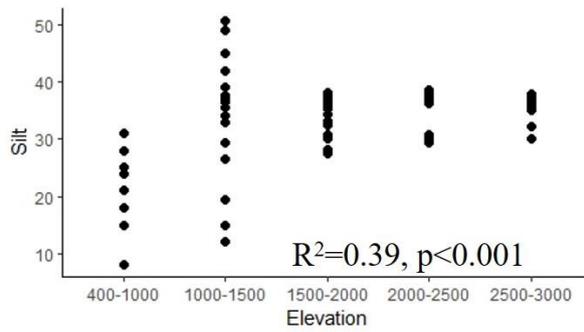
814



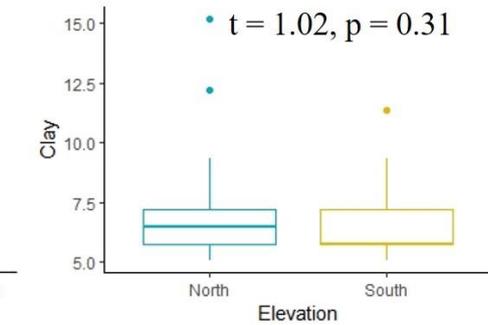
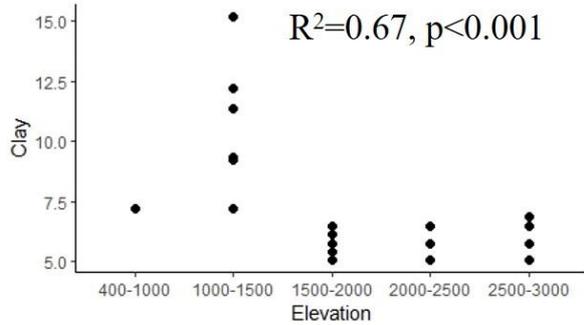
815



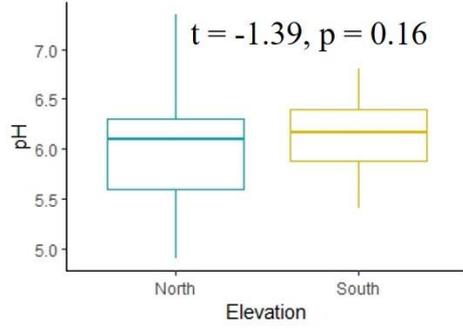
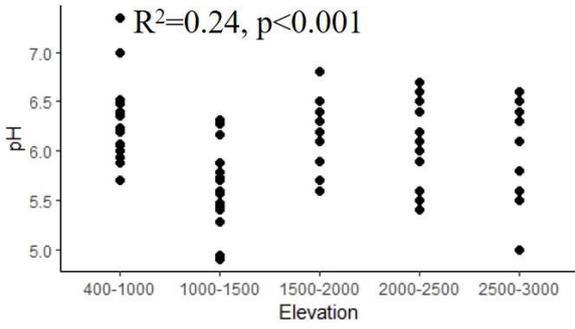
816



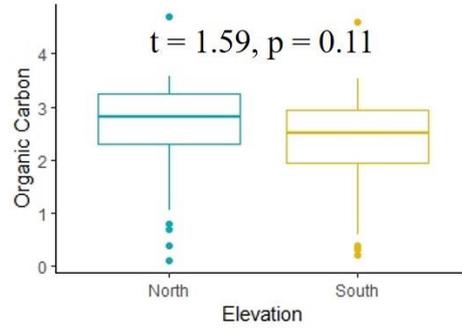
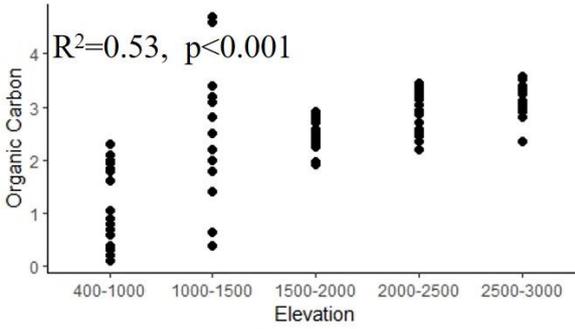
817



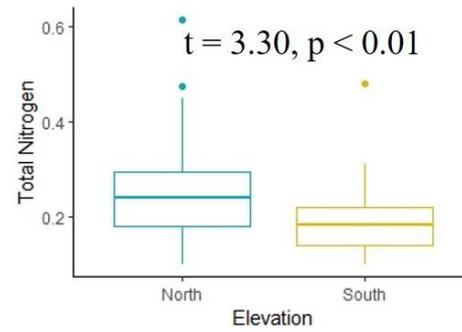
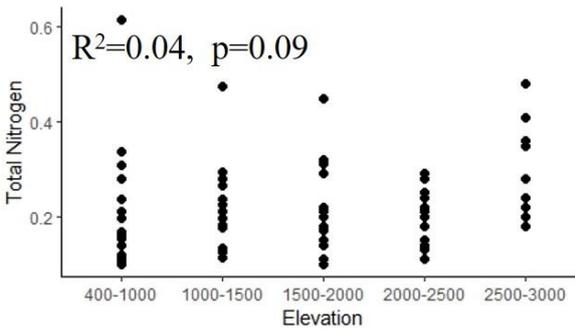
818



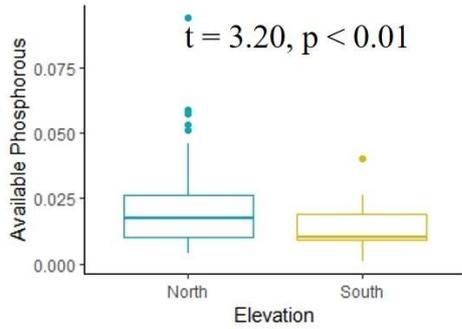
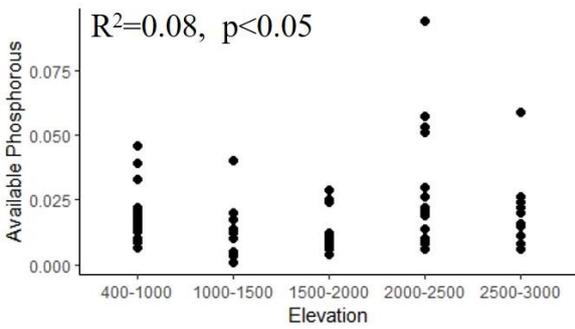
819



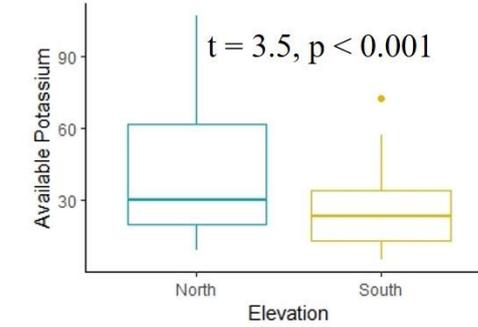
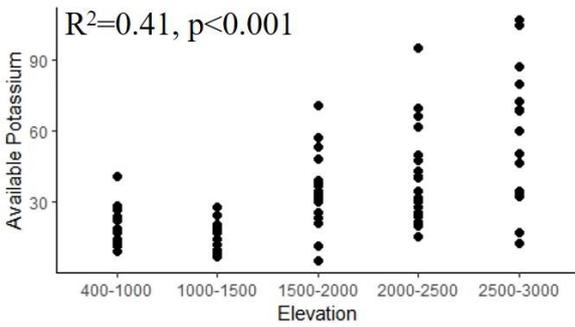
820



821



822



823

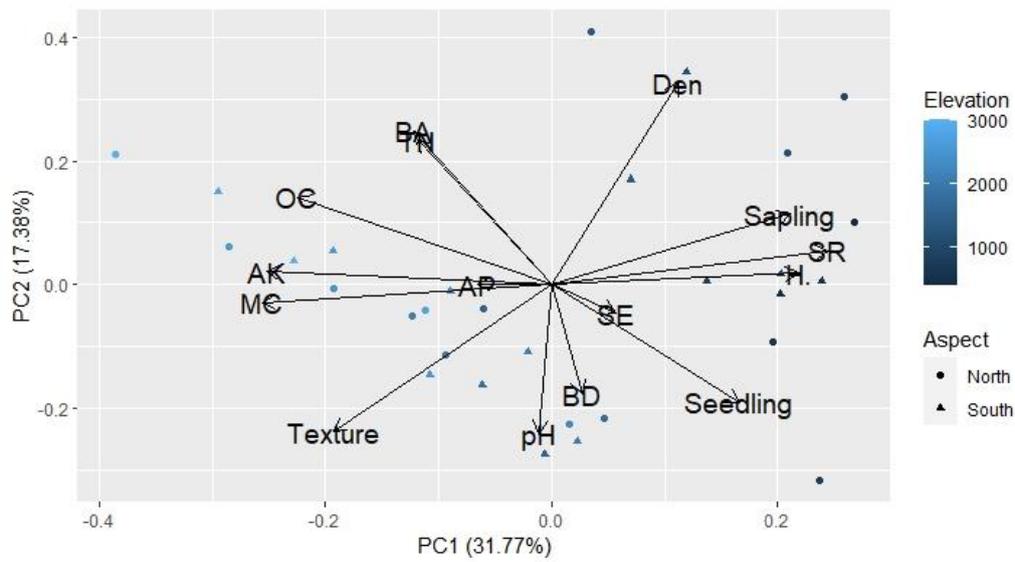
824 **Fig. 9.** Linear regression analysis of soil properties along increasing elevation  
825 [Moisture Content (MC %), Bulk Density (BD g cm<sup>-3</sup>), pH (unitless),  
826 Texture-Sand, Silt and Clay (%), Organic Carbon (OC %), Total Nitrogen  
827 (TN %), Available Potassium (AK %), Available Phosphorous (AP %)].



828 Right panel: Box plot with t-test showing variation in soil properties with varying slope aspect:  
829 North (blue) and South (yellow). The limits of boxes indicate the first and third quartiles, and  
830 the horizontal line within boxes corresponds to the median. The upper whisker extends from  
831 the third quartile to the highest value within  $1.5 \times \text{IQR}$  (interquartile range) of the third quartile.  
832 The lower whisker extends from the first quartile to the lowest value within  $1.5 \times \text{IQR}$  of the  
833 first quartile.

834

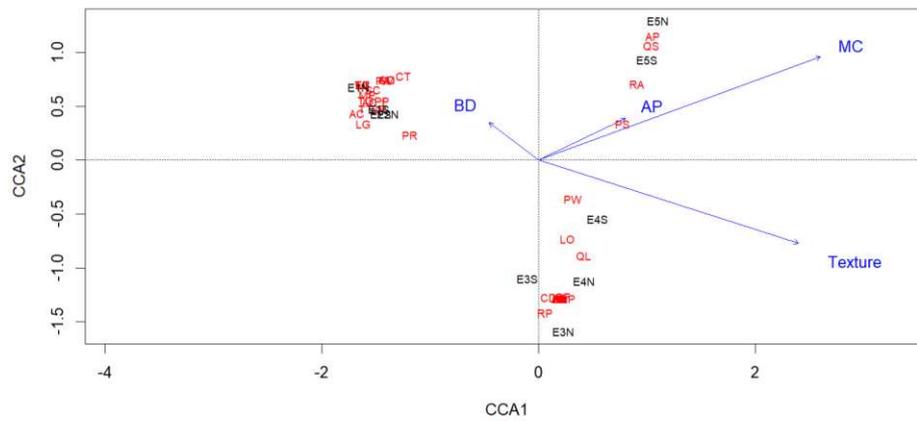
835



836

837 **Fig 10.** Principal Component Analysis of vegetation attributes and soil parameters among sites.  
838 Abbreviations: Density (Den, individuals ha<sup>-1</sup>), Basal Area (BA, m<sup>2</sup> ha<sup>-1</sup>), Seedling and Sapling  
839 (individuals ha<sup>-1</sup>), Shannon-Weiner Diversity (H', unitless), Species Richness (SR, unitless),  
840 Species Evenness (SE, unitless), Moisture Content (MC %), Bulk Density (BD g cm<sup>-3</sup>), pH  
841 (unitless), Texture-Ratio of Sand, Silt and Clay (%), Organic Carbon (OC %), Total Nitrogen  
842 (TN %), Available Potassium (AK %), Available Phosphorous (AP %).

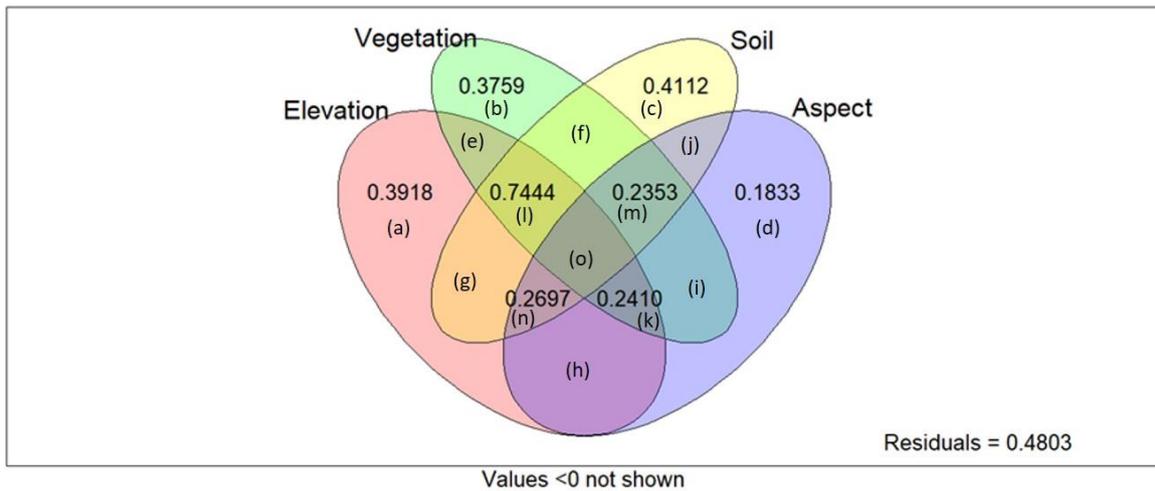
843



844

845 **Fig. 11.** CCA ordination diagram of tree species (red) among the study sites (black) to analyze  
 846 the major gradients among the combination of explanatory variables. The length of vectors in  
 847 the ordination diagram represents the strength of the correlation, while the angle between two  
 848 vectors shows the degree of correlation among variables with each axis. Species abbreviations  
 849 are mentioned in Figure S2.

850



851

852 **Fig. 12.** A Venn diagram showing the partitioning of variation according to four groups of  
 853 independent variables, Elevation, Vegetation (Density, Basal area and Species Richness), Soil  
 854 properties (Moisture content, Texture and soil nutrients) and Slope aspect. The rectangle  
 855 corresponds to the total variation in the dependent (species regeneration) data. Each area of  
 856 overlap of the four ellipses is representative of the intersection of the four groups in terms of  
 857 their explained variation. The area of the rectangle (total variation) that the four ellipses do not  
 858 cover represents the unexplained variation (residuals) (refer to Table S2 for negative adjusted  
 859 R-square values of each class).

## Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- [Supplementaryinfo.docx](#)