

YSSP Report
Young Scientists Summer Program

Trait-based modelling of temperate forests in Western Himalaya, India

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It was finished by **Shipra Singh** and has not been altered or revised since.

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Abstract

A central goal of ecology is to understand how ecological communities assemble and how species assemblages determine ecosystem functioning (reflected in 'effect traits') in response to environmental factors (reflected in 'response traits'). In this study, we aim to characterize the spatial variability of major plant functional traits along an environmental gradient in temperate forests of western Himalaya, and to assess the extent to which this variability differs between broad-leaved and conifer tree species. Further, to analyze the effect of traits on vegetation dynamics mechanistically, we calibrated the Plant and Plant-FATE vegetation models. Four functional traits were selected to incorporate information on both the leaf and the wood economic spectra: maximum tree height, wood density, leaf mass per area and leaf phosphorous content.

We found that environmental filtering shapes local species composition and associated functional characteristics in the region – particularly, elevation, light intensity, and soil texture are the most important determinants of vegetation dynamics which affect plant functional trait variation and determine vegetation carbon storage in the temperate forests of Western Himalaya. Moreover, most of the plant functional trait variability was determined at the level of individual plants, thus suggesting higher trait variation within species than between species. To further investigate how these environmental drivers affect the size distribution of trees, we calibrated trait-based eco-evolutionary vegetation models (Plant and Plant-FATE) capable of predicting species-specific size distributions. We found that predicted height and DBH distributions of trees successfully match with field observations, suggesting that inclusion of the mechanistic factors driving intraspecific trait variation is crucial for linking environmental variation to changes in community assemblage processes and emergent ecosystem functioning. Our approach has the potential to improve the prediction of ecosystem services under future climate change scenarios for the Himalayan region.

Acknowledgments

Pride, praise and perfection belong to almighty. Every creation is motivated by purpose and all purposes have destiny predestined by the creator. I thank almighty for bestowing me with the fruitful purpose to enlighten the obscure spheres of my life.

Words cannot suffice my eternal affection and deepest regards towards my parents and elder siblings. As I intend to manifest the sense of selflessness, deep kindness and love that I inherited from them in my endeavors, the quantum of their eternal blessings revolutionize my mortal being.

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1. Introduction

Understanding how species are distributed in nature and how local processes influence patterns of structure and diversity across varied environmental gradients remains central to the conceptual development of community ecology (Kraft et al. 2011; Hulshof et al. 2013). For a long time, ecologists have worked on gaining insight into the processes that govern the assembly of natural communities, striving to find general 'assembly rules' determining species composition at a certain site and the constraints on community structure and composition (Tansley 1920; Diamond 1975; Tilman 1988; Grime 2002). This has led to the emergence of functional ecology which suggests categorisation of species not by their taxonomic identity only, but also by their biological characteristics through the measurement of functional traits. Plant functional traits can be used to study either as an effect on ecosystem processes or as a response to environmental variables. Two common applications of plant functional traits are to (i) characterize community responses to changes in the environment, including community assembly processes and to (ii) quantify the influence of community shifts on ecosystem processes. Hence, to study the effect-response framework (**Figure 1**), it is necessary to prefer plant functional groups over individual species to analyze the response of plant communities to environmental factors. Plant functional traits are very important in analyzing patterns in species composition, community structure, and its relationship with deterministic environmental effects (Casanoves et al. 2011). Such relationships between abiotic environmental factors and biotic interactions between species competing for limiting resources determine, on the one hand, species success in a given environment (Naeem and Wright 2003), and, on the other hand, the contribution of that species to ecosystem level fluxes of carbon, water and nutrients (Petchey and Gaston 2006). Plant functional traits integrate the ecological and evolutionary history of a species. Shifts in species composition (in response to disturbances and climate change) affect plant functional trait composition, which in turn affects the ecosystem functioning that depends both on the traits of species that decline or disappear and the traits of species that replace them (Diaz et al. 2007; Lavorel et al. 2007). Therefore, plant functional traits cannot only be used to predict the species-specific response to disturbance but also to assess the functioning of forest ecosystems.

Defining community assembly processes with respect to functional trait values instead of species identity will likely be independent of taxonomy, and easier to construct and apply (Diaza and Cabido 2001; Weiher and Keddy 1995). Rules based on functional trait values, moreover, allow for a more mechanistic view of species interactions (McGill et al. 2006). In the past, very few studies have considered the role of plant functional traits in defining species ranges and forest structure. An important exception is a recent comprehensive framework for studying trait-, size- and patch-structured met populations of plants by Falster et al. (2011) i.e., the Plant model, and its extension to more realistic environmental responses, i.e., Plant-FATE model, which can be used to study how forests respond on demographic timescales to varied environmental gradients. Vegetation dynamics processes like plant growth, demography and competition are governed by traits and size of the species, which ultimately influence dynamics temporally (Griffith et al. 2016; Rees and Ellner 2016). The model allows us to understand how plants are influenced

by its trait, size and varied radiation intensity as a function of topography. The model requires four traits i) Leaf Mass per unit Area (LMA), ii) Maximum height (HT), iii) Wood density (WD), and iv) Seed mass (SM) for parameterization. The fundamental idea of the model is to model the short-term physiological functioning of an individual plant and how this is influenced by its traits, size, and light environment and disturbance regimes (Falster et al. 2011).

Topographical gradients provide opportunities to explore environmental controls on forest structure and functioning (Singh et al. 2018). Since forest habitats vary locally at any given elevation, simply based on slope angle, aspect and radiation intensity this spatial heterogeneity affects canopy structural properties and functional forest ecosystem processes. This study is an attempt to understand the role of plant functional trait variation on ecosystem services provided by temperate forests of Western Himalaya. Selection of plant functional traits has been done following Westoby (1998) and Grime (1977) who suggested to summarize plant life-history strategy through three major axes: resource exploitation, competition ability, and response to disturbance. Leaf traits (leaf mass per unit area, LMA and leaf phosphorus content, LPC) represent resource use, whereas stem traits (wood density, WD) and whole-plant traits (maximum height, HT, measured as the 90th percentile of observed heights in each plot) represent competitiveness. By analyzing plant functional trait distribution in temperate forests of Western Himalaya across an elevational gradient, we attempted to address the following research questions: 1) How do gradients in environmental parameters and resource availability affect species composition and vegetation dynamics? 2) How do plant functional traits vary across such a gradient? 3) How does environmental heterogeneity and associated variation of plant functional traits affect vegetation carbon storage? 4) Can we mechanistically predict ecosystem functioning based on plant functional traits? The main objectives of this research addressing the abovementioned research question were to: i) Analyze the influence of topography on plant species composition and vegetation dynamics ii) Assess the variation of plant functional traits (maximum height, leaf area, wood density and seed mass) along gradients of temperature, water availability, light availability and soil type iii) Evaluate the effect of environmental gradients and plant functional traits on vegetation carbon storage; and iv) Calibrate the Plant and Plant-FATE models to predict the effect of plant functional traits on forest dynamics across environmental gradients.

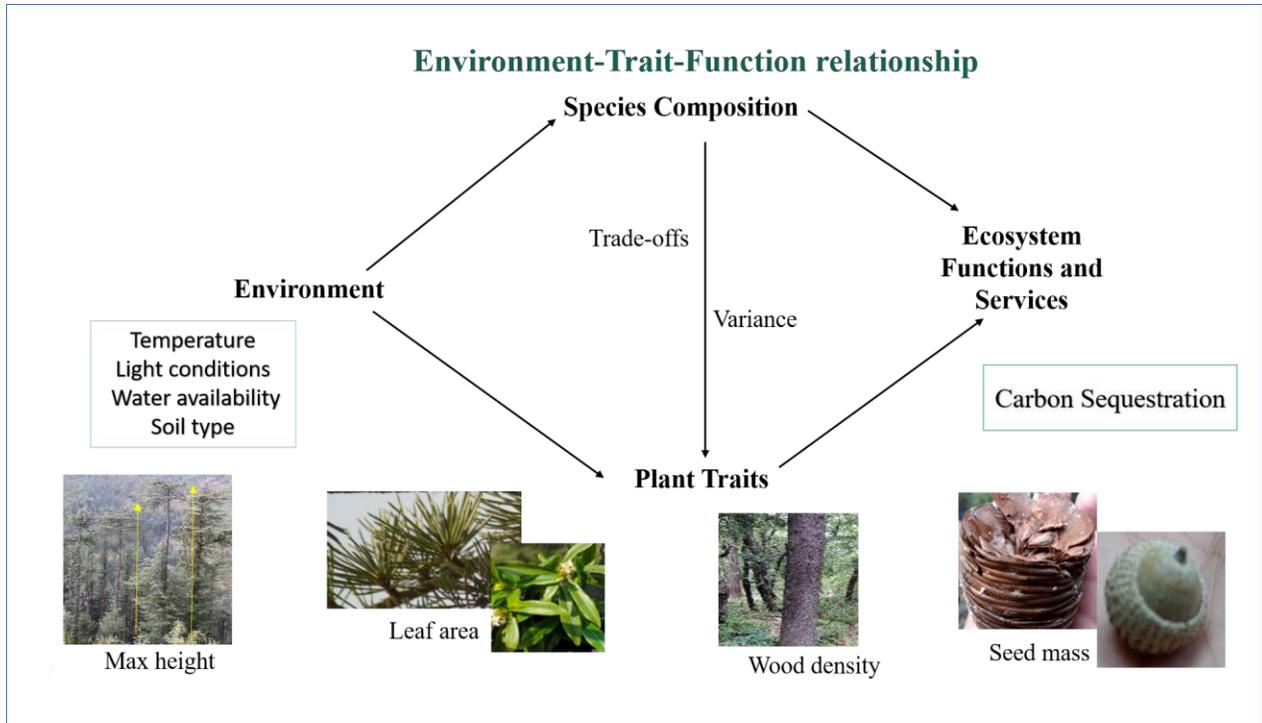


Figure 1. A conceptual framework of Environment-Trait-Function relation suggesting environmental conditions like change in temperature, light availability, water availability and soil type causes variation in plant traits (Max height, Leaf area, Wood density and Seed mass). Further, environment also affects species composition which ultimately affects trait-based trade-offs and variance among species. Ultimately these traits affect ecosystem functioning and services such as carbon sequestration.

2. Study area

The study was carried out in Sawana Reserved Forest located in Rajgarh range of Sirmour district, Himachal Pradesh (**Figure 2**). The study region ($30^{\circ} 86' N - 31^{\circ} 01' N$ and $77^{\circ} 38' E$ and $77^{\circ} 49' E$) covers an area of 1395.38 ha with an altitudinal variation of 1537 m to 3164 m asl. Climate varies from moderate and cold to very cold at higher elevations. Temperature ranges from $10^{\circ}C$ to $30^{\circ}C$ and rainfall is about 1250 mm annual (Himachal Pradesh Forest Department Report 2009). The forest is classified under Group 12-Himalayan moist-temperate forest as per Champion and Seth (1968) forest classification. Vegetation is dominated by *Cedrus deodara* along with various other species as *Abies pindrow*, *Picea smithiana*, *Pinus wallichiana*, *Quercus semecarpifolia*, etc. These forests occur in pure as well as mixed forms. The soil type is sandy to clayey loam up to 3000 m and silty loam soil above 3000m asl. The main rock types found are granite, gneiss, micaceous, schist, quartzite and phyllite.

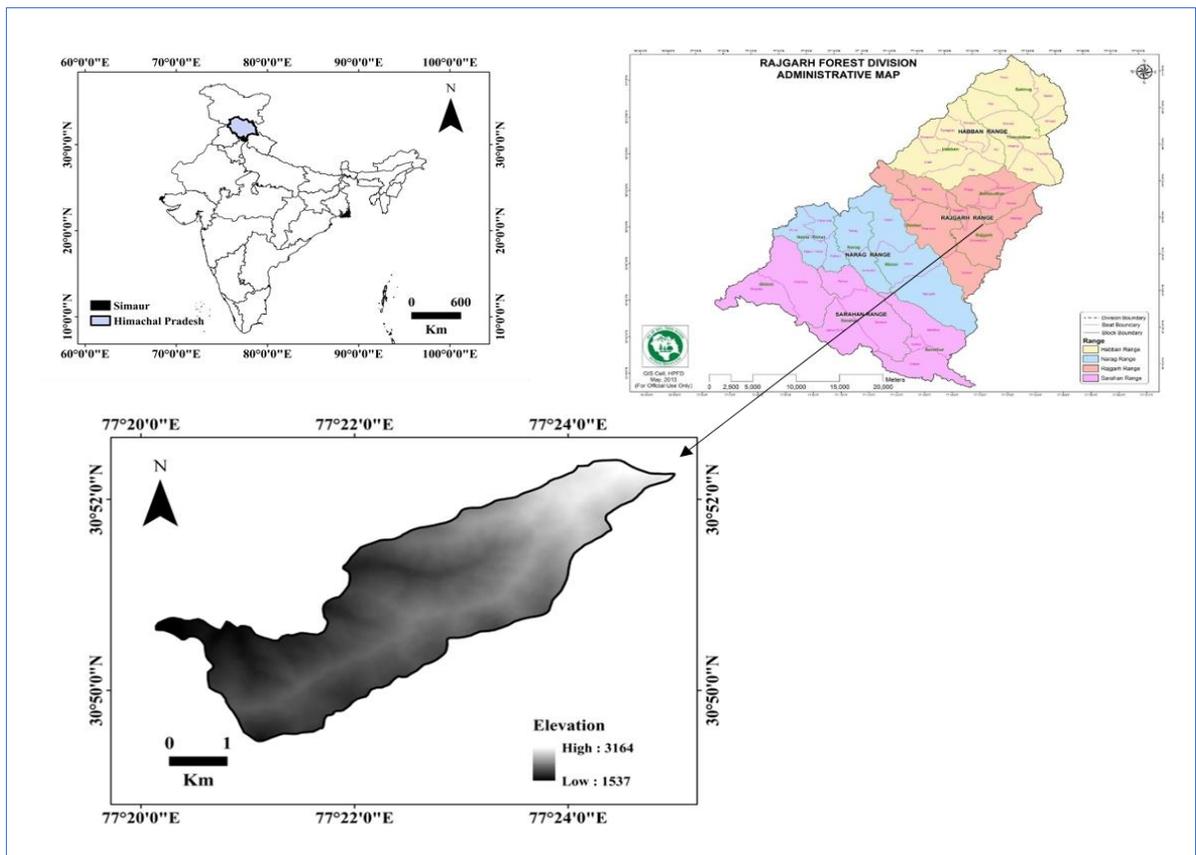


Figure 2. Location of study area (Sawana Reserved Forest) in Rajgarh Forest Division, Sirmour district, Himachal Pradesh India

3. Methods

3.1. Sampling design

Eighteen Plots of 0.1 hectare were established along three elevation classes (1500m-2000m, 2000m-2500m, 2500m-3000m). Six Plots, of which three plots represent northern (N) and southern (S) aspect per elevation class (E.C.), respectively (i.e., 3N+3S×3 E.C. =18Plots) have been identified along the altitudinal gradient to sample woody vegetation (live trees $\geq 10\text{cm}$ DBH (Diameter at Breast Height) and shrubs). In the following, the six sites are indicated as **NL**: Northern aspect at Lower elevation, **SL**: Southern aspect at Lower elevation, **NM**: Northern aspect at Middle elevation, **SM**: Southern aspect at Middle elevation, **NH**: Northern aspect at Higher elevation, **SH**: Southern aspect at Higher elevation. Plot borders were delineated using measuring tape, magnetic compass and a rope. Elevation and geographical coordinates were located using GPS-Garmin, aspect was estimated using Magnetic compass, slope angle was measured using clinometer and relative radiation intensity was calculated following Vetaas (1992).

3.2. Floristic surveys and collection of plant functional traits

Tree species in the study sites were identified with the help of the glossary of forest flora provided by the Rajgarh Forest Department, Sirmour. CBH (circumference at breast height) was measured during the field survey which was later converted into DBH (diameter at breast height for determination of tree basal area). The data were quantitatively analyzed to calculate stem density, frequency, and abundance following Curtis and McIntosh (1950) for each plot. Similarly, the Shannon–Wiener diversity index (H') (Shannon and Weaver 1963) and SR (Margalef 1958) were also calculated for each site. Following stem girth measurements and species identification, a list was composed with all species sorted from most to least abundant, based on the sum of each species' basal area (BA). All species that contributed to more than 80% of plot basal area (in decreasing order of species basal area) were identified for sampling. Above-ground Biomass and Carbon Stocks were calculated based on species-specific volumetric equations for each individual (**Appendix 1, Table A1**) (FSI 1996). In each plot, individuals were further divided based on their DBH class and three individuals for each DBH class were sampled to study the functional traits chosen for study. The study design accounts for three nested ecological scales (among individuals within a species; among species within a plot; among plots). Following species abundance, eight dominant species were selected in the study region (*Pinus roxburghii*, *Cedrus deodara*, *Quercus floribunda*, *Quercus leucotrichophora*, *Pinus wallichiana*, *Picea smithiana*, *Abies pindrow* and *Quercus semicarpifolia*). In total, 250 individuals were sampled for eight dominant tree species in 2019-20. In each plot, trait measurement for each individual was done following Cornelissen et al. (2003) and Perez-Harguindeguy et al. (2013).

3.3. Soil properties

Five randomly located soil samples were collected from each plot using a soil corer of 5 cm diameter and dividing cores into layers of 0-10cm, 10-20cm and 20-30cm. Soil moisture content (MC) was calculated following Misra (1968) whereas soil pH was measured using a multi-parameter ion meter (pH/Cond 340i

SET 1) following Jackson (1973). Soil Bulk Density was calculated following Anderson and Ingram (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 and Gathua 2002). Organic carbon (OC) of the soil sample was measured with dichromate oxidation using air-dried sample of 1g and titrating with FeSO₄ based on modified Walkley and Black method (1947).

3.4. Statistical analysis

Data normality was assessed based on Shapiro–Wilk's test and homogeneity of variance was tested by Levene's test. Traits were log-transformed prior to the analyses to satisfy normality assumptions. Trait data were segregated into broad-leaved and conifers species since the functional traits differed markedly between both the classes. Linear regression models were used to test for patterns in trait variability along environmental gradients of increasing elevation (ggplot package). One-way ANOVA followed by Tukey *post hoc* test was conducted to evaluate the effect of topography (elevation and slope aspect) on vegetation structure, above ground carbon stocks and species diversity, and the differences were reported significant at $p < 0.001$. Species composition with increasing elevation were determined using non-metric multidimensional scaling (NMDS) approach followed by PERMANOVA analyses (vegan package). To explore the relationships between each plant functional trait and the selected environmental and edaphic factors, we fitted linear mixed models using each of the four functional traits as dependent variables. Variance inflation Factor (vif) was used to check the multicollinearity among the environmental and soil variables ($vif < 5$) (car package). Plots were introduced as a random factor. Starting from the saturated model consisting of all the parameters, and sequentially removed predictors which were insignificant, to arrive at the final model. Coefficients of determination were used to assess the percentage contribution of fixed effects alone (R^2 marginal) and both fixed and random effects (R^2 conditional) in explaining functional trait variability (Nakagawa & Schielzeth 2013) (MuMIn package). To quantify the extent to which the four functional traits covary in a multidimensional space, and to determine if covariation among traits varies depending on the ecological scale considered, we performed a principal components analysis (PCA) for both broad-leaved and conifer species (ggfortify package). We performed variance partitioning to separate different components driving trait variation across three nested ecological scales: species, population and individual level (lme4 package). We further used structural equation modeling (SEM) to study the influence of environmental gradients and plant traits on carbon stocks (piecewiseSEM package). The best model was selected based on lowest AIC value and significant p-value. We applied principal component analysis (PCA) to reduce multicollinearity among soil variables across environmental gradients and thus computed principal components of soil variables (PC1) for SEM analysis. PC1 accounted for 24.58% of variation among the variables Sand content, pH and Bulk Density. All statistical analyses were conducted using R version 3.5.0 (R Core Team 2018).

4. Results and Discussion

4.1. Environmental filtering shapes local species composition and vegetation dynamics

Statistical analysis based on permutational analysis of variance revealed that species composition was associated to elevation and thus significantly differed between the three-elevation zones evaluated in this study, such that species composition at lower elevation was found to be completely different from that at higher elevation, while the mid-elevation zone created an ecotone between the lower and higher elevation plots (**Figure 3**). To further analyze the effect of elevation and slope aspect on community composition and forest structure, we used one-way ANOVA followed by Tukey post hoc test (**Figure 4**). Species diversity (H') did not vary across the study sites ($p < 0.3$). However, values for H' were greater for mid-elevation sites, whereas total basal area and tree density were found to be maximum for the higher elevation site and least for the lower elevation site, respectively. Above-ground biomass was found to be maximum for mid-elevation sites (**Appendix 2 Table A2**). A density-diameter curve was drawn to understand the distribution of individuals in different DBH class for each site (**Figure 5**). Population structure was found to be inverted-J shaped for lower and middle elevation site indicating greater number of seedlings and saplings than adults. This represents expanding population indicating young forest. In case of higher elevation, the population represented more or less bell-shaped curve indicating maximum number of individuals having medium DBH class. Vegetation structure and above ground biomass increased with elevation suggesting elevation to be an important parameter governing species composition and forest structure. Species diversity was found to be maximum in mid-elevation site that could be attributed to differences in management practices (Toledo et al. 2012) as well as recruitment of new species due to scattered canopy (Kumar 2000) at lower and mid-elevation site. Local disturbance causes tree gaps resulting in scattered canopy that creates patches of greater light availability and availability of optimum resources and nutrients for lower subcanopy and regenerating species (Raghubanshi and Tripathi 2009). Foregoing studies suggested that mild disturbances provide greater opportunity for species turnover, establishment, and colonization, thus leading to higher diversity (Whittaker and Likens 1975; Connell 1978; Mishra et al. 2004). Additionally, other factors might contribute to the differences among study sites, such as topographical heterogeneity and environmental conditions in the study region.

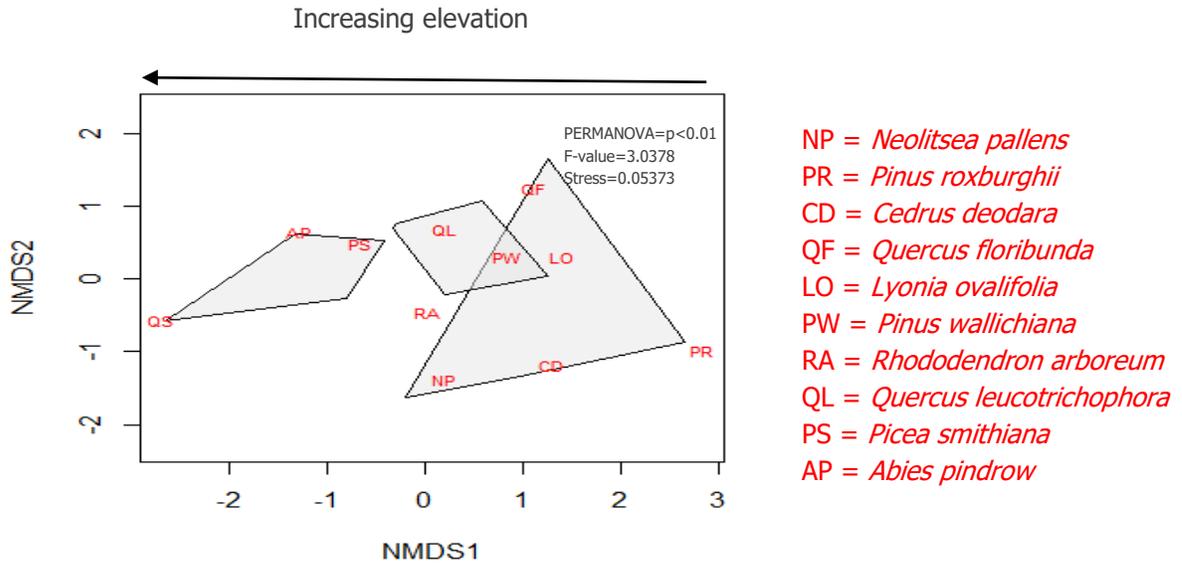


Figure 3. Non-metric Multi-Dimensional Scaling followed by PERMANOVA for all the species in the study site

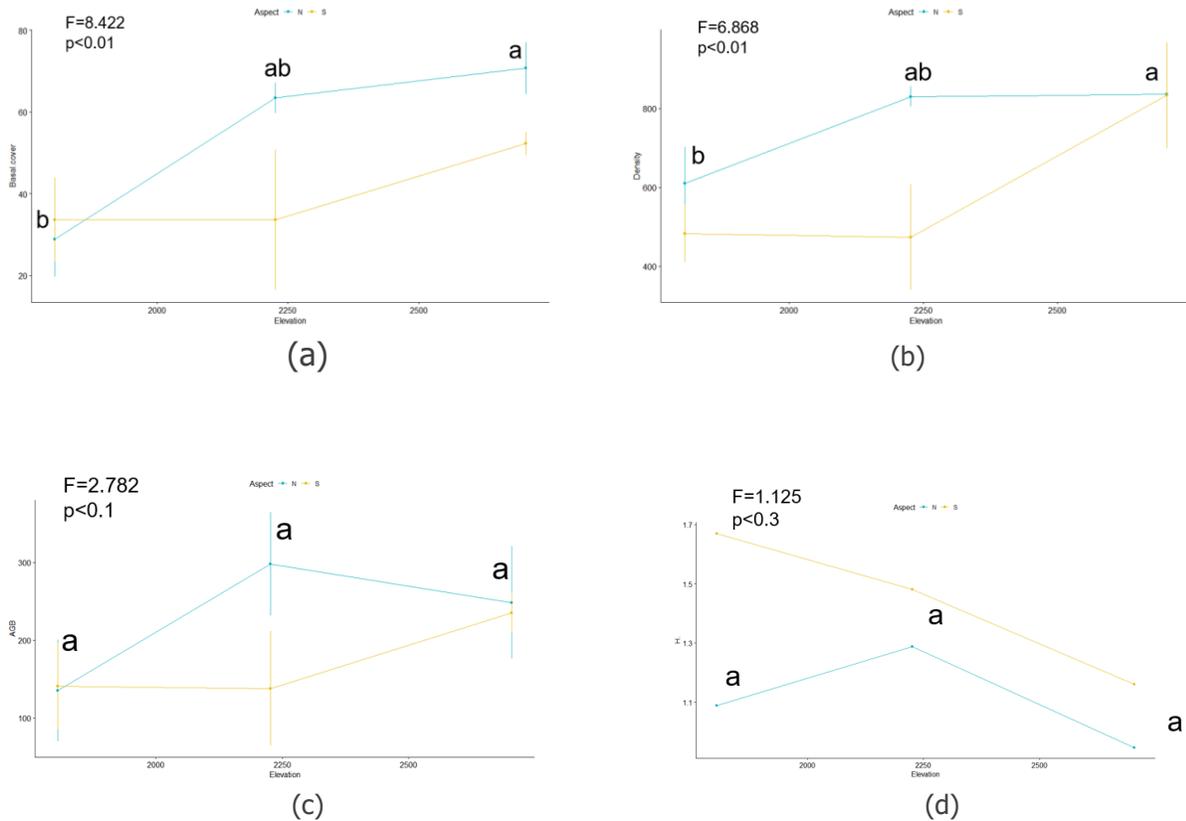


Figure 4. showing the comparison of (a) Basal cover, (b) Density (c) Above-ground Biomass (AGB) and (d) Shannon-Weiner Diversity (H') using One-way ANOVA followed by Tukey post hoc test

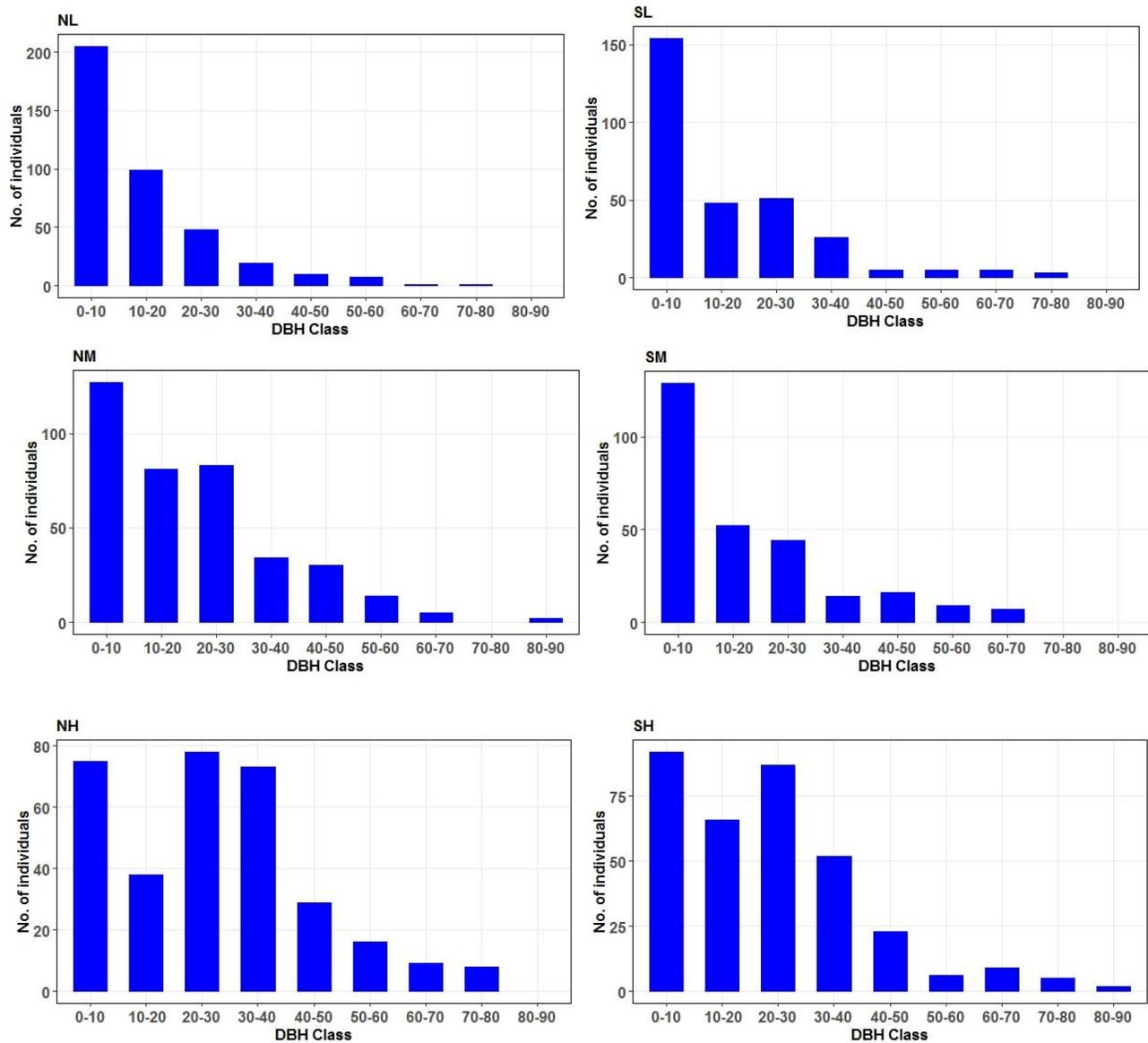


Figure 5. Population structure of tree species Where the DBH Class has been divided into 0-10 cm, 10-20 cm, 20-30 cm, 30-40 cm, 40-50 cm, 50-60 cm, 60-70 cm, 70-80 cm, 80-90 cm. (Abbreviations: NL: Northern aspect at Lower elevation, SL: Southern aspect at Lower elevation, NM: Northern aspect at Middle elevation, SM: Southern aspect at Middle elevation, NH: Northern aspect at Higher elevation, SH: Southern aspect at Higher elevation).

4.2. Soil Texture and Light Intensity are the most important determinants of trait variation

To analyze how plant functional traits vary with environmental conditions, we used linear mixed effect models. Environmental parameters such as Relative Radiation Index (light intensity), Elevation, Soil Texture, Soil pH, Soil Moisture Content (water availability) were introduced as fixed effects, whereas plots were introduced as random effects. We found that, elevation and soil texture significantly affect all plant functional traits investigated in this study. Light intensity and water availability did not explain much of the observed trait variation individually, but significantly affected trait variation in combination with other factors (i.e., interaction terms were significant). Fixed effect variance (R^2 marginal) due to environmental factors (soil texture and light intensity) was greatest for HT followed by WD whereas, leaf traits especially LPC had the least variance (**Table 1 and 2**). Fixed effect variance for conifers were also greatest for height and least for wood density suggesting HT to be strongly under the environmental control than any other traits followed by wood density, whereas leaf traits, especially LPC, had the least variance due to environmental factors suggesting the management activities as an important factor that affects trait distribution. Our results were in line with Vilà-Cabrera et al. (2015) who studied trait variation for dominant tree species in Mediterranean region. For conifers, we did not find the interaction to be significantly contributing to the trait variation rather than the individual environmental factors themselves. For both broad-leaved and conifer species, elevation remains to be the most important contributing factor for all traits followed by the light intensity and soil texture. With increasing elevation, we found HT of the species to reduce with increasing elevation for both broad-leaved and conifer species (**Figure 6, Appendix 3 Table A3**). However, for conifers, R^2 explained 66% of the variance suggesting plant height to reduce significantly with increasing elevation. WD decreased significantly with increase in elevation for both broad-leaved and conifers explaining 35% and 51% variance respectively. With increasing elevation and thus reducing temperature, water becomes more viscous and to maintain that flux, lower wood density is required for a given plant individual. LMA was found to increase with increase in elevation for broad-leaves suggesting high investment in leaf defense mechanism and thus longer leaf life span due to abiotic stresses at higher elevation. For conifers we found the opposite trend due to disturbances at lower level. Pine and cedar species at lower elevation show higher LMA due to anthropogenic disturbances at lower elevation. But from mid-elevation to higher elevation there is an increase in LMA with increasing elevation due to extreme environmental conditions (**red line, Figure 6**). Species at higher elevation were found to have greater LMA, and such individuals tend to have longer leaf life spans causing lower growth rates (Louault et al. 2005). Lower LMA in broad-leaves suggest the species to be resource-acquisitive indicating the competitive nature of the species whereas higher LMA in conifers suggest the species to be resource conservative indicating resistance to extreme environments and hence stable. LPC did not vary much for broad-leaved species whereas for conifers we found it to increase significantly with increasing elevation. This suggests the leaf economic spectrum to be affected by external factors such as management intensity for broad-leaved species since the local people cut down the branches for fuel and fodder purposes. This also holds true for conifers at lower elevation. Similar results were found in a study conducted in European vineyards

indicating higher photosynthetic capacity and growth rates in bare soil vineyards (Hall et al. 2020). This suggests a faster turnover of plants in response to disturbance (Kazakou et al. 2016). HT was found to be lowest for the high elevation site, thus suggesting less light-demanding species to be shorter (Falster and Westoby 2005). This suggests that additional factors such as topography (slope aspect and elevation), species composition, and environmental conditions (Castro-Luna et al. 2011) might be important in governing plant traits and processes in the region. Therefore, the inclusion of the combined effect of disturbances, topographical heterogeneity, forest types, and environmental conditions might play an important role in the observed variation of plant functional traits in this study.

4.2.1. Intra-specific trait variation greater than inter-specific trait variation

To analyze how traits covary, we used principal component analysis (**Appendix 4, Figure A1**). First and second principal component explained around 63% variance for broad-leaved and about 74% variance for conifers. We found LMA to be the first axis of variance whereas LPC, HT and WD forms the second axes of variance. But for conifers we found LMA and LPC together formed the first axes of variance whereas WD and HT formed the second axes of variance. This suggests the functional differences to be high between broad-leaved and conifers. The fact that trait variance occurs mostly at the class level reflects high trait conservatism within angiosperms and gymnosperms and provides further evidence for the known divergence in functional strategies between these two major classes (Brodribb et al. 2012; Carnicer et al. 2013b). To assess the percentage of variance at different ecological levels, variance partitioning was done for broad-leaved and conifers at nested hierarchical level from species to individual level. We found trait variation to be greater at individual level or population level whereas interspecific trait variation was comparatively lower (**Appendix 4, Figure A2**). The results are in contrast with the general expectation that inter-specific trait variation is higher than intra-specific trait variation along environmental and resource gradients (Hulshof and Swenson 2010; Jackson et al. 2013). Since we have already segregated the species at class level, we conclude that intra-specific variation results from management activities at lower elevation zones. Variance partitioning for the leaf economic spectrum (LMA and LPC) shows low differentiation between species, suggesting that external factors such management activities are affecting the trait distribution at different ecological levels.

Table 1. showing Linear mixed model summary for broad-leaved species.

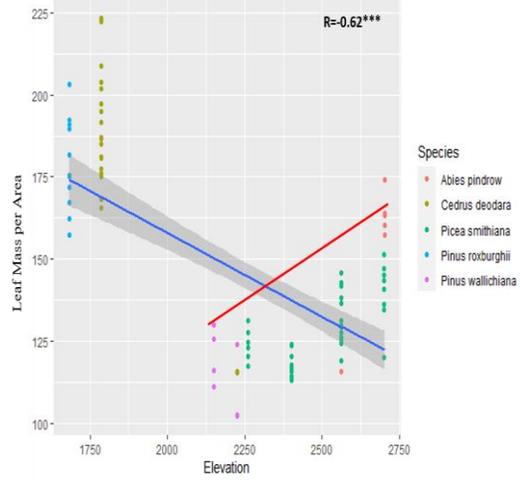
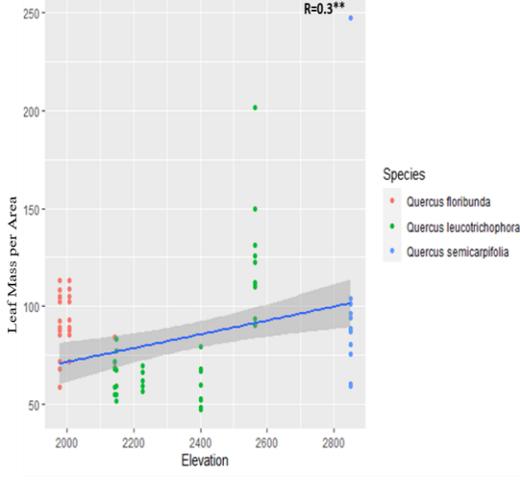
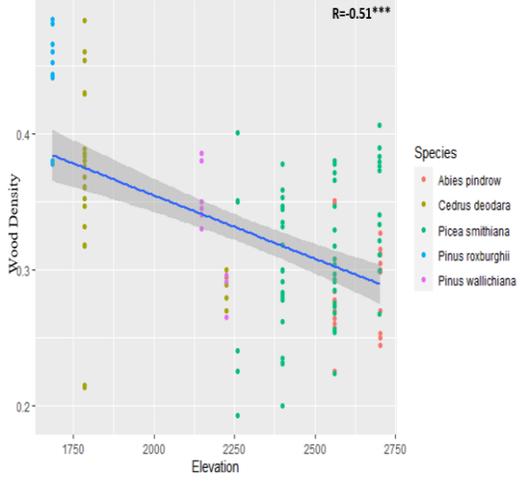
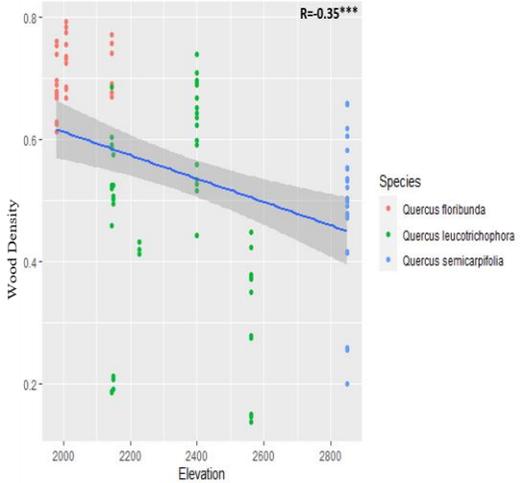
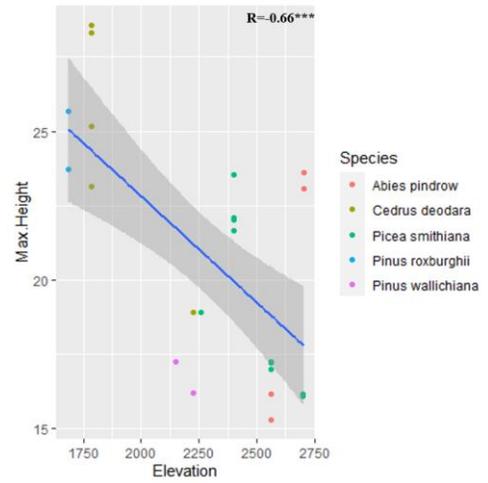
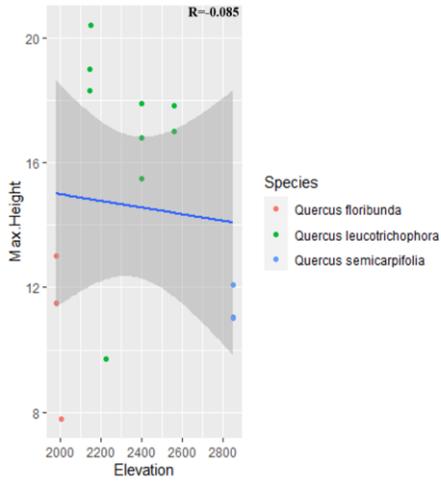
RRI: Relative Radiation Index, SMC: Soil Moisture Content, n.i.: not included; Null model includes only Plot as random factor; Values after \pm indicate standard error; p-values <0.001 '***', <0.01 '**', <0.05 '*'. R²(m/c) indicates fixed effect due to marginal /fixed effect due to conditional.

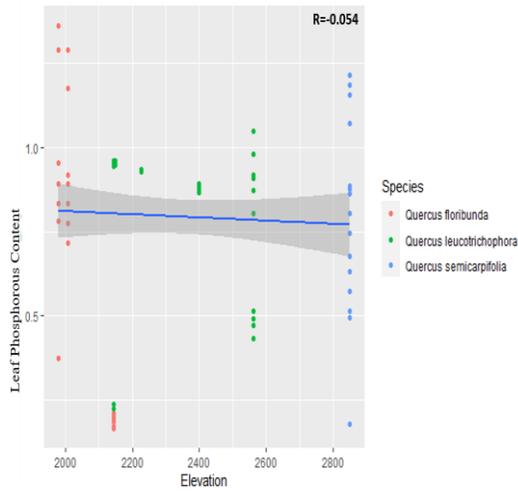
Linear Mixed Models	Max. Height	Wood Density	Leaf Mass per Area	Leaf Phosphorous Content
Intercept	-0.16±0.09	-0.48±0.09***	0.14±0.11	0.22±0.14
Elevation	-0.44±0.12**	-0.15±0.15***	0.37±0.12*	0.84±0.35*
SMC	n.i.	0.47±0.08***	n.i.	n.i.
Soil pH	n.i.	n.i.	1.49±0.31***	n.i.
Texture	-1.12±0.21***	n.i.	-1.25±0.23***	1.66±0.64*
RRI	n.i.	1.07±0.11***	-1.09±0.26***	n.i.
Elevation:RRI	n.i.	0.67±0.11***	n.i.	0.34±0.27
Elevation:SMC	n.i.	0.69±0.12***	n.i.	n.i.
Texture:RRI	n.i.	n.i.	0.49±0.19*	n.i.
Texture:Elevation	n.i.	n.i.	n.i.	1.05±0.46*
Texture:SMC	0.65±0.09***	n.i.	n.i.	n.i.
RRI:SMC	-2.02±0.23***	n.i.	n.i.	1.20±0.55*
R²(m/c) (%)	91/97	72/76	40/46	11/18

Table 2. showing Linear mixed model summary for conifer species.

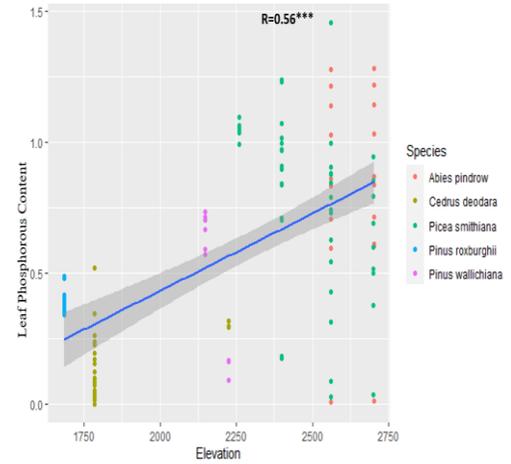
RRI: Relative Radiation Index, SMC: Soil Moisture Content, n.i.: not included; Null model includes only Plot as random factor; Values after \pm indicate standard error; p-values <0.001 '***', <0.01 '**', <0.05 '*'. $R^2(m/c)$ indicates fixed effect due to marginal /fixed effect due to conditional.

Linear Mixed Models	Max. Height	Wood Density	Leaf Mass per Area	Leaf Phosphorous Content
Intercept	-0.02±0.13	-0.008±0.10	0.12±0.16	0.01±0.09
Elevation	-0.87±0.15***	-0.33±0.11*	-0.96±0.19***	0.66±0.11***
SMC	n.i.	n.i.	0.92±0.25**	n.i.
Texture	n.i.	0.26±0.10*	n.i.	n.i.
Temperature	n.i.	n.i.	n.i.	0.55±0.13**
RRI	0.66±0.15***	-0.27±0.11*	n.i.	0.34±0.11*
Texture:Elevation	n.i.	n.i.	0.88±0.28**	n.i.
R²(m/c) (%)	75/94	33/41	62/90	35/40





Broad-leaved species



Conifer species

Figure 6. Variation of functional traits with increasing elevation for broad-leaved (left panel) and conifer species (right panel) indicating HT and WD decrease with elevation (blue line). Exception: LMA increases with elevation (red line). Different color points indicate different species

4.3. Plant Functional Traits drive Vegetation Carbon Storage

Structural equation models have been used to analyze the relation between environment factors (RRI, elevation as a proxy for change in temperature, SMC and Soil PC1) and ecosystem function (vegetation carbon stocks, calculated using species-specific volumetric equations) using plant functional trait i.e., WD (Figure 7). We found that elevation, light availability (RRI), species richness (SR) and soil water availability (SMC) were the most important variables governing trait variability and carbon stocks for both broad-leaved (Fig. 7 left panel) and conifer species (Fig. 7 right panel). Arrows with red color indicate negative relationship whereas the green indicate positive relationship among the variables. Arrow width indicates effect strength, and numbers are significant standardized path coefficients ($p < 0.05$). The finding suggest that Carbon stocks increases significantly with increases in WD for both the classes. It also suggests the dominant tree species to play an important role in carbon storage in the region. Thus, trait variability could be a useful indicator to predict carbon sequestration at large spatial scales.

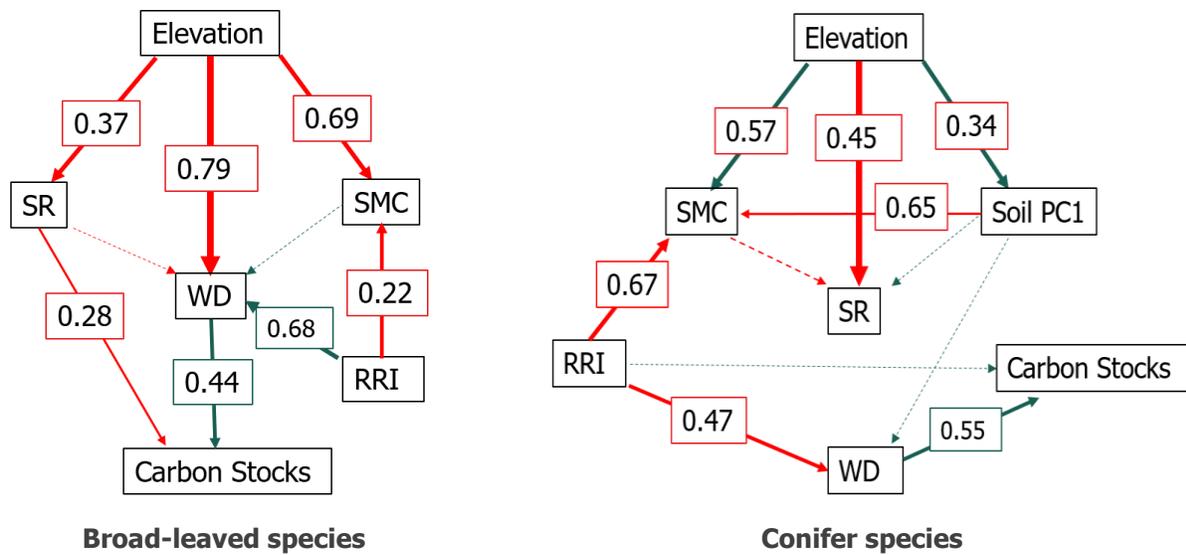


Figure 7. showing Structural Equation Model framework showing relation between environment-trait-ecosystem function. Trait selected is Wood density (WD) and ecosystem function is Carbon Stocks.

4.4. Plant and Plant-FATE model calibration (Preliminary results)

To analyze the effect of traits on ecosystem functioning and associated services we calibrated the Plant and Plant-FATE models using the height distribution of trees from our study site. These models use four traits (maximum height, wood density, leaf mass per area, and seed mass) to account for trait-driven tradeoffs in individual plant functioning, and scale-up the functioning of individual plants to the level of plant communities. They predict emergent ecosystem properties such as 1) Species number and abundance (biodiversity), 2) Height and DBH distribution of trees, 3) Height / DBH growth rates, 4) Leaf Area Index, 5) Gross Primary Productivity, 6) Standing biomass. We initialized these models with observed trait data for two species occurring in two mono-specific plots, and calibrated their predictions with corresponding observed size-distribution data. We found that the model's predictions match field observation for the two species, *Quercus floribunda* (**Figure 8**) and *Neolitsea pallens* (**Figure 9**). The calibrated models can now be used to predict emergent ecosystem properties for temperate forests of Western Himalaya.

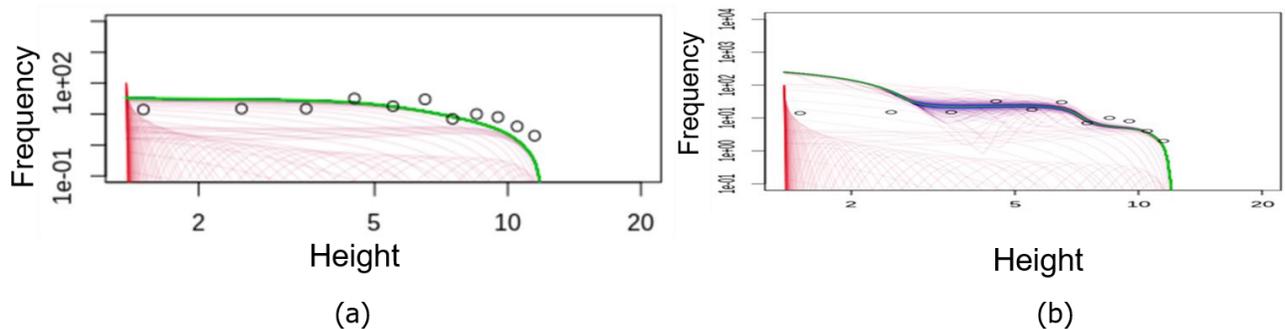


Figure 8. showing Height distribution of *Quercus floribunda* with time for (a) Plant model and (b) Plant FATE model

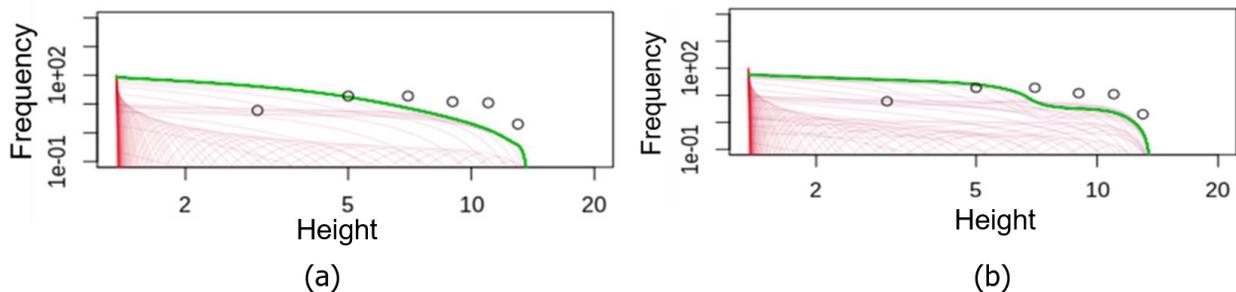


Figure 9. showing Height distribution of *Neolitsea pallens* with time for (a) Plant model and (b) Plant FATE model

5. Conclusions and potential implications for sustainable forest management

The plant functional traits investigated in this study, especially HT, WD and LMA, were found to be tightly linked to the environmental heterogeneity of the study site for both broad-leaved and conifer tree species. Environmental filtering shapes local species composition and associated plant functional traits in the study site and we found elevation, light intensity and soil texture to be the most important environmental factors affecting plant functional trait distribution. Contrary to our expectations, we found higher intra-specific variation than inter-specific trait variation for both broad-leaved and conifer tree species. While inter-specific variation typically results from changes in species composition between study sites located in different elevations along environmental gradients in resource availability, intra-specific variation results from individual adaptation to local site conditions. It is therefore not surprising that we found the leaf economic spectrum to be strongly affected by local management practices. Therefore, inclusion of management practices, especially for broad-leaved species, and the inclusion of the sources and causes for intraspecific trait variation is crucial for linking environmental changes to changes in species distribution and ecosystem functions and services. We also found that plant functional traits are important predictors of vegetation carbon storage suggesting that differences in species composition determine vegetation carbon storage in the region. Eventually, using our results to calibrate a trait-based eco-evolutionary model, we successfully predicted the size distribution of two species at our sites. The calibrated models can thus be used to project crucial ecosystem services under future climate change scenarios. Overall, our study findings indicate that species with more conservative ecological strategies would be more prone to continued disturbance intensity, and therefore highly fragile temperate forests in the Himalaya should be sustainably managed to maintain crucial ecosystem services and avoid further loss of biodiversity in the region.

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Appendix 1

Table A1 showing species-specific volumetric equations for the dominant species. V=volume, D=Diameter at breast height, H= Height and n=number of samples.

Sl. No.	Species name	Volumetric equations	References	n	R ²	General /Local
1	<i>Pinus roxburghii</i>	$V=(0.2283/D^2-1.7288/D+9.05)*D^2$	FSI (1996)	388	0.4945	Local
2	<i>Quercus leucotrichophora</i>	$V=(0.0854/D^2-1.2582/D+7.703)*D^2$	FSI (1996)	600	0.6028	Local
3	<i>Quercus floribunda</i>	$V=(0.0988/D^2-1.5547/D+10.1631)*D^2$	FSI (1996)	355	0.6686	Local
4	<i>Cedrus deodara</i>	$V=-0.0017+8.2098D^2$	FSI (1996)	221	0.9393	Local
7	<i>Pinus wallichiana</i>	$V=0.2232-2.3509D+11.9067D^2$	FSI (1996)	86	0.9627	Local
8	<i>Picea smithiana</i>	$V=0.26072/D^2-3.29692/D+14.71246D^2$	FSI (1996)	427	-	Local
9	<i>Quercus semicarpifolia</i>	$V=(0.13581/D^2-1.84908/D+10.82341-0.6276*D)*D^2$	FSI (1996)	291	0.6061	Local
10	<i>Abies pindrow</i>	$V=0.17507+0.22606D^2H$	FSI (1996)	22	0.9525	General

Appendix 2

Table A2. showing the vegetation structure and soil properties in the study site with units in the bracket.

Plots	Elevation	Density (ind ha ⁻¹)	Basal cover (m ² ha ⁻¹)	AGB (t ha ⁻¹)	H'	SMC (%)	pH	Sand (%)	Clay (%)	Silt (%)
1	1596	430	10.81	6.95	1.088	10.34	5.93	60.52	5.76	34.44
2	1684	340	27.71	80.07	1.67	11.88	6.33	62.20	5.52	32.28
3	1785	660	40.07	179.76	1.088	22.82	5.93	60.48	5.88	33.64
4	1785	530	53.65	252.76	1.67	21.86	6.53	58.85	6.00	35.15
5	1980	740	35.63	219.47	1.088	19.58	6.17	63.84	5.64	30.52
6	2007	580	19.48	90.53	1.67	31.25	6.23	56.84	5.52	37.64
7	2144	850	61.35	293.92	1.287	13.99	5.87	57.17	5.04	37.79
8	2149	360	15.07	55.25	1.48	12.69	5.63	63.96	5.52	30.52
9	2260	860	58.3	184.41	1.287	24.57	6.37	61.51	6.00	32.49
10	2226	320	17.86	73.91	1.48	15.90	6.37	57.99	5.28	36.73
11	2400	780	70.66	415.39	1.287	9.66	6.13	61.51	5.76	32.73
12	2400	740	67.92	284.77	1.48	11.87	6.33	62.68	5.28	32.04
13	2562	630	59.4	104.6	0.946	35.88	6.50	58.01	5.76	36.23
14	2562	580	57.31	185.35	1.16	17.04	6.53	59.51	5.52	34.97
15	2703	950	81.39	307.45	0.946	23.18	6.17	59.75	5.76	34.49
16	2700	880	52.07	263.82	1.16	21.62	6.33	62.08	5.76	32.16
17	2850	930	71.35	333.41	0.946	38.42	5.43	57.77	5.52	36.71
18	2850	1040	47.56	257.3	1.16	32.15	6.03	58.69	5.88	35.43

Appendix 3

Table A3. showing species level mean trait values (unit) in each plot along the elevation gradient in the study site with respective units in the bracket.

Plots	Elevation	Species name	Htmax(m)	LMA(kg/m ²)	WD(kg/m ³)	SM(kg)	LPC(%)
1	1596	<i>Neolitsea pallens</i>	13.50	0.130	290.40	0.0003	0.249
2	1684	<i>Pinus roxburghii</i>	25.67	0.178	437.33	0.0001	0.398
3	1785	<i>Cedrus deodara</i>	28.56	0.176	346.75	0.0001	0.142
4	1785	<i>Cedrus deodara</i>	25.15	0.199	380.42	0.0005	0.138
5	1980	<i>Quercus floribunda</i>	13.00	0.091	685.42	0.0041	0.776
6	2007	<i>Quercus floribunda</i>	7.80	0.096	734.00	0.0046	0.950
7	2144	<i>Quercus floribunda</i>	8.00	0.072	714.71	0.0043	0.180
7	2144	<i>Quercus leucotrichophora</i>	19.00	0.062	478.75	0.0018	0.830
8	2149	<i>Quercus leucotrichophora</i>	20.40	0.064	413.00	0.0017	0.967
8	2149	<i>Pinus wallichiana</i>	17.25	0.118	355.17	0.0020	0.660
9	2260	<i>Picea smithiana</i>	18.90	0.124	293.33	0.0002	1.040
10	2226	<i>Cedrus deodara</i>	18.90	0.116	282.83	0.0006	0.300
10	2226	<i>Quercus leucotrichophora</i>	9.70	0.063	424.00	0.0059	0.930
10	2226	<i>Pinus wallichiana</i>	16.20	0.110	284.00	0.0010	0.140
11	2400	<i>Picea smithiana</i>	23.55	0.117	311.42	0.0001	0.960
11	2400	<i>Quercus leucotrichophora</i>	12.89	0.059	635.75	0.0022	0.883
12	2400	<i>Picea smithiana</i>	22.00	0.120	290.75	0.0001	0.805
12	2400	<i>Quercus leucotrichophora</i>	17.89	0.061	582.44	0.0027	0.886
13	2562	<i>Abies pindrow</i>	16.15	0.116	282.17	0.0001	0.861
13	2562	<i>Picea smithiana</i>	16.32	0.130	273.89	0.0002	0.587
14	2562	<i>Quercus leucotrichophora</i>	17.83	0.124	313.75	0.0032	0.697
14	2562	<i>Picea smithiana</i>	17.24	0.133	334.58	0.0001	0.764
15	2703	<i>Abies pindrow</i>	23.60	0.164	291.42	0.0001	0.844
16	2700	<i>Picea smithiana</i>	15.95	0.139	348.17	0.0001	0.576
17	2850	<i>Quercus semicarpifolia</i>	11.05	0.096	565.25	0.0035	0.752
18	2850	<i>Quercus semicarpifolia</i>	12.10	0.114	444.33	0.0037	0.792

Appendix 4

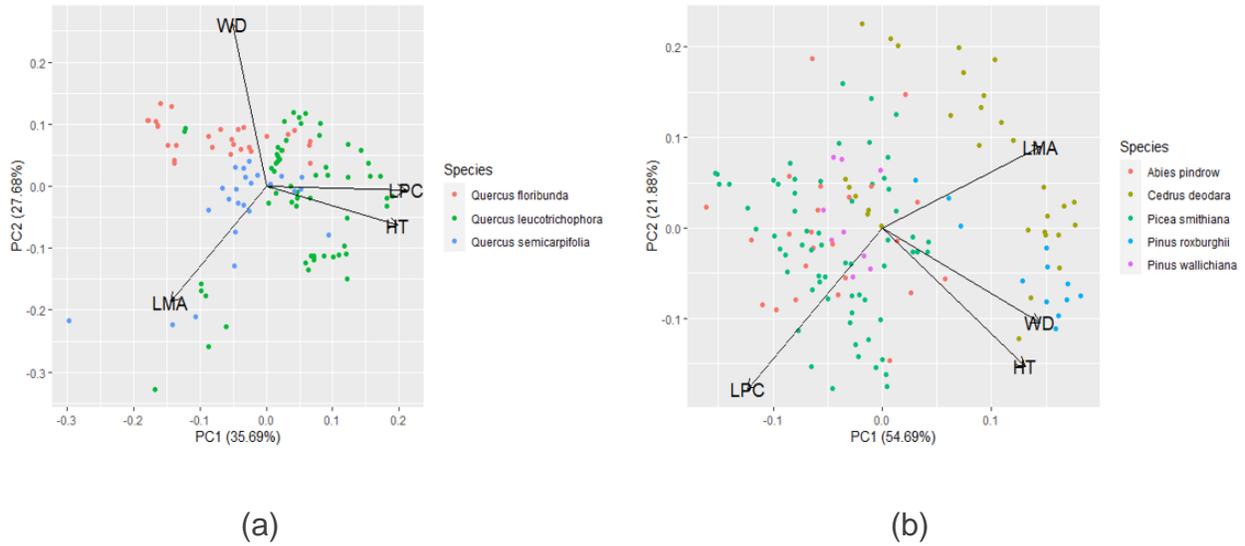


Figure A1. Graphic representation of first and second components of the Principal Component Analysis of functional traits within (a) Broad-leaved species (left panel) and (b) Conifer species (right panel).

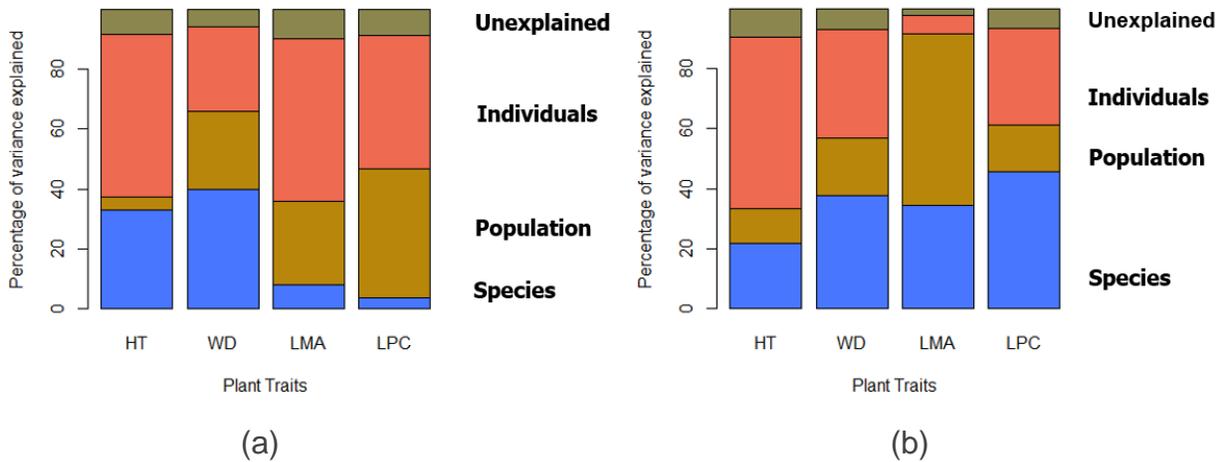


Figure A2. Variance partitioning for broad-leaved and conifer species at nested hierarchical level (Species/Population/Individuals/Unexplained) within (a) Broad-leaved species (left panel) and (b) Conifer species (right panel).

