SPECIES EXHIBITING POSITIVE ASSOCIATION DEMONSTRATE HIGH ABOVE-GROUND BIOMASS ACCUMULATION IN THE SUBTROPICAL HIMALAYAN FOREST ECOSYSTEM, INDIA

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Abstract. Species interaction is vital in regulating community function, structure, formation, succession, and maintenance in the forest. The present study aimed to understand the interactions within mixed plant communities and their impact on individual tree above ground biomass (AGB) accumulation in the Himalayan sub-tropical forest, INDIA. Using the variance ratio (VR) and Spearman correlation coefficient (SRCC), population dynamics and spatial associations were examined between species pairs and AGB accumulation. Results showed species richness of 46 and average Shannon-Wiener index of 2.40. The variance ratio of 2.443, exceeding the critical value of 1.51, indicated a significant positive association among species, contributing to a stable forest structure. Significant positive covariance ($r \geq 0.511$, $p \leq 0.01$); and negative covariance ($r < -0.398$, $p < 0.05$) were identified, with *Acacia catechu* and *Ehretia leavis* showed the highest positive pairing (33.13%) with other species and species with a DBH of 5-10 cm accumulated the highest AGB. The study revealed that 98% of species showed positive associations, significantly enhancing AGB accumulation, while 2% showed negative associations. These findings suggested that mixed-species plantations upholding species diversity are more effective for biomass generation than monoculture plantations and these novel identified species pairs are recommended for plantation in sub-tropical forested regions for high biomass generation with medicinal importance. The study offers a new perspective on AGB accumulation through mutualism among species, emphasizing the ecological and practical benefits of mixed-species plantations for carbon sequestration and forest stability.
Keywords: *species interaction, biomass accumulation, ecological stability, species diversity, community dynamics*

Introduction

Above-ground biomass (AGB) is an important phenomenon of forests that reflect their health and functions. Forests act as carbon sinks that contribute to high biomass accumulation owing to the presence of diverse plant species. These mixed plant communities consist of individuals of various species that interact locally with each other and also form a network of species for their interactions. Communities in such forests are the sum of co-occurring individuals of different species (Michalet et al., 2014). Therefore, the response of tree communities to mixed species is influenced by the combined effects of numerous small-scale interactions among these individuals (Potvin and Dutilleul, 2009; Williams et al., 2017; Van de Peer et al., 2018). Thus in the natural forests mixed tree species have faster growth and greater survival rates (Liang et al., 2016; Liu et al., 2018). These interactions vary in the neighbourhood of individual trees due to diverse ecological and physiological factors, which either benefit or hinder tree growth. Positive associations, such as niche differentiation or facilitation, occur when different species

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complement each other, enhancing overall community function. In contrast, negative associations, such as competition for resources, arise when neighbouring trees compete, potentially limiting growth (Wright et al., 2014).

Positive associations among species occur when species have a common response to unlimited resources. In this case, species mutually enhance their survival probabilities, and they swing unanimously when the availability of resources is limited (Ludwig and Reynolds, 1988; Chesson, 2000; HilleRisLambers et al., 2012). Species facilitate the growth and establishment of other species by increasing water availability, improving soil fertility and help in nitrogen fixation (Maestre et al., 2003; Bishop et al., 2013). The negative association between species interferes with their growth due to competition for resources or their different resources requirements (Ludwig and Reynolds, 1988; Chesson, 2000). Competition arises in plant communities due to the sharing of limited resources (such as light, water, and nutrient availability), which results in decrease in the success rate of the competing plants (Wilson, 2007; Bittebiere et al., 2012). Past studies have shown that competition and facilitation occur simultaneously in communities, and the balance of these is influenced by the degree of abiotic stress (Callaway et al., 2002; Maestre and Cortina, 2004).

While in literature most of the studies based on the biomass estimation in subtropical Himalayan forests (Li et al., 2020; Opelele et al., 2021; Zhang et al., 2023; Chen et al., 2024) but lack in define the relationship of biomass with species association. Studying ecological species groups and the interspecific relationship among plant species is essential for uncovering the process and mechanisms that enable species coexistence (Su et al., 2015). Therefore, the present study aimed to understand the interactions within mixed plant communities and their impact on the AGB accumulation of individual trees. Studying the spatial pattern and association of tree species in natural forests provides significant insight into the process of biomass accumulation and the carbon sink potential of species. Mixed forests, which contain a variety of tree species, are likely to be more resilient and adaptable to climate change compared to forests dominated by a single species (Zhang et al., 2012). Mixed forests are believed to maintain a minimum level of functioning despite changing environmental conditions (Jucker et al., 2014) and are expected to exhibit more stable functioning over time under various management practices. Additionally, these forests are often more resistant to biotic disturbances, such as attacks by pathogens or herbivorous insects, compared to monospecific forests (Damien et al., 2016; Kambach et al., 2016; Jactel et al., 2017).

Thus, it is imperative to explore the species association of mixed forests as viable alternatives, for the regions where monospecific forests are planted. This exploration is crucial for ensuring which pair of species associations will maximize the provision of ecosystem goods and services, enhancing forest resilience, maintaining ecosystem functions, and mitigating the impacts of environmental changes, particularly in the face of climate change (Cordonnier et al., 2018). Our goal is to estimate the AGB of subtropical mixed Himalayan forest and identify species pair associations that demonstrate high AGB. The finding is novel as it has not been earlier reported in the context of the sub-tropical Himalayan forest. Understanding species associations is crucial for forest managers in restoration and regeneration efforts. Insights from this study can guide the selection of alternative species for biomass generation, significantly enhancing ecosystem services. By leveraging positive species interactions, forest management practices can be optimized to improve biodiversity, carbon sequestration, and overall forest health.

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Materials and methods

Study area

The study area Dhaulasidh sub-tropical Himalayan Forest located at 31.80477 N latitude and 76.43964 E longitude in the Hamirpur district of Himachal Pradesh, India (*Fig. 1*). This is a 142.6 ha area having an elevation ranging from 469 to 869 m AMSL. The annual mean temperature of the region varies between 17.96 to 27.9º C and the rainfall is 1,020–1,275 mm.

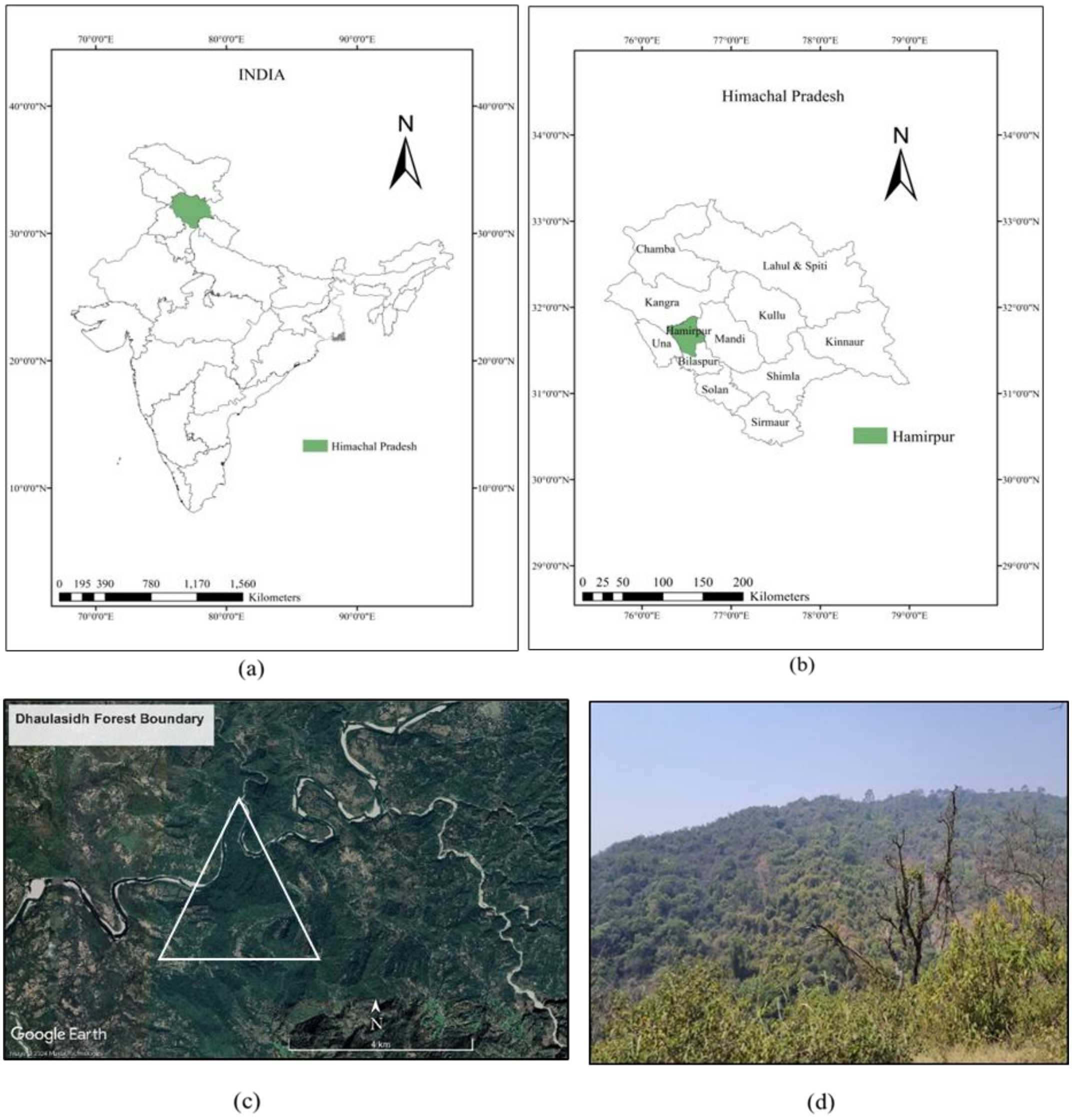

Figure 1. *(a) Study area located on country map, state map (b) and in the field (c, d)*

Methods

Estimation of Above Ground Biomass (AGB)

The study area is under the control of the Himachal state forest government (Hamirpur forest circle). The present study utilized tree inventory data, based on the compartmental basis comprises with 10 compartments (from year 2020-2021), with each compartment

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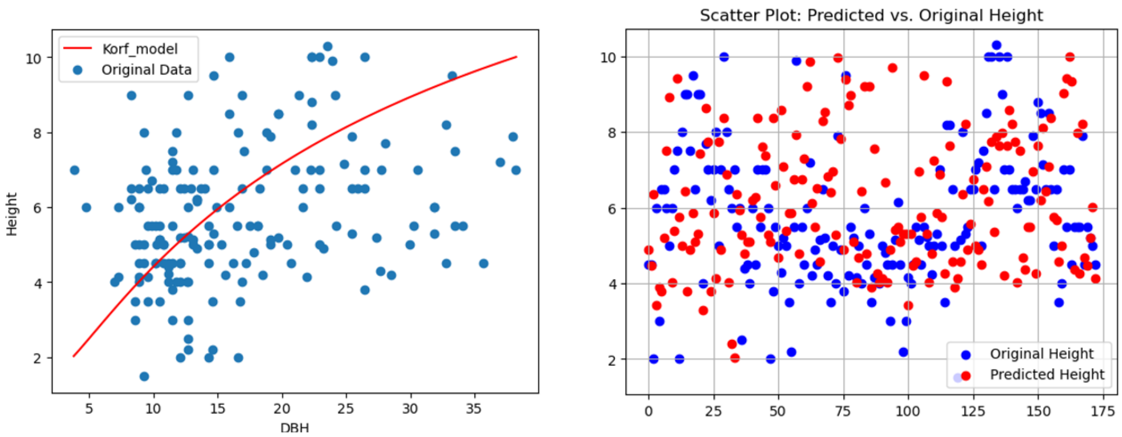
spanning an area of 1.5 hectares, providing total surveyed area of 15 hectares. The survey was conducted systematically from the forest's start to end and organized in a way that compartments 1, 2 and 3 marked as forest's starting sections, compartments 4, 5, 6, and 7 covered the middle, and compartments 8, 9, and 10 represented the end point. Overall, Diameter at Breast Height (DBH) measurements were recorded for 9,608 trees by forest officials using a measuring tape at 1.3 meters above ground level. Further, in each compartment, species composition and dominance patterns analysed for the spatial variations in AGB accumulation. Since the AGB calculation (*Equation 2*) requires tree height values, the heights of trees were estimated using a non-linear Korf/Lundqvist (KL) model equation using the DBH data (*Equation 1*).

$$H = 1.3 + a \times e(-b \times DBH^{-c}) \quad \text{(Eq.1)}$$

where, DBH = Diameter at breast height; a = asymptote; b = scale parameter; c = shape parameter; e = base of natural logarithm.

Here, the calculated values for a, b, and c estimated in python libraries are 20.18,7.38 and 0.59, respectively.

In order to validate the accuracy of Equation1, field surveys were conducted in the forest, height (using clinometer) and DBH (measured meter tape at 1.3 m) of 187 trees were measured randomly. The comparison between observed and predicted height (*Fig. 2*) showed 95% accuracy (mean absolute error = 1.7, mean square error = 4.47 and root mean square error = 2.11).



(a) (b)

Figure 2. *(a) Korf model and (b) Scatter plot between original and predicted height*

Ultimately, using a mixed species allometry model, AGB was estimated for individual trees (*Equation 2*). The specific gravity of each tree was used from the literature (Nath et al., 2019).

$$AGB(kg/m^3) = 0.32 \times p \times D^2 \times H^{0.75} \times 1.34 \quad \text{(Eq.2)}$$

where, p= Wood Density, D = Diameter at Breast Height, H = Height of tree.

The forest tree species diversity was calculated using Shannon diversity index (*Equation 3*).

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$$H' = -\sum pi \times (Ln\, pi) \quad \text{(Eq.3)}$$

where, pi = n_i/N (N and i is the total number of individuals per study plot), n_i = the number of individuals per species, p_i = proportion of individuals in species i.

The species evenness was calculated using *Equation 4*.

$$\mathrm{E} = \frac{\mathrm{D_{max}}}{\mathrm{D}} \quad \text{(Eq.4)}$$

D_{max} represents maximum possible value of D in a community where all species are equally abundant. For a community with S species, D_{max} = $1-1/S$. Where, D =1−∑(n_i/N)2 (n_i = number of individuals of the ith species, N = total number of individuals in the sample). The evenness index ranges between '0' and '1', where '1' indicates perfect evenness (all species are equally abundant) and values closer to '0' indicate uneven distribution among species. Thus, Species richness was calculated compartments-wise to check the variation of species richness in the study area.

Estimation of rarefaction curve

Rarefaction curves estimate species richness in habitat by accounting for the variability in sampling size based on the hypergeometric distribution model (Sanders, 1968; Hurlbert, 1971). These curves are widely used to compare the biodiversity of varying sample sizes (Gotelli and Colwell, 2001). It is created by plotting the average number of species found in each compartment. Python libraries (Pandas and Matplotlib) were used for estimation of rarefaction curve.

Estimation of Important Value Index (IVI)

IVI serves as a comprehensive quantitative measure to delineate the significance of each species within the community (Erman and Helm, 1971). A higher IVI signifies greater dominance of a tree species within the plot. The IVI was computed according to the following formula:

IVI = Relative abundance + Relative frequency + Relative dominance/3 (Curtis and McIntosh, 1951).

Estimation of Variance Ratio (VR)

In the present study, firstly overall association of species was calculated using a VR test (*Equation 5*) (Ludwig and Reynolds, 1988; Gu et al., 2017).

$$VR = \frac{S_T^2}{\sigma_T^2} = \frac{\frac{1}{N}\sum_{J=1}^{N}(T_j - t)^2}{\sum_{i=1}^{S}\frac{n_i}{N}(1-\frac{n_i}{N})} \quad \text{(Eq.5)}$$

where, N represents the total number of quadrats, T_j is the number of species in the jth quadrat, S is the total number of species, t is the average number of species in the quadrats and n_i denotes the number of quadrat in which the ith species occurred.

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Estimation of Spearman's Rank Correlation Coefficient (SRCC)

VR test doesn't provide pairwise or interspecies spatial association but only limited to revealing overall species association in a forest stand. Therefore, SRCC index (*Equation 6*) were used to determine the species spatial association between all possible species pairs of high AGB accumulation. SRCC is a non-parametric technique that uses the rank of data to evaluate the correlation between independent variables or the degree of linear association. It has an advantage over other correlations because of the tolerance of small data sets and includes insensitivity in population distribution (Gauthier, 2001). VR test and SRCC were calculated in Python version 3.11 using libraries Pandas, Numpy, Seaborn, Scipy and Matplotlib.

$$r_s(i,j) = 1 - \frac{6\sum_{k=1}^{n} d_k^2}{N^3 - N} \quad \text{(Eq.6)}$$

where N is the total number of quadrat, $r_s(i,j)$ is the Spearman's rank correlation coefficient, $d_k = (x_{ik}-x_{jk})$, x_{ik} is the rank of species i in quadrat k, and x_{jk} is the rank of species j in quadrat k.

Results

Refraction curve of data set

In the analysis of the rarefaction curve it was observed that compartment 2 showed high species occurrence, while compartment 1 exhibited the least number of species. The number of observed species increased with the sample size (*Fig. 3*). The x-axis of the plot represents the number of individuals, while the y-axis represents the number of species.

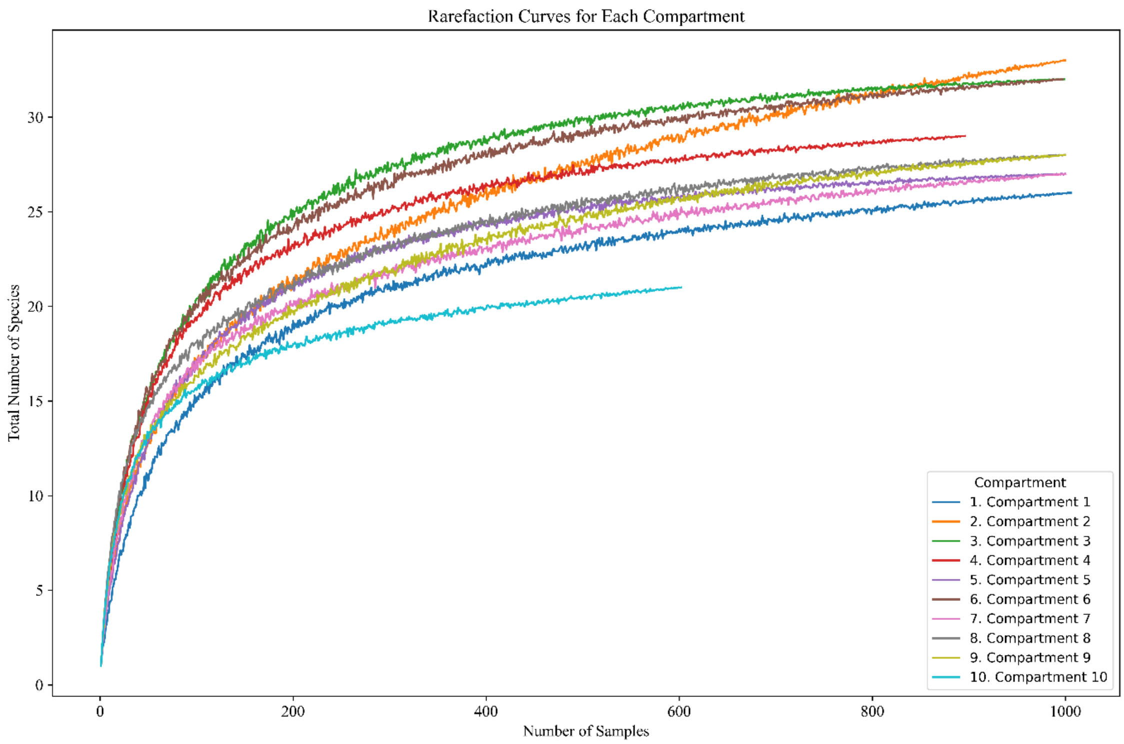

Figure 3. *Species rarefaction curve of species in different compartments*

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Important Value Index (IVI) of tree species

A total of 46 tree species were observed from beginning to end of the forest, with the highest IVI found for *Mallotus philippinensis* (33.37) and *Acacia catechu* (17.74) (*Table 1*) with respective of 3,872 and 525 individuals. The IVI for other species ranged from 0.01 to 3.47, highlighting the dominance of these two species in the study area.

Table 1. *Basal area, Relative density, abundance, frequency and IVI of species in the study area*

Species	Basal area (m^2)	Relative Density (%)	Relative Abundance (%)	Relative Frequency (%)	IVI
Kydia calycina	74.69	2.44	3.12	2.92	2.83
Acacia catechu	1283.01	41.94	5.81	5.45	17.74
Aegle marmelos	0.67	0.02	0.02	0.02	0.02
Albizia chinensis	52.15	1.70	0.62	0.58	0.97
Albizia lebbak	72.56	2.37	1.33	1.25	1.65
Albizia odoratissima	62.7	2.05	2.69	2.53	2.42
Anogeissus latifolia	7.91	0.26	0.90	0.84	0.67
Bauhinia verregata	57.17	1.87	3.38	3.17	2.81
Bombax malabaricum	62.45	2.04	2.56	2.40	2.34
Casearia elliptica	3.92	0.13	0.33	0.31	0.26
Cassia fistula	52.26	1.71	4.49	4.22	3.47
Catunaregam spinosa	0.25	0.01	0.03	0.03	0.02
Cedrela toona	1.77	0.06	0.18	0.17	0.13
Celtis ausorails	3.12	0.10	0.18	0.17	0.15
Cordia dichotoma	6.78	0.22	0.17	0.16	0.18
Cordia vestita	29.54	0.97	1.53	1.44	1.31
Crataeva religiosa	19.55	0.64	0.98	0.92	0.84
Dalbergia sissoo	40.73	1.33	1.05	0.99	1.12
Diospyros melanoxylon	49.1	1.61	2.35	2.21	2.05
Ehretia laevis	36.45	1.19	1.54	1.45	1.39
Emblica officinalis	37.06	1.21	1.22	1.14	1.19
Eugenia jambolana	93.39	3.05	1.66	1.56	2.09
Ficus auriculata	33.63	1.10	2.26	2.12	1.83
Ficus benghalensis	12.5	0.41	0.04	0.04	0.16
Ficus glomerata	14.08	0.46	0.26	0.24	0.32
Ficus religiosa	149.85	4.90	0.83	0.78	2.17
Ficus rumphii	1.39	0.05	0.03	0.03	0.04
Flacourtia indica	3.32	0.11	0.09	0.08	0.09
Grewia optiva	65.16	2.13	3.38	3.17	2.90
Holoptellea integrifolia	4.49	0.15	0.16	0.15	0.15
Jatropha curcas	14.75	0.48	1.01	0.95	0.81
Mallotus philippinensis	516.29	16.88	42.94	40.30	33.37
Mangifera indica	2.86	0.09	0.04	0.04	0.06
Melia azedarach	3.35	0.11	0.22	0.21	0.18
Morus alba	14.49	0.47	0.83	0.78	0.70
Morus laevigata	0.3	0.01	0.02	0.02	0.02
Nerium Indicum	1.62	0.05	0.02	0.05	0.02
Oroxylum indicum	2.18	0.07	0.09	0.08	0.08
Ougenia dalbergiodes	13.92	0.46	1.66	1.56	1.23
Pyrus pashia	61.03	2.00	4.77	4.48	3.75
Sapindus mukorossi	77.8	2.54	4.36	4.09	3.66
Syzygium cumini	11.56	0.38	0.38	0.35	0.37
Terminalia arjuna	1.48	0.05	0.09	0.08	0.07
Toona ciliata	4.47	0.15	0.27	0.25	0.22
Xeromphis spinosa	0.32	0.01	0.01	0.01	0.01
Ziziphus mauritiana	0.85	0.03	0.11	0.10	0.08

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The frequency distribution of species revealed varying occurrences of individuals in the data set. After *Mallotus philippinensis* and *Acacia catechu: Grewia optiva*, *Cassia fistula*, and *Sapindus mukorossi* had frequencies of 419, 405 and 392 respectively. However, species like *Pyrus pashia*, *Bauhinia verregata*, and *Albizia odoratissima* exhibited lower frequencies 330, 307 and 296. While *Albizia chinensis*, *Ficus rumphii*, and *Mangifera indica* were the species with the least occurrence 2, 5 and 4. *Mallotus philippinensis* exhibited the highest frequency 63.65%, 38.44%, 47.54%, 52.20%, 35.01%, 48.60%**,** and 24.30%. across all compartments, expect the end of the forest (10th compartment) where *Bauhinia variegata* displayed the highest frequency of 23.92%. The analysis of tree density and cover in all studied compartments revealed that *Mallotus philippinensis* exhibited the highest tree density 254.30 ha^{-1}, In contrast, *Acacia catechu* demonstrated a lower density of 24.12 ha^{-1}. The species with the lowest density, at 0.10 ha^{-1}, were *Zizyphus mauritiana* and *Xeromphis spinose*, indicated a sparse presence in the forest community.

Above Ground Biomass (AGB) of tree species

The tree species were categorized into eleven DBH classes of varying diameter ranges such as 0-5 cm, 5-10 cm, 10-15 cm, 15-20 cm, 20-25 cm, 25-30 cm, 30-35 cm, 35-40 cm, 40-45 cm, 45-50 cm, and >50 cm (*Fig. 4*). The majority of species fall in the 5-10 cm DBH class, except *Catunaregam spinose*. The *Aegle marmelos, Ficus benghalensis, Morus laevigata, Nerium indicum,* and *Xeromphis spinosa* were absent in the 0–5 cm DBH category. Only *Acacia catechu* and *Eugenia jambolina* had DBH greater than 50 cm, and it is the sole species that represented all the DBH categories, indicated its broad diameter range. Interestingly, despite the prevalence of maximum individuals of *Mallotus philippinensis*, *Acacia catechu* emerged as the dominant species, having the highest AGB compared to other species and the *Xeromphis spinose* had the lowest AGB (101 kg/m^3). It was found that the DBH classes 0-5, 5-10, 10–15, 15–20, 20–25, 25–30, 30–35, 35–40, 40–45, 45–50, and >50 cm exhibited AGB values of 81,559.5 kg/m^3, 260,397.4 kg/m^3, 129,824.64 kg/m^3, 129,750.3 kg/m^3, 191,389.7 kg/m^3, 225,981 kg/m^3, 132,539.7 kg/m^3, 79,687.6 kg/m^3, 11,216.6 kg/m^3, 219,264 kg/m^3, and 797,253 kg/m^3 respectively (*Fig. 4*). Thus in total 1,266.435 tonnes of AGB estimated in the study area. And 5-10 DBH classes possess the highest AGB amongst all other DBH classes. The 55.72% of the total AGB was accounted by *Acacia catechu*, while other significant contributors for the AGB include *Mallotus philippinensis* (11.23%), *Ficus religiosa* (4.19%), *Eugenia jambolana* (3.93%), *Kydia calycina* (2.12%), *Albizia lebbeck* (2.10%), *Sapindus mukorossi* (1.97%), *Grewia optiva* (1.68%), *Pyrus pashia* (1.50%), and *Diospyros melanoxylon Roxb* (1.42%). Also in the starting of forest (compartment 2), *Acacia catechu* witness highest 71% of tree cover than other species.

It was observed that *Acacia catechu* and *Ficus benghalensis* were distinctive species, with 75th percentile of AGB values falling up to 2000 kg/m^3 (*Fig. 5*). This sets them apart from other species. The AGB values of most other species are notably lower, generally below 100 kg/m^3, with some exceptions in the case of *Kydia calycina*, *Aegle marmelos*, *Albizia chinensis*, *Eugenia jambolana*, *Ficus religiosa*, *Holoptellea integrifolia*, and *Mangifera indica* exhibiting AGB values exceeding 100 kg/m^3 at the 75th percentile. Despite the substantial population size of 3,872 individuals, the AGB of *Mallotus philippinensis* stands at 40.74 kg/m^3 in the 75th percentile.

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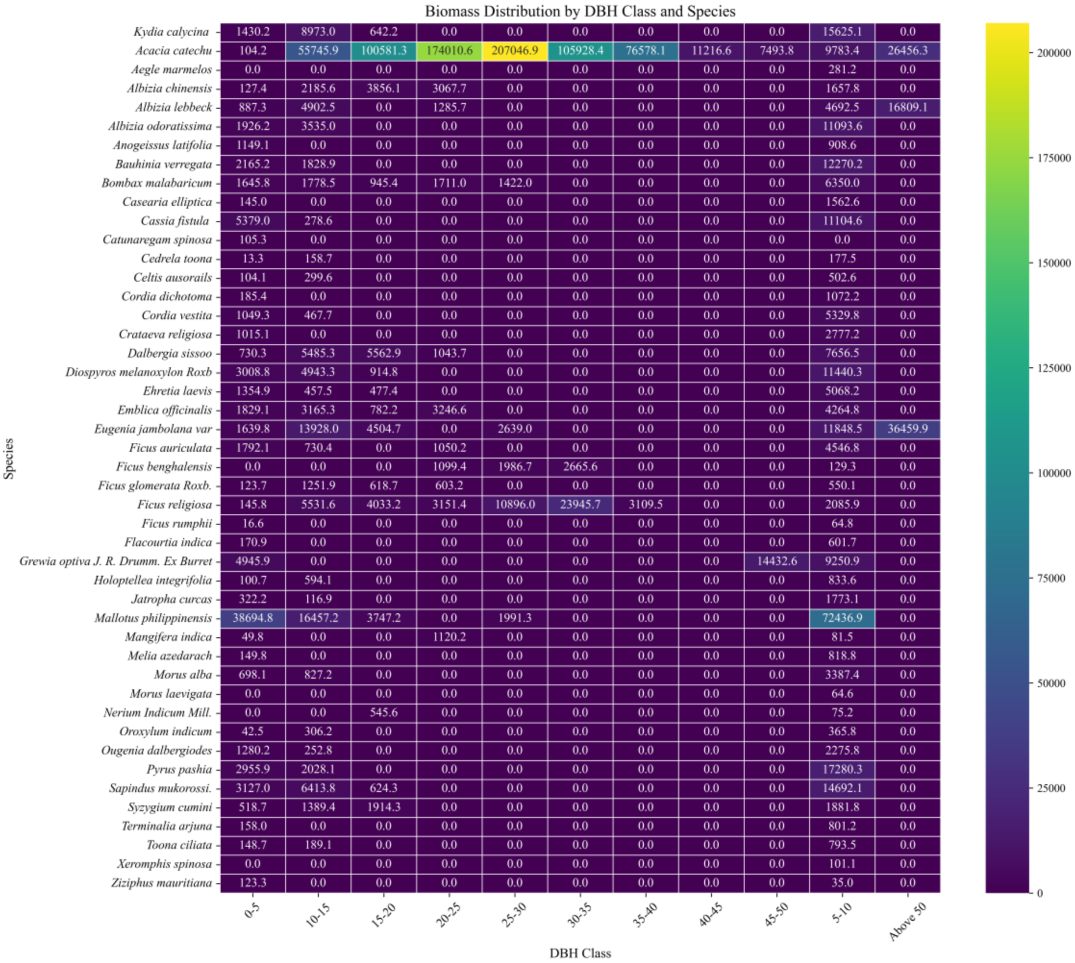

Figure 4. *AGB distribution in each DBH class of species in the study area*

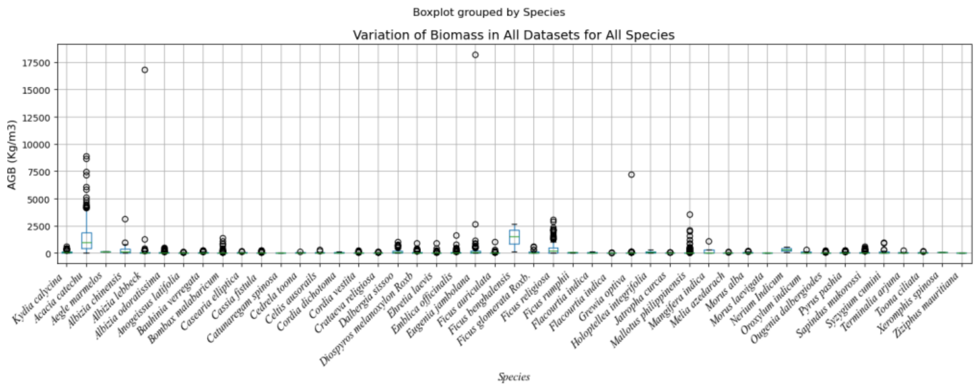

Figure 5. *Variation of AGB among species*

The average Shannon-Wiener index value of 2.40 for all compartments indicated a moderate level of species diversity having good and well-distribution in study area. The unique species richness amongst all compartments was 46 which varied between 27, 36, 33, 30, 28, 33, 27, 29, 30 and 21 from compartments 1-10. The species evenness ranged from 0.70-0.81 in all the compartments and indicated most of the species in the

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community are relatively evenly distributed. Linear regression between species richness and AGB shows a positive correlation $R^2 = 0.59$ (*Fig. 6*). It was found that the beginning of the forest (Compartment 2) possesses the highest aboveground biomass (AGB) at 2,810.80 kg/m³ (or 281.08 tons) as well as the highest species richness (36), indicated that higher AGB is associated with greater species richness. Although there was not any significant relationship found between species evenness and AGB.

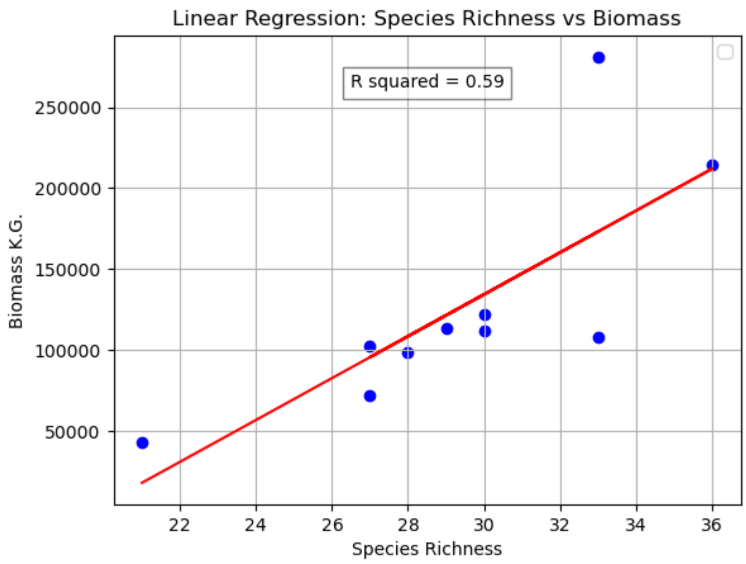

Figure 6. *Linear regression between species richness and above-ground biomass*

VR of tree species

VR predicts an overall association between all possible species pairs under the null hypothesis of independence, the expected value of VR is 1. When VR > 1, the species exhibits a positive association and when VR < 1, a negative association is observed (Ludwig and Reynolds, 1988; Gu et al., 2017). Here, the VR was observed 2.443 with a critical value of 1.51, indicated a significant positive association of species in the sub-tropical Himalayan forest, resulted in a stable state of forest structure and species composition. This VR test showed overall association of species in a forest, but it does not reveal pairwise intra/interspecies spatial associations. Therefore, Spearman's rank correlation coefficient (SRCC) was further used to determine the species spatial association between all possible species pairs.

SRCC of tree species

All possible pairs of species association generation based on the unique species present in the combined dataset. In each compartment the ranks of species calculated based on their AGB values and SRCC calculated for each pair of species across all compartments. The species pairs were classified based on the threshold of the correlation values obtained from the correlation matrix (*Fig. 7*). Mainly three categories were identified, such as highly significant positive covariance, ($r \geq 0.511$, $p \leq 0.01$) significant negative covariance ($r < -0.398$, $p < 0.05$) and no covariance ($-0.398 < r < 0.398$, $p > 0.05$).

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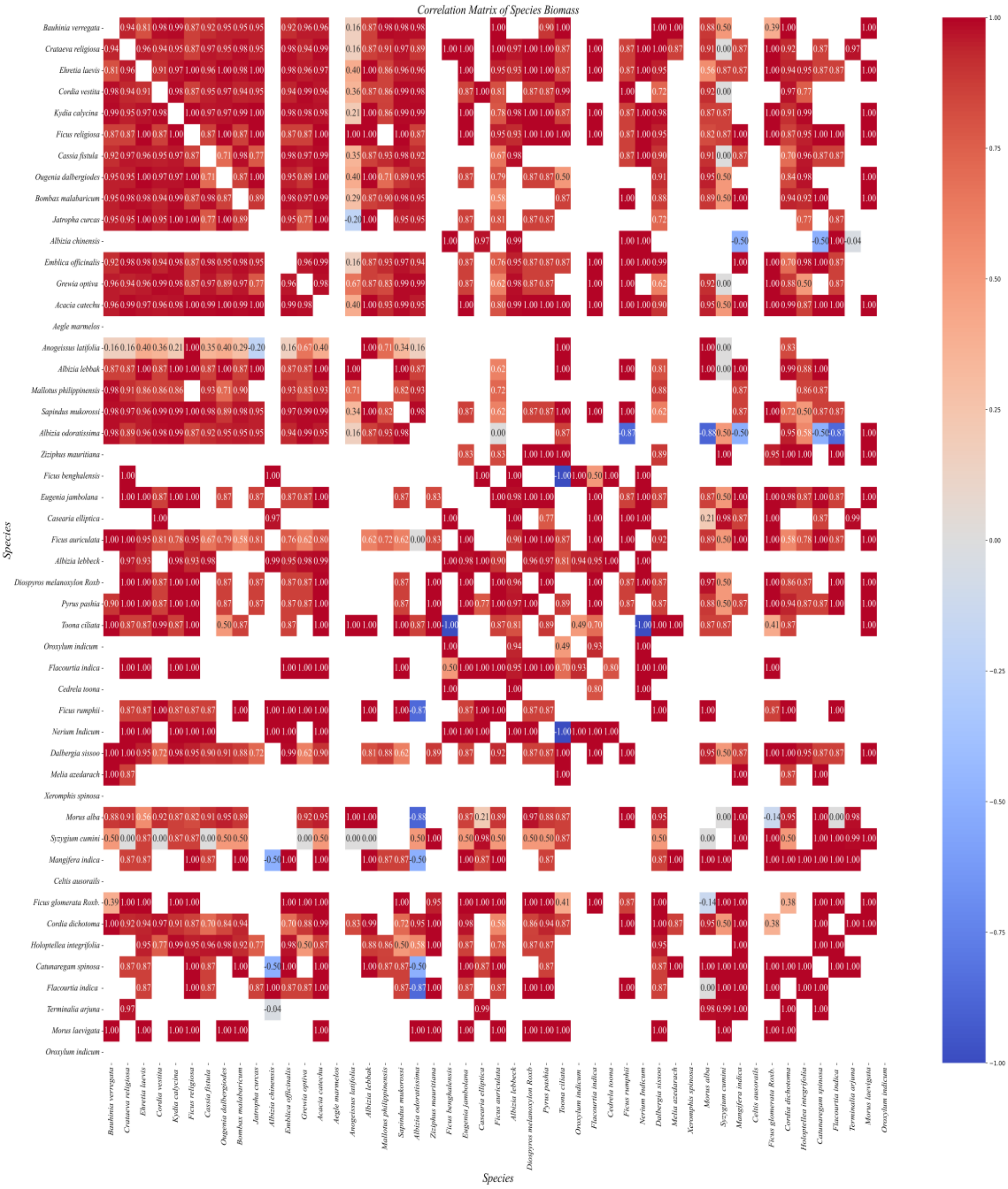

Figure 7. *SRCC matrix of different species pair*

It’s an iterative process, where for each pair of species (excluding cases where the species are the same), the correlation value against the defined threshold values was checked and the species pair was classified into one of the covariance categories based on correlation value. For each sorted dictionary of pairs, iterates over the sorted items were calculated based on percentage of pairs for each species relative to the total number of pairs. Finally, species pairs were categorized by covariance relationships and their corresponding percentages. In total 1006 species pairs were identified, where 98% of pairs had significant positive covariance and 2% had negative covariance. The *Acacia catechu* and *Ehretia leavis* exhibited the highest pairing with other tree species (33.13%) (*Fig. 8*) and the *Mallotus philippinensis* made 20.95% positive covariance with other species while *Bombax malabaricum* and *Kydia calycina* were associated in all compartments, along with *Acacia catechu*. Although *Albizia odoratissima, Toona ciliate, Ficus rumphi, Flacourita indica, Caserria elleptica, and Nerium indicum* possess strong negative covariance with other species.

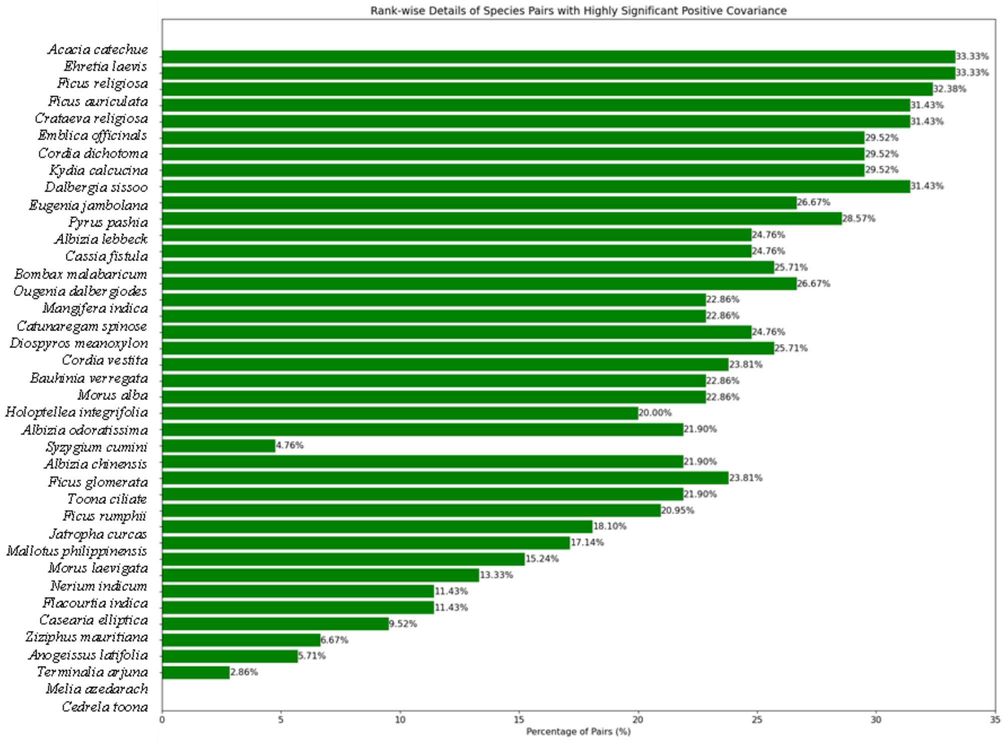

Figure 8. *Percentage wise pair of species for positive association*

The SRCC analysis revealed that the top pair of *Acacia catechu* exhibited significant positive covariance with other species. Specifically, *Acacia catechu* showed a positive covariance with the following species: *Bombax malabaricum*, *Kydia calycina*, *Grewia optiva* , *Ficus religiosa*, *Cordia vestita*, *Emblica officinalis*, *Albizia lebbeck*, *Albizia odoratissima*, *Jatropha curcas*, *Anogeissus latifolia*, *Ehretia laevis*, *Mallotus philippinensis*, *Bauhinia variegate*, *Ougenia dalbergiodes*, *Sapindus mukorossi*, *Cassia fistula*, *Flacourtia indica*, *Eugenia jambolana*, *Toona ciliata*, *Ficus rumphii*, *Pyrus pashia*, *Diospyros melanoxylon Roxb*, *Nerium Indicum Mill.*, *Ficus auriculata*, *Dalbergia sissoo*, *Syzygium cumini*, *Mangifera indica*, *Ficus glomerata Roxb.*, *Morus alba*, *Cordia dichotoma*, *Holoptellea integrifolia*, *Catunaregam spinosa*, *Morus laevigata*, *Flacourtia indica*, *Crataeva religiosa.* This indicated that, as the abundance or presence of *Acacia catechu* increases, the resource utilization and facilitation of these species for growth in AGB accumulation may increases and suggesting a possible ecological or environmental relationship among these species within the studied habitat. Also, the rank-wise detail of every pair is shown in *Fig. 8* which demonstrate *Cordia vistea* species formed less positive covariance with other species.

The SRCC analysis also identified significant negative covariance among certain species. Notably, *Albizia odoratissima* exhibited a negative covariance of 4.76% with the following species: *Flacourtia indica*, *Ficus rumphii*, *Mangifera indica*, *Morus alba*, and *Catunaregam spinosa*. In contrast, *Albizia chinensis* exhibited a negative covariance of

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1.90% with both *Mangifera indica* and *Catunaregam spinosa*. Additionally, *Mangifera indica* showed a negative covariance of 1.90% with *Albizia chinensis* and *Albizia odoratissima*. Similarly, *Catunaregam spinosa* showed a negative covariance of 1.90% with *Albizia chinensis* and *Albizia odoratissima*. *Toona ciliata* displayed a negative covariance of 1.90% with *Ficus benghalensis* and *Nerium indicum*. Furthermore, *Flacourtia indica* showed a negative covariance of 0.95% with *Albizia odoratissima*. *Ficus rumphii* exhibited a negative covariance of 0.95% with *Albizia odoratissima*, and *Morus alba* also showed a negative covariance of 0.95% with *Albizia odoratissima*. *Ficus benghalensis* demonstrated a negative covariance of 0.95% with *Toona ciliata*, while *Nerium indicum* exhibited a negative covariance of 0.95% with *Toona ciliata*.

This negative covariance (*Fig. 9*) indicated that as the presence or abundance of these species increases the abundance or presence of other species tends to decrease. Further indicated potential competitive interactions or differing ecological preferences among these species within the studied habitat.

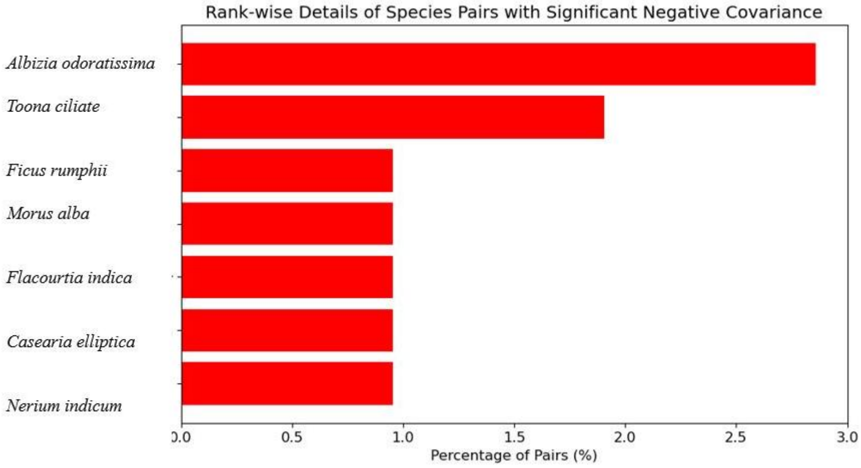

Figure 9. *Negative covariance of species*

Discussion

The positive association of species pairs with *Acacia catechu* has led to high AGB accumulation. The *Acacia catechu* though present in all DBH classes. But 5-10 cm DBH class accumulated the highest AGB, which comprises almost all species. This doesn't imply that all species restricted to grow after reaching the 5-10 cm DBH range. Instead, they continue to grow and attains different DBH ranges, and thus represent AGB in other classes. But adults were observed to contribute more to AGB in warmer lower-latitude regions (Lutz et al., 2018). Similarly, the small DBH 1-10 cm trees contributed to the highest AGB than larger trees because their abundance in the wet or moist tropical forests is maximum (Wright and Connell, 2006) due to the seasonal environment's greater (multilayer) lifespan of leaves for broadleaves understory trees (Coley, 1988), which reduces the cost of deploying leaves and ensures their survival in the low-light environments.

In past studies a positive relationship was confirmed between the AGB and species diversity in sub-tropical forests. Existing studies have evidence that an increase in the abundance of dominant species on a large scale is influenced by the species richness of tall trees, which is dependent on the macroclimate, which enhances light use efficiency

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in tall tree strata (Oberle et al., 2009). In diverse tree communities, strong and positive biodiversity-productivity relationships are often driven by increased species diversity and complementary light utilization strategies between shade-tolerant and intolerant species (Ray et al., 2023). Therefore, this may be the reason behind the abundance of *Acacia catechu* and *Mallotus philippinensis,* as species richness was higher for tall trees (*Ficus* and all other trees), and their high DBH range was present in every compartment, probably the high DBH trees having large height observed. The high biomass in the 5-10 cm DBH class is due to tall tree species, as tall tree species richness significantly boosts the short tree biomass. It also noticed that short trees have a greater relationship between species richness and above-ground biomass. This probably the region behind high biomass in 5-10 DBH class (Li et al., 2018). Especially mountainous subtropical broadleaf short tree species followed the complementarity effect with tall tree species (Li et al., 2015), which promotes site resource utilisation and prevents strong interspecific competition (Zhang et al., 2017). The coexistence of small tree species enhances resource use efficiency such as nutrient uptake, water use efficiency, control of herbivore disease, niche partitioning facilitation, etc., which increases woody biomass production (De Aguiar et al., 2013).

Our results align with the hypothesis that tree species diversity positively influences biomass indirectly by enhancing structural complexity within forest stands. As greater the species richness within a plot so does greater the structural complexity and wood productivity of the stand (Zhang et al., 2024).

Maximum individuals of *Mallotus philippinensis* in the study site may be due to vegetative propagation through ramet production and sprouting. Ramets can spread rapidly through vegetative propagation which allows them to colonize new habitats and increase their population (Pandy et al., 2001). In mixed natural growth forests, the least disturbed communities had the maximum proportion of *Mallotus philippinensis* seedlings but gradually decreased the number of individuals noticed at a different seedling to tree ages (Pathak and Shukla, 2004). That's probably the cause *Mallotus philippinensis* didn’t attain well after attaining the 5-10 DBH range; only a few individuals of 25-30 DBH were found in the study area that acquired AGB of 2 Ton. On the other hand, *Acacia catechu* is the least sprouting tree species (Pandey and Shukla, 2001) but high carbon density (10 tons per year) noticed in tropical forests. In one of the study site of Chaturvedi et al. (2011), *Acacia catechu* found the highest carbon accumulation of 817 kg (Cm^2 yr^{-1}) with an annual DBH increment of 0.46 cm yr^{-1} $tree^{-1}$. However, *Acacia catechu* is a primary successional species, i.e., a pioneer species that grows in moist areas (Dwivedi et al., 2006). Pioneers species follow some characteristics like high growth rates, early reproduction, sparse branching, and wide ecological ranges (Bazzaz, 1991), as these are defined by light availability at seed and seedling stages (Swaine and Whitmore, 1988). Other late successional native species might have been facilitated by pioneer species (Padilla and Pugnaire, 2006), and *Acacia catechu* has an open canopy; therefore, it might facilitate shade-tolerant species that grow under canopy, and that may be the reason that so many species associated with *Acacia catechu*. The major association of *Acacia catechu* was found with *Dalbergia sissoo* (Dwivedi et al., 2006) which is also prominent in our case.

The *Albizia odoratissima* was the top species among negative associations, which is a fast-growing large woody tree reaching heights up to 10–25 m. It annually grows up to 87 cm in height but is not a gregarious tree (Orwa et al., 2010), neither poses competition to other tree species nor facilitates them. The results from SRCC analysis indicated static

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relationships among all species in the community having a predominant significant positive association, suggesting that the community maintains a relatively stable state (Su et al., 2015; Gu et al., 2017). Species pairs exhibiting significant positive associations often share similar ecological characteristics and thrive under the same site conditions, indicating a high likelihood of close association and effective coexistence (Zhao et al., 2012; Hao et al., 2007).

Hao et al. (2007) found a positive association between saplings and adult trees in the *Quercuswu taishanica*. Du Zhi et al. (2013) also identified a positive association of *Pinus koraiensis* in the lower forest layer and the dominant layer. Several researchers have linked these associations to the limited seed dispersal capabilities and shade tolerance of the saplings (Hao et al., 2007). This positive interspecific association between saplings and adult trees may be attributed to niche differentiation for resource utilization among species pairs (Sushma and Singh, 2006; Yuan et al., 2018). Hao et al. (2007) suggested that this phenomenon is due to the relatively broad niche of many sapling species, enabling them to thrive under the canopy of various other tree species. This suggests the transformation of monoculture into uneven-aged mixed species to generate above-ground biomass for carbon sequestration. Diversity-biomass relationships (DBRs) in natural ecosystems exhibit considerable variability, making them challenging to predict (Wang et al., 2019). It is also important to note that previous research on DBRs has found that positive DBRs are not universal due to various theoretical and experimental insights (Hagan et al., 2021; Van Der Plas et al., 2023). Instead, environmental factors, along with their interaction with diversity, have been identified as key factors in predicting ecosystem functioning across scales (Daleo et al., 2023). Furthermore, as environmental heterogeneity increases over larger spatial scales, a higher number of species may be necessary to achieve similar levels of ecosystem functionality as observed at smaller scales (Thompson et al., 2021). Therefore, positively associated species can be used for enrichment with plantations (Wang and Meng, 2018). Thus, it is crucial to plant positively associated, high-values, and late-successional tree species to foster regeneration.

Conclusion

The rank-wise species pair detail may be used by policymakers for high biomass generation in the sub-tropical Himalayan region for high carbon sequestration. Also, these positive associations of species bring a new dimension for biomass generation to tackle climate change. All these species have some medicinal values; therefore, these will be beneficial from an economic perspective. Positive association allows individuals to grow in mutualism or facilitation among species. Therefore, these positive association species pairs provide novel findings among their associations for sharing resources in their habitat and facilitate each other and are recommended in the regeneration process in the subtropical Himalayan area.

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Author Contributions. Vivek Dhiman: Review of literature, Field survey, Data processing and Analysis, manuscript preparation. Amit Kumar: Performed Conceptualization, manuscript editing, and overall work execution.

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Data availability. The authors declare that all the raw, processed and analysed data related to the present study is with us and may be made available from the corresponding author upon reasonable requests, which is subject to further official formalities and approval from the competent authority.

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