

**Evolutionary Ecology of Woody Plants and Above Ground Carbon Accumulation in
Tropical Forest Communities**

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ABSTRACT

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Biodiversity-rich tropical forests act as critical carbon sinks, regulating the global carbon cycle. However, deforestation and degradation threaten these ecosystems, causing biodiversity loss and shifting them into carbon sources. Understanding how woody plant communities assemble and how their functional and phylogenetic diversity influence aboveground carbon (AGC) accumulation is crucial for gaining insights into their evolutionary ecology and role in global carbon dynamics. The niche complementarity hypothesis, which suggests species occupying distinct ecological niches more efficiently use resources and enhance AGC. In addition, the mass ratio hypothesis posits that a few dominant species with traits promoting high growth and survival drive AGC accumulation. To evaluate these perspectives, I analysed functional trait and phylogenetic diversity using presence, abundance and size weighted metrics in relation to spatial and temporal patterns of AGC storage and accumulation in the tropical forests of the Western Ghats biodiversity hotspot in India. First, I examined climatic drivers of woody plant community assembly across four vertical strata, including lianas. Stronger phylogenetic clustering in understory and lianas under high climatic water deficit (CWD) suggested environmental filtering under water-limited conditions. Conversely, greater phylogenetic divergence with elevation in emergent and canopy layers indicated niche differentiation in montane habitats. Second, I assessed the independent and additive effects of functional and phylogenetic diversity on AGC stocks while accounting for environmental stress. AGC declined with increasing stress but increased with elevation. Abundance and size weighted phylogenetic divergence increased AGC and supported the mass ratio hypothesis. Combined functional and phylogenetic diversity metrics and environmental variables significantly improved AGC prediction. Third, I analysed temporal AGC accumulation across forest types. Evergreen forests had the highest accumulation rates, while El Nino-induced CWD significantly reduced AGC accumulation. A few dominant species disproportionately contributed to carbon dynamics. Dense-wooded species enhanced carbon storage in drier forests, and large-seeded species boosted accumulation in evergreen forests. Abundance-weighted phylogenetic basal divergence and size-weighted terminal divergence enhanced AGC accumulation, further supporting the mass ratio hypothesis. By highlighting the mechanisms shaping spatial and temporal patterns of AGC storage and accumulation, this study provides insights to maximize conservation and restoration efforts in tropical forests of Western Ghats.

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Table of Contents

List of Tables	viii
List of Figures	xii
INTRODUCTION.....	1
Chapter 1 - Phylogenetic Structure and Assembly of Woody Plant Communities Across Tropical Forest Strata.....	7
1.1 Introduction	7
1.2 Methods.....	11
1.2.1 Data description	11
1.2.2 Environmental variables	12
1.2.3 Phylogeny reconstruction	12
1.2.4 Phylogenetic diversity metrics.....	12
1.2.5 Statistical analysis.....	13
1.3 Results	14
1.3.1 Phylogenetic Structure Across Biogeographic subregions of the Western Ghats	14
1.3.2 Environmental Drivers of Phylogenetic Structure.....	16
1.4 Discussion	17
1.4.1 Phylogenetic Structure Across Biogeographic subregions of the Western Ghats	17
1.4.2 Environmental Drivers of Phylogenetic Structure.....	21
1.5 Conclusion	23
1.6 Figures and Tables.....	25
Chapter 2 - Structurally Dominant Tree Species and Their Evolutionary Diversity Drive Aboveground Carbon Storage in Tropical Forests.....	49
2.1 Introduction	49
2.2 Methods.....	52
2.2.1 Data description	52
2.2.2 Estimation of above ground biomass and carbon	52
2.2.3 Environmental variables	52
2.2.4 Functional traits diversity	52
2.2.5 Phylogeny reconstruction	53
2.2.6 Phylogenetic signal.....	53
2.2.7 Phylogenetic diversity metrics.....	53
2.2.8 Statistical analysis.....	54
2.3 Results	54

2.3.1 Phylogenetic Signal	54
2.3.2 Independent effects of functional and phylogenetic diversity on AGC.....	55
2.3.3 Additive Effects of Diversity Metrics on AGC.....	55
2.4 Discussion	56
2.5 Conclusion.....	59
2.5 Figures and Tables.....	61
Chapter 3 - Above Ground Carbon Accumulation Rates across Forest Types in the Western Ghats Biodiversity Hotspot.	86
3.1 Introduction	86
3.2 Methods.....	90
3.2.1 Data description.....	90
3.2.2 Estimation of Above Ground Biomass Carbon and accumulation	91
3.2.3 Environmental variables	91
3.2.4 Functional traits diversity	92
3.2.5 Phylogeny reconstruction	92
3.2.6 Phylogenetic diversity metrics.....	92
3.2.7 Statistical analysis.....	93
3.3 Results	94
3.3.1 Disproportionate AGC storage and temporal patterns in accumulation rates between forest types.....	94
3.3.2 Effects of abiotic variables on AGC accumulation rates	95
3.3.3 Effects of Community Weighted Means (CWM) on AGC accumulation rates	95
3.3.4 Effects of functional diversity on AGC accumulation rates	96
3.3.5 Effects Phylogenetic diversity on AGC accumulation rates.....	96
3.3.6 Shifting contributions of environment, functional and phylogenetic diversity across unweighted, abundance and size-weighted models	96
3.4 Discussion	98
3.5 Conclusion.....	107
3.6 Figures and Tables.....	109
CONCLUSION	141
REFERENCES.....	143

List of Tables

Table 1: Species richness distribution between deciduous and evergreen phenology among tropical forest plots within Western ghats. _____	28
Table 2: Variation inflation factor (VIF) among environmental variables measured across forest sites in the Western Ghats. _____	33
Table 3: Model selection results from generalized least squares (GLS) analyses testing spherical, exponential, Gaussian, and rational spatial correlation structures to account for spatial autocorrelation in phylogenetic community structure across forest strata of the Western Ghats. Values represent Akaike Information Criterion (AIC) scores, with lower values indicating better model fit. _____	35
Table 4: Species richness and Shannon's alpha diversity among tropical forest plots within Western ghats. _____	37
Table 5: Mean pairwise phylogenetic distance (MPD) and mean nearest taxon distance (MNTD) across forest strata and biogeographic subregions of the Western Ghats. Both unweighted (presence-absence) and abundance-weighted values are presented for each stratum (liana, understory, subcanopy, canopy, and emergent) and for all woody plants combined. MPD reflects average evolutionary distances among all co-occurring taxa (basal divergence), whereas MNTD emphasizes the mean phylogenetic distance to each species closest relative (terminal divergence). Higher values denote greater phylogenetic divergence among co-occurring species, while lower values indicate stronger evolutionary relatedness. _____	39
Table 6: Results of standardized effect sizes of mean pairwise distance (SESMPD), representing basal phylogenetic structure, across biogeographic subregions of the Western Ghats. Values are shown for both unweighted (presence-absence) and abundance-weighted versions, separately for each forest stratum (liana, understory, subcanopy, canopy, and emergent) and for all woody plants combined. Negative SESMPD values indicate phylogenetic clustering (co-occurrence of more closely related species than expected by chance), whereas positive values indicate phylogenetic overdispersion. Associated p-values denote the significance of deviation from null expectations. _____	40
Table 7: Results of standardized effect sizes of mean nearest taxon distance (SESMNTD), representing terminal phylogenetic structure, across biogeographic subregions of the Western Ghats. Values are presented for both unweighted (presence-absence) and abundance-weighted versions, separately for each forest stratum (liana, understory, subcanopy, canopy, and emergent) and for all woody plants combined. Negative SESMNTD values indicate phylogenetic clustering (closely related species co-occurring more than expected by chance), whereas positive values reflect phylogenetic overdispersion. Associated p-values indicate the significance of departure from null expectations. _____	41
Table 8: Results of generalized least squares (GLS) models examining the influence of environmental gradients on phylogenetic community structure, expressed as standardized effect sizes of mean pairwise distance (SESMPD), with unweighted (presence-absence) version across all woody plants and individual forest strata. Reported values include regression estimates, standard errors (SE), t-values, and p-	

values for each predictor including Elevation, Rainfall, and Climatic Water Deficit (CWD). Significant positive coefficients indicate increased phylogenetic divergence (reduced clustering) with increasing predictor values, whereas significant negative coefficients reflect stronger phylogenetic clustering.	43
Table 9: Results of generalized least squares (GLS) models examining the influence of environmental gradients on phylogenetic community structure, expressed as standardized effect sizes of mean pairwise distance (SESMPD), with abundance weights across all woody plants and individual forest strata.	44
Table 10: Results of generalized least squares (GLS) models examining the influence of environmental gradients on phylogenetic community structure, expressed as standardized effect sizes of mean nearest taxon distance (SESMNTD), with unweighted (presence-absence) version across all woody plants and individual forest strata.	45
Table 11: Results of generalized least squares (GLS) models examining the influence of environmental gradients on phylogenetic community structure, expressed as standardized effect sizes of mean nearest taxon (SESMNTD), with abundance weight version across all woody plants and individual forest strata.	46
Table 12: Summary of functional trait data availability at the species level for 592 woody plant species across 111 one-hectare plots in the Western Ghats.	63
Table 13: Variation inflation factor (VIF)	75
Table 14: Model selection results comparing four spatial correlation structures (exponential, Gaussian, spherical, and rational quadratic) for the generalized least squares (GLS) model of above-ground carbon (AGC) as a function of Chave's Environmental Stress index and elevation. Model fit was evaluated using Akaike's Information Criterion (AIC).	77
Table 15: Results of independent t-tests comparing above-ground carbon (AGC), species richness, functional richness, and standardized effect size of Faith's phylogenetic diversity between deciduous and evergreen forest types in the Western Ghats.	79
Table 16: Blomberg's K statistics testing for phylogenetic signal (phylogenetic conservatism) in functional traits and above-ground carbon (AGC) of woody plant species in the Western Ghats. Values of K close to 0 indicate weak phylogenetic signal, whereas values closer to 1 indicate strong conservatism of traits along the phylogeny.	79
Table 17: Independent effects of environmental variables on above-ground carbon (AGC) as estimated from generalized least squares (GLS) models.	79
Table 18: Independent effects of community-weighted means (CWMs) of functional traits (WD - Wood density, SDM - Seed diaspore mass, LN - Leaf Nitrogen, LMA - Leaf mass per area, LA - Leaf area) on above-ground carbon (AGC) under three modeling frameworks: unweighted, abundance-weighted, and size-weighted generalized least squares (GLS) models.	80
Table 19: Independent effects of functional traits diversity on above-ground carbon (AGC) under three modeling frameworks: unweighted, abundance-weighted, and size-weighted generalized least squares (GLS) models.	80
Table 20: Independent effects of phylogenetic diversity (standardised effect size (SES) mean pairwise distance (SES MPD) and mean nearest taxon distance (MNTD) on above-	

ground carbon (AGC) under unweighted, abundance-weighted, and size-weighted generalized least squares (GLS) models. _____	81
Table 21: Model comparisons examining the independent and combined effects of Chave's environmental stress (CES), elevation, community-weighted means of functional traits (CWM), functional diversity, and phylogenetic diversity on above-ground carbon (AGC). Models were evaluated under unweighted, abundance-weighted, and size-weighted frameworks using Akaike's Information Criterion (AIC), Δ AIC, and explained variance (R^2). _____	83
Table 22: Generalized least squares (GLS) model results testing the independent effects of environmental gradients (Chave's Environmental Stress index and elevation), community-weighted means (CWM) of functional traits, and multiple dimensions of functional diversity on above-ground carbon (AGC) under unweighted, abundance-weighted, and size-weighted frameworks. _____	84
Table 23: Generalized least squares (GLS) model results testing the combined effects of environmental gradients (Chave's Environmental Stress index [CES] and elevation), community-weighted means (CWMs) of functional traits (WD -Wood density, SDM -Seed diaspore mass, LN -Leaf Nitrogen, LMA -Leaf mass per area, LA - Leaf area), functional (functional richness, evenness, divergence, and dispersion), and phylogenetic diversity (SES MPD and SES MNTD) on above-ground carbon (AGC) under unweighted, abundance-weighted, and size-weighted frameworks. _____	85
Table 24: Characteristics of long-term Forest Dynamics Plots (FDPs) established across the Western Ghats biodiversity hotspot. The table summarizes site names, elevation, plot dimensions, number of plots, total area, and years of repeated censuses for tropical evergreen, dry deciduous, and scrub forest sites. _____	114
Table 25: Proportion of functional trait data available at the species levels. Values indicate the number and percentage of species with trait data directly measured at the species level. _____	114
Table 26: Variation inflation factor (VIF) _____	126
Table 27: Variations in above-ground carbon (AGC; $\text{Mg ha}^{-1} \text{ yr}^{-1}$) and AGC gains across census intervals at 17 one-hectare sites spanning four forest types in the Western Ghats. Values represent mean AGC and mean annual AGC gains ($\pm$ SD) for Southern Western Ghats mid-elevation evergreen (SWG-M-EV), Central Western Ghats low-elevation evergreen (CWG-L-EV), Dry Deciduous Forest (DDF), and Scrub Forest (SCRUB). _____	128
Table 28: Above-Ground Carbon (AGC) storage (Mg ha^{-1}) and accumulation rates (Mg ha^{-1}) of dominant tree species across forest types in the Western Ghats. _____	129
Table 29: Occurrence and intensity of El Niño and La Niña events between 1990 and 2021, classified as weak, moderate, strong, or very strong based on the Oceanic Niño Index (ONI). The table summarizes the frequency and duration of each category, highlighting interannual variability in the strength of ENSO phases across three decades. _____	130
Table 30: Results of linear mixed-effects models testing the effects of elevation and maximum climatic water deficit (MCWD) on above-ground carbon (AGC) accumulation. Forest type and census interval were included as random effects to account for spatial and temporal variability. _____	132

<i>Table 31: Results of linear mixed-effects models testing the relationships between community-weighted mean (CWM) functional traits-calculated using presence-based, abundance-weighted, and size-weighted approaches-and above-ground carbon (AGC) accumulation. Forest type and census interval were included as random effects to account for spatial and temporal variability.</i>	133
<i>Table 32: Results of linear mixed-effects models testing the relationships between functional trait diversity - calculated using presence-based, abundance-weighted, and size-weighted frameworks - and above-ground carbon (AGC) accumulation. Forest type and census interval were included as random effects to account for spatial and temporal variability.</i>	134
<i>Table 33: Results of linear mixed-effects models testing the relationships between phylogenetic diversity - calculated using presence-based, abundance-weighted, and size-weighted frameworks - and above-ground carbon (AGC) accumulation. Forest type and census interval were included as random effects to account for spatial and temporal variability. Phylogenetic diversity was assessed using SES MPD (standardized effect size of mean pairwise distance) and SES MNTD (standardized effect size of mean nearest taxon distance).</i>	135

List of Figures

- Figure 1: Conceptual representation of the community assembly processes of woody plants, shaped by stochastic processes including dispersal and deterministic processes including competition, environmental filtering. _____ 25
- Figure 2: Conceptual illustration of stress gradient hypothesis (SGH). _____ 26
- Figure 3: Spatial distribution of 1280 (25 x 25 m - 0.06 ha) forest plots (indicated with black dot) across the Western Ghats biodiversity hotspot overlaid on a climate water deficit (CWD) gradient (mm/yr) , ranging from higher moisture availability (blue) to greater water deficit (red). _____ 27
- Figure 4: Spatial distribution of 1280 (25 x 25 m - 0.06 ha) forest plots across the Western Ghats biodiversity hotspot categorized into Northern, Central, and Southern biogeographic subregions, separated by the Palghat Gap. Circles represent proportion of deciduous species in a plot distinguishing dry forest (red) to wet (black) forests Overlaid on a climate water deficit (CWD) gradient (mm/yr) gradient ranging from higher moisture availability (blue) to greater water deficit (red). _____ 28
- Figure 5: Phylogenetic tree of 925 woody plants species highlighted by Liana, Understory, Subcanopy, Canopy and Emergent strata species including deciduous (orange circles) and evergreen species (green circles). _____ 30
- Figure 6: Histograms of standardised effect sizes of mean pairwise distance (SESMPD) across forest strata in the western ghats. Blue bars represent unweighted SESMPD, while red bars represent abundance weighted SESMPD. Vertical red dashed lines indicate SESMPD =0. Negative SESMPD values reflect phylogenetic clustering, whereas positive values indicate phylogenetic overdispersion. _____ 31
- Figure 7: Histograms of standardised effect sizes of mean nearest taxon distance (SESMNTD) across forest strata in the western ghats. Blue bars represent unweighted SESMNTD, while red bars represent abundance weighted SESMNTD. Vertical red dashed lines indicate SESMNTD =0. Negative SESMNTD values reflect phylogenetic clustering, whereas positive values indicate phylogenetic overdispersion. _____ 32
- Figure 8: Correlation among environmental variables measured across forest sites in the Western Ghats. Variables include elevation (elev), mean annual temperature (temp), annual rainfall (rain), climatic water deficit (cwd), latitude (lat), and longitude (lon). _____ 33
- Figure 9: Moran's scatter plot illustrating spatial autocorrelation in SESMPD (unweighted) across study plots in the western ghats. The plot shows positive autocorrelation pattern, with a Moran's I statistic of 0.33, indicating that sites with similar SESMPD values are spatially clustered rather than randomly distributed. _____ 34
- Figure 10: Species richness and Shannon's alpha diversity among tropical forest plots within Western ghats. Colors represent biogeographic subregions: Central WG (red), Nilgiris (green), Northern WG (blue), and Southern WG (purple). _____ 36
- Figure 11: Standardized effect sizes of mean pairwise phylogenetic distance (SESMPD) and mean nearest taxon distance (SESMNTD) across forest communities including Liana, T1 - Understory, T2 -Subcanopy, T3 -Canopy and T4 -Emergent strata in the Western Ghats, showing divergence from null model expectations. Filled circles indicate statistically

- significant values ($p < 0.05$). Colors represent biogeographic subregions: Central WG (red), Nilgiris (green), Northern WG (blue), and Southern WG (purple). _____ 38
- Figure 12: Results of stratum-specific and scale-dependent environmental drivers of phylogenetic clustering and divergence with slope estimates ($\pm$ SE) of generalized least squares (GLS) models particularly testing the influence of climatic water deficit (CWD), rainfall, and elevation on phylogenetic community structure across vertical forest strata of the Western Ghats. Phylogenetic structure is quantified as standardized effect sizes of mean pairwise distance (SESMPD; basal divergence) and mean nearest taxon distance (SESMNTD; terminal divergence) with unweighted (red) and abundance-weighted (blue) versions. Filled symbols indicate significant relationships ($p < 0.05$), while open symbols denote non-significant results. _____ 42
- Figure 13: Relationship between deciduousness and the standardized effect size of mean pairwise distance (SESMPD) for a different forest stratum, including all strata combined (All), Liana, Understory, Subcanopy, Canopy, and Emergent. The blue and red lines represent results from models without weights presence and weighted by abundance respectively. _____ 47
- Figure 14: Relationship between deciduousness and the standardized effect size of mean nearest taxon distance (SESMNTD) for a different forest stratum, including all strata combined (All), Liana, Understory, Subcanopy, Canopy, and Emergent. The blue and red lines represent results from models without weights presence and weighted by abundance respectively. _____ 48
- Figure 15: Conceptual framework linking functional and phylogenetic divergence, environmental stress, and above ground carbon dynamics. Forest sites experiencing lower environmental stress and greater co-occurrence of evolutionarily distant woody plant species are hypothesised to exhibit higher above ground carbon (AGC) stocks. In contrast, plots under higher environmental stress with greater co-occurrence of closely related species are predicted to show reduced AGC stocks. _____ 61
- Figure 16: Map showing the locations of 111 one-hectare forest plots across the western ghats, India (gray boundary). Deciduous plots are indicated in blue and evergreen plots in black. _____ 62
- Figure 17: Boxplots showing variations in community-weighted means (CWMs) of functional traits under three weighting schemes: unweighted (presence-absence), abundance-weighted, and size-weighted. Traits include maximum height (Max H), maximum diameter (Max DBH), wood density (WD), leaf area (LA), leaf nitrate mass (LNM), leaf mass per area (LMA), and seed diaspore mass (DM). _____ 64
- Figure 18: Density plots illustrating the distribution of community-weighted means (CWMs) of functional traits under unweighted (presence-absence), abundance-weighted, and size-weighted frameworks. Traits include maximum height (Max H), maximum diameter (Max DBH), wood density (WD), leaf area (LA), leaf nitrate mass (LNM), leaf mass per area (LMA), and seed diaspore mass (DM). _____ 65
- Figure 19: Boxplots showing variation in functional diversity metrics under unweighted (presence-absence), abundance-weighted, and size-weighted frameworks. Metrics

include functional richness, functional evenness, functional divergence, and functional dispersion.	66
Figure 20: Density plots showing the distribution of functional diversity metrics under unweighted (presence–absence), abundance-weighted, and size-weighted frameworks. Metrics include functional richness, functional evenness, functional divergence, and functional dispersion.	67
Figure 21: Phylogenetic tree of 592 woody plant species recorded across 111 one-hectare plots in the Western Ghats. Functional trait values are mapped onto the phylogenetic tree with gradients ranging from high (in red) to low (in blue). Traits include maximum attainable height (max H), maximum attainable diameter at breast height (max DBH), Wood density (WD), Seed diaspore mass (DM), Leaf Nitrogen (LN), Leaf mass per area (LMA), Leaf area (LA).	69
Figure 22: Boxplots showing variation in phylogenetic diversity metrics under unweighted (presence–absence), abundance-weighted, and size-weighted frameworks. Metrics include the standardized effect size of mean pairwise distance (SES MPD), reflecting basal evolutionary divergence, and the standardized effect size of mean nearest taxon distance (SES MNTD), reflecting terminal divergence.	70
Figure 23: Density plots showing the distribution of phylogenetic diversity metrics under unweighted (presence–absence), abundance-weighted, and size-weighted frameworks. Metrics include the standardized effect size of mean pairwise distance (SES MPD), representing basal divergence, and the standardized effect size of mean nearest taxon distance (SES MNTD), representing terminal divergence.	71
Figure 24: Correlation matrix showing relationships between abiotic variables (e.g., Chave’s Environmental Stress index, elevation) and UNWEIGHTED biotic variables, including community-weighted means of functional traits, functional diversity metrics, and phylogenetic diversity (SES MPD and SES MNTD).	72
Figure 25: Correlation matrix showing relationships between abiotic variables (e.g., Chave’s Environmental Stress index, elevation) and ABUNDANCE weighted biotic variables, including community-weighted means of functional traits, functional diversity metrics, and phylogenetic diversity (SES MPD and SES MNTD).	73
Figure 26: Correlation matrix showing relationships between abiotic variables (e.g., Chave’s Environmental Stress index, elevation) and SIZE weighted biotic variables, including community-weighted means of functional traits, functional diversity metrics, and phylogenetic diversity (SES MPD and SES MNTD).	74
Figure 27: Moran’s scatter plot illustrating spatial autocorrelation in above-ground carbon (AGC) across study plots in the Western Ghats. The plot shows a positive spatial autocorrelation pattern, with a Moran’s I statistic of 0.258, indicating that sites with similar AGC values are spatially clustered rather than randomly distributed.	76
Figure 28: Empirical variogram showing spatial autocorrelation in above-ground carbon (AGC) across study plots in the Western Ghats. The variogram indicates positive spatial autocorrelation at shorter distances, with semivariance increasing as distance between plots increases, demonstrating that nearby sites are more similar in AGC than distant ones.	77

- Figure 29: Comparison of above-ground carbon storage (AGC; Mg ha^{-1}), species richness (species ha^{-1}), functional richness (FRic; ha^{-1}), and standardized effect size of phylogenetic diversity (SES Faith's PD; ha^{-1}) between deciduous and evergreen forest plots in the Western Ghats _____ 78
- Figure 30: Independent effects of environmental gradients (Chave's Environmental Stress index and elevation), community-weighted means of functional traits (CWMs), functional diversity metrics (functional richness, evenness, divergence, and dispersion), and phylogenetic diversity (SES MPD and SES MNTD) on above-ground carbon (AGC) under unweighted, abundance-weighted, and size-weighted generalized least squares (GLS) models. _____ 82
- Figure 31: Conceptual framework linking phylogenetic community structure, environmental stress, and above ground carbon dynamics. Forest sites experiencing lower environmental stress and greater co-occurrence of evolutionarily distant woody plant species are hypothesised to exhibit higher above ground carbon (AGC) accumulation rates. In contrast, plots under higher environmental stress with greater co-occurrence of closely related species are predicted to have lower AGC accumulation rates. _____ 109
- Figure 32: Location and elevation (m) of 1-ha long-term vegetation monitoring plots in the Western Ghats. The central panel shows peninsular India with the Western Ghats biodiversity hotspot boundary and locations of forest dynamics sites. The upper left inset depicts low-elevation tropical evergreen plots in the central Western Ghats with rectangular linear dimensions of $20 \times 350 \text{ m}$. The lower left inset shows mid-elevation wet evergreen plots in the southern Western Ghats with rectangular dimensions of $40 \times 250 \text{ m}$. The right inset illustrates the distribution of square $100 \times 100 \text{ m}$ tropical dry forest plots in the Western Ghats, where blue plots represent dry deciduous forests (DDF) and black plots represent scrub jungles. _____ 110
- Figure 33: Distribution of square $100 \times 100 \text{ m}$ tropical dry forest plots in the Western Ghats, where blue plots represent dry deciduous forests (DDF) and black plots represent scrub jungles. _____ 111
- Figure 34: The upper inset depicts low-elevation tropical evergreen plots in the central Western Ghats with rectangular linear dimensions of $20 \times 350 \text{ m}$. The lower inset shows mid-elevation wet evergreen plots in the southern Western Ghats with rectangular dimensions of $40 \times 250 \text{ m}$. _____ 112
- Figure 35: Distribution of square $100 \times 100 \text{ m}$ tropical dry forest plots in the Western Ghats, where blue plots represent dry deciduous forests (DDF) and black plots represent scrub jungles. _____ 113
- Figure 36: Variations in community-weighted means (CWM) of functional traits calculated using presence-based, abundance-weighted, and size-weighted approaches across forest types. Symbols denote forest types: plus, sign (+) for SWG-M-EV, open circles for CWG-L-EV, triangles for DDF, and squares for SCRUB. _____ 115
- Figure 37: Density plots showing variation in community-weighted means (CWM) of functional traits under presence-based, abundance-weighted, and size-weighted frameworks. Colors distinguish the distributions for each weighting scheme, highlighting differences in trait values. _____ 116

- Figure 38: Variations in functional trait diversity metrics calculated using presence-based, abundance-weighted, and size-weighted approaches across forest types. Symbols denote forest types: plus, sign (+) for SWG-M-EV, open circles for CWG-L-EV, triangles for DDF, and squares for SCRUB. _____ 117
- Figure 39: Density plots showing variation in functional traits diversity metrics under presence-based, abundance-weighted, and size-weighted frameworks. Colors distinguish the distributions for each weighting scheme, highlighting differences in functional diversity. The density for functional evenness appears highly skewed, with a sharp peak at one end. This suggests a lack of variability in this metric across the weighting schemes. _ 118
- Figure 40: Phylogenetic tree of the 212 species recorded in the study, representing 144 genera and 50 families. _____ 119
- Figure 41: Phylogenetic tree of 212 woody plant species recorded across forest dynamics plots in the western ghats. Functional trait values are mapped onto the phylogenetic tree with gradients ranging from high (in red) to low (in blue). _____ 120
- Figure 42 : Phylogenetic tree of 212 woody plant species recorded across forest dynamics plots in the western ghats. Functional trait values are mapped onto the phylogenetic tree with gradients ranging from high (in red) to low (in blue). _____ 121
- Figure 43: Variations in phylogenetic divergence metrics calculated using presence-based, abundance-weighted, and size-weighted approaches across forest types. Symbols denote forest types: plus, sign (+) for SWG-M-EV, open circles for CWG-L-EV, triangles for DDF, and squares for SCRUB. _____ 122
- Figure 44: Density plots showing variation in phylogenetic diversity metrics under presence-based, abundance-weighted, and size-weighted frameworks. Colors distinguish the distributions for each weighting scheme, highlighting differences in phylogenetic diversity. _____ 123
- Figure 45: Histograms and Q–Q plots showing the distribution of above-ground carbon (AGC) gain data before (top) and after square root transformation (bottom). The transformation improved normality, as indicated by closer alignment of sample quantiles with the theoretical quantiles in the Q–Q plot. _____ 124
- Figure 46: Pearson correlation matrices showing relationships between response and predictor variables. Panels represent (top left) unweighted, (top right) abundance-weighted, and (bottom) size-weighted functional and phylogenetic metrics. Strong positive and negative correlations are indicated by color gradients, with significant associations highlighted. _____ 125
- Figure 47: Temporal variation in above-ground carbon (AGC; $\text{Mg ha}^{-1} \text{yr}^{-1}$) accumulation across 17 one-hectare long-term monitoring sites representing four forest types in the Western Ghats. The x-axis denotes the midpoint year of each census interval. Forest types include Southern Western Ghats mid-elevation evergreen (SWG-M-EV), Central Western Ghats low-elevation evergreen (CWG-L-EV), Dry Deciduous Forest (DDF), and Scrub Forest (SCRUB). _____ 127
- Figure 48: Results of linear mixed-effects models testing the influence of community-weighted means, functional diversity, and phylogenetic diversity metrics on above-ground carbon (AGC) accumulation. Models were analyzed under presence-based (brown), abundance-

weighted (blue), and size or size-weighted (black) frameworks. Site and census interval were included as random effects to account for spatial and temporal autocorrelation. Filled circles indicate significant effects, and horizontal lines represent 95 % confidence intervals. To assess whether a slope differs significantly from zero, the 95% confidence interval (CI) for the slope parameter was calculated as the estimate $\pm (1.96 \times \text{standard error})$. If the CI includes zero, the slope is not significantly different from zero at the 0.05 level; if it excludes zero, the effect is considered statistically significant. _____ 131

Figure 49: Venn diagram showing the variance partitioning of above-ground carbon (AGC) accumulation among four predictor groups: Environmental Variables, Community-Weighted Means (CWM), Functional Diversity, and Phylogenetic Diversity. Values in overlapping regions represent shared contributions of predictors, whereas non-overlapping sections indicate the unique variance explained by each predictor. _____ 136

Figure 50: Venn diagram showing the variance partitioning of above-ground carbon (AGC) accumulation among four predictor groups: Environmental Variables, abundance weighted Community-Weighted Means (CWM), Functional Diversity, and Phylogenetic Diversity. _____ 137

Figure 51: Venn diagram showing the variance partitioning of above-ground carbon (AGC) accumulation among four predictor groups: Environmental Variables, size weighted Community-Weighted Means (CWM), Functional Diversity, and Phylogenetic Diversity. _____ 138

Figure 52: Annual variation in above-ground carbon (AGC; Mg ha^{-1}) across diameter at breast height (DBH) classes, shown by forest type. The figure highlights temporal dynamics (C1–C5 census intervals) and structural contributions of different size classes to overall carbon storage. _____ 139

Figure 53: Annual variation in above-ground carbon (AGC; Mg ha^{-1}) accumulation across diameter at breast height (DBH) classes over census intervals C1–C5, grouped by forest type. The figure highlights both temporal dynamics and structural contributions to carbon accumulation. _____ 140

INTRODUCTION

Tropical forests harbor more than 70% of global biodiversity (Slik et al. 2015; 2018), and play a crucial role in regulating the global carbon cycle. These ecosystems sequester more than 40% of atmospheric carbon through high rates of plant productivity thus acting as one of the largest carbon sinks (Joseph Wright 2013; Phillips and Lewis 2014; Pan et al. 2011; Hubau et al. 2020), and regulate the global climate (Anderson-Teixeira et al. 2021). However, these tropical forests are subject to anthropogenic impacts of deforestation and forest degradation leading to rapid loss of significant number of species (McNicol et al. 2018; Menon and Bawa 1998) and becoming a source of carbon emission (Baccini et al. 2017) contributing to climate change (Hubau et al. 2020). The spatial and seasonal variability in temperature and precipitation associated with the latitude and topography influences the spatial and temporal distribution patterns of taxonomic diversity and growing conditions of woody plants (Jucker et al. 2018; Shen et al. 2016; Shivaprakash et al. 2018; Bose et al. 2019) and affect carbon stocks and accumulation rates. Although there are a few studies on the biodiversity and ecosystem function relationships in the tropical forests (Souza et al. 2019; Mensah et al. 2024) exist, the detailed studies on the evolution of woody plant communities and its influence on spatial and temporal dynamics of above ground carbon storage in tropical forests at local, regional and global scales are limited (Nawalage et al. 2025).

The spatiotemporal diversity patterns of organisms in tropical forests are determined by stochastic and deterministic community assembly processes, including dispersal, drift, speciation, selection, and environmental filtering (Vellend 2016) (Figure 1). Quantifying ecological adaptations that result from species-to-species differences across functional traits is necessary to understand community assembly mechanisms (Cadotte et al. 2011). There are large number of morphological and physiological traits responsible for the establishment and survival of a species and quantifying each trait for all species is time consuming and costly (Nawalage et al. 2025). Ecological adaptations are shaped by abiotic and biological interactions experienced by a species ancestor, as all organisms are products of their evolutionary history. Because of similar resource use, competition among closely related species is stronger than competition between distantly related species, which in turn influences species coexistence (Darwin 1859; Elton 1946; Williams 1964; Simberloff 1970; Enquist et al. 2002). Furthermore, phylogenetically closely related species have similar trait values due to a shared evolutionary history, occupying common preferred ecological and environmental niches (MacArthur and Levins 1967). This pattern of closely related taxa sharing characteristics related to their environmental niche is called phylogenetic niche conservatism (Wiens and Graham 2005). Therefore, assuming phylogenetic conservatism, the phylogenetic relatedness of species in a community can be used as a proxy for functional trait relationships. Additionally, phylogenetic niche conservatism assumes that functional traits of species are conserved between ancestors and descendants and therefore may be linked through phylogeny (Webb 2000). In phylogenetic clustering, species in a community are more evolutionarily closely related to each other than would be expected by chance (Nawalage et al. 2025; Divya and Karanth 2018). In this scenario, they are expected to consist of closely related

species with analogous niches, only able to establish through environmental filtering. This would occur when the environment selects species from a larger species pool or filters them into the observed community based on suitable characteristics to establish and survive in the given environment (Webb et al. 2002). In contrast, species in a diverged community are more evolutionarily distantly related than would be expected by chance. They are therefore likely to thrive occupying different ecological and environmental niches, primarily due to limited similarity (Webb et al. 2002). Therefore, the phylogenetic relationships of species in communities can provide insight not only into the processes that structure community assembly but also into the relative contribution of stochastic and deterministic mechanisms that play a role in creating the composition of a community with observed species (Nawalage et al. 2025; Divya and Karanth 2018). In addition to within-community (alpha) phylogenetic diversity metrics, intercommunity (beta) phylogenetic diversity metrics that show species evolutionary compositional turnover across spatial, environmental, temporal, disturbance, and successional gradients can also reflect the deterministic and stochastic community assembly processes (Nawalage et al. 2025; Divya and Karanth 2018). Large-scale topographical and latitudinal heterogeneity-induced environmental gradients at local and regional scales are considered to be major drivers in shaping species diversity and distribution (Condit et al. 2002; Pascal 1988). According to the stress gradient hypothesis (SGH), environmental conditions constrain the range of ecological adaptations in more stressed locations and thus have a filtering effect on the extent of potential adaptations (Kraft et al. 2015) (Figure 2). For example, high temperature and rainfall seasonality may represent ecophysiological limits. Due to strong environmental filtering and phylogenetic niche conservatism favoring a subset of lineages adapted to harsh environments, communities in abiotically harsher environments have been hypothesized to consist of more closely related species that form phylogenetically clustered communities (Nawalage et al. 2025; Divya and Karanth 2018). Conversely, conditions of aseasonality and resource diversity should lead to greater niche diversification and limitation of similarity due to competition. Therefore, it has been hypothesized that greater lineage diversity should be found in conjunction with a wider range of adaptations, leading to phylogenetically overdispersed communities in an adiabatic, stable, and stress-free environment (Nawalage et al. 2025; Divya and Karanth 2018). Several studies have found that increasing phylogenetic clustering results in increasing the cooccurrence of closely related woody plant species in tropical forests from south to north and west to east, thereby increasing rainfall seasonality and decreasing rainfall gradient within the Western Ghats biodiversity hotspot (Shivaprakash et al. 2018; Bose et al. 2019; Divya et al. 2020). Meanwhile, several studies in the Himalayas highlight that increasing elevation leads to phylogenetic clustering in plant communities, highlighting environmental filtering as a major force in the assembly process (Manish and Pandit 2018; Shooner et al. 2018). The existence of habitats in extremely stable climates, which may also act as a reflection of past ideal environmental conditions for the inhabiting species, is mainly influenced by complex topography, including high elevations with high rainfall and lesser dry periods (Gunatilleke et al. 2017). Such habitats act as a refugium and remain isolated, sheltering species during periods of unfavourable climate conditions across evolutionary or geological time scales (Willis and Whittaker 2000). As the climate becomes more favourable and stable, maladapted species retreat to, persist, and may

extend from refugia habitats (Keppel et al. 2012; Grant et al. 2023). Several criteria may reflect refugia; they not only have species richness and environmental stability that exceed the surrounding ecosystems but also the presence of remnant taxa and diverse anatomy in the ecosystem. Additionally, relict taxa may be phylogenetically distinct due to their unique evolutionary history, such as the mixture of both old and new lineages, and therefore disproportionately contribute to the phylogenetic diversity and structure within the community (Shooner et al. 2018; Grant et al. 2023). Therefore, it is hypothesized that less climatically stable regions may harbour assemblages of survivors or species able to recolonize after local extinctions, resulting in phylogenetic clustering. Conversely, it is hypothesized that more climatically stable regions are comprised of distantly related lineages that could persist better through evolutionary time and diversify over a broad ecological spectrum, resulting in phylogenetic overdispersion.

Although, there are many studies highlight environmental filtering as the main community assembly mechanism of woody plants (Shooner et al. 2018; Shivaprakash et al. 2018; Manish and Pandit 2018; Bose et al. 2019; Divya et al. 2020; Grant et al. 2023). However, this ignores the fact that the species composition varies considerably in the various vertical layers of the forest, including liana, understory, canopy and emerging trees due to the filtering of the environment by variable light profiles. Each vertical strata have different species pools (Draper et al. 2021) due to regional differences in forest structure and turnover rates (Pascal 1990; 1986). Based on this link, I can hypothesize that canopy and emergent species which are known to accumulate and store large proportions of carbon are phylogenetically clustered because the maximum potential tree size has a significant phylogenetic signal (Shivaprakash et al. 2018), meaning those species capable of occupying canopy and emergent strata are concentrated in particular lineages (families or orders), mainly within a few deep clades (for example *Dipterocarpaceae*) (Pascal 1990; 1988; Pascal et al., n.d.). Such above canopy species have to endure high solar radiation, high temperatures, higher rainfall and low humidity, these conditions offer limited niche space and are likely to filter for a particular set of functional traits that may have evolved only in species belonging to some particular lineages (Draper et al. 2021). Seed dispersal of tall trees for instance based on winged seeds in Dipterocarps tend to disperse better than understory woody plants, and at least some common lineages are well dispersed across evolutionary time scales (Bansal et al. 2022). The strongest competitors for the canopy layers may have been able to spread uniformly for millennia, becoming dominant, as a result of their increased capacity for dispersal (Thomson et al. 2018; Bansal et al. 2022). Conversely, however, I can hypothesize that species in understory layers are more phylogenetically dispersed because of dispersal limitation (Draper et al. 2021; Thomson et al. 2018; Givnish 1999). And, understory species are locally abundant, have rapid regeneration (Ganesan and Davidar 2003) and negative density dependent mortality (Comita et al. 2014). Also, they must compete with saplings and juveniles of canopy species. Moreover, the understory shade environment is spatially more heterogeneous due to variation in forest structure and the frequency and size of forest gaps, magnitude of forest fire potentially leading to increased niche partitioning and adaptation in understory trees. Furthermore, forest structure including leaf phenology varies in the wet to dry tropical forest. For instance, the leaf phenology of both canopy and understory woody

plants at high elevations and lower climatic stress are evergreen. On the other hand, in the lower elevations and higher climatic stress leaf phenology of both canopy and understory trees are deciduous. In addition, in semievergreen forests the canopy species will have deciduous leaf phenology and understory trees will have evergreen leaf phenology (Pascal 1990; 1986; 1988). Therefore, I can say that understory species may be exposed to different abiotic and biotic filters over large spatial scales and develop greater local specialisation associated with different types of functional characteristics.

Understanding the evolution and organization of woody plant species into communities, or community assembly mediated through functional traits is important for gaining insights into carbon sequestration in forest communities. The taxonomic diversity metrics alone have limited ability to explain the spatial and temporal distribution patterns of carbon sequestering in tropical forests because they often do not account for evolutionary ecology and functional trait diversity that directly impacts carbon accumulation and storage through variations in traits such as wood density and leaf area that determine and occupy unique ecological niche of given species in the tropical forest ecosystem (Cadotte and Davies 2016). For example, within tropical forests, species of individuals with larger leaf area and lower wood density tend to grow faster and live only for a short time, thus accumulating less above ground carbon (AGC), whereas individuals of species with smaller leaf area and higher wood density tend to grow slower and live longer, thereby accumulating higher levels of AGC (Cadotte et al. 2011). Niche complementarity hypothesis suggests that different species occupying distinct ecological niches can more efficiently utilize resources, thereby leading to higher productivity and improved carbon sequestration (Cadotte et al. 2008). In addition the selection or mass ratio hypothesis postulates that variation of ecosystem functions including above ground carbon storage is mainly determined by few dominant species with particularly distinctive traits that influence high growth and survival rates leading to efficient carbon storage (Cadotte et al. 2008).

Incorporating abundance and structural dominance-weighted functional and phylogenetic relatedness metrics aligns with the selection or mass-ratio hypothesis to infer the role of dominant species in ecosystem processes like carbon storage (Tucker et al. 2017). The selection or mass-ratio hypothesis suggests that biodiverse communities likely include species with beneficial traits, while abundance-weighted measures focus on how predominant species with traits enhancing carbon sequestration drive ecosystem functions. Many studies have incorporated abundance in community weighted means, functional (Hao et al. 2018) and phylogenetic diversity metrics (Cadotte et al. 2012; Castaño et al. 2024; Souza et al. 2019). Structurally dominant metrics, emphasizing tree size and biomass, complement this by showing how the traits of larger trees influence carbon storage, reflecting the mass-ratio hypothesis. This combined approach offers a comprehensive view of biodiversity's role in ecosystem functioning, particularly in mature forests where large trees are vital (Lutz et al. 2018). Many studies have used structural dominance (e.g., basal area or biomass) in functional traits community weighted mean (CWM) and functional diversity, evenness and dispersion metrics (Finegan et al. 2015; Sande et al. 2017; Yuan et al. 2018; Hao et al. 2020; Prado-Junior et al. 2016). However, the abundant species may not necessarily need to be structurally

dominant in terms larger diameter and height. For instance, *Terminalia anogeissina* in dry forest and *Agrostistachys boornensis* in evergreen forest are highly abundant but structurally smaller trees but accumulate and stock large quantity of AGC due to their sheer abundance (Pascal 1988). However, species like *Dipterocarpus indica*, *Cullenia exarillata* and *Vateria indica* are large statured trees accumulating and stocking large proportions of AGC with in few individuals (Pascal 1988). Therefore, I chose to use both unweighted, abundance and structurally dominance weighted functional and phylogenetic metrics in the analyses. Similarly, as community weighted mean (CWM) of functional traits with abundance or structurally dominant species weights depicts plants reproductive, growth and survival performance (Finegan et al. 2015; Sande et al. 2017), phylogenetic diversity metrics are restricted to abundance in a few studies (Mensah et al. 2024; Castaño et al. 2024; Satdichanh et al. 2019). To my knowledge, there are no studies that incorporated structural dominance (e.g., biomass, carbon or basal area) in phylogenetic diversity metrics. Integrating such metrics aligns with the mass-ratio hypotheses, which suggest that dominant species with beneficial traits drive key ecosystem processes such as carbon storage and accumulation (Tucker et al. 2017).

The environmental variables such as altitude, temperature, and precipitation seasonality can distort the relationships between biodiversity and carbon. At higher altitudes, lower temperatures may limit plant growth and carbon storage, even in areas with high biodiversity, while lower altitudes with more favourable growing conditions may store more carbon despite lower biodiversity. Likewise, temperature fluctuations can affect species growth rates, and rainfall seasonality can influence water availability for the survival, which in turn impacts carbon storage potential. These environmental factors create variations in how biodiversity related to carbon storage, emphasizing the importance of incorporating such variables into models of carbon storage and biodiversity to develop more effective climate change mitigation strategies (Chisholm and Dutta Gupta 2023).

Carbon-biodiversity co-benefits can occur in areas where priority locations for carbon storage overlap with locations of high biodiversity and human dominated landscapes including biodiversity hotspots (Osuri et al. 2020). Therefore, analysing the relationship between AGC stocks and diversity metrics at taxonomic, functional and phylogenetic levels is not only important to understand spatial distribution patterns of AGC but also crucial for predicting consequences of natural and anthropogenic induced changes in climate on AGC accumulation in biodiversity hotspots (Chisholm and Dutta Gupta 2023). Although there are many studies explaining the biotic and abiotic mechanisms determining distribution and abundance of deciduous and evergreen trees (Shivaprakash et al. 2018), there is still a lack of empirical evidence on how AGC diversity relationships differ across forest types, and the contributions of niche complementarity and the selection or mass-ratio hypotheses to biodiversity effects on carbon are not yet fully understood.

I hypothesize that lower environmental stress and increased co-occurrence of evolutionarily distantly related woody plant species enhance above-ground carbon stocks and carbon accumulation rates in forest communities. Conversely, higher environmental stress and increased

co-occurrence of evolutionarily closely related woody plant species reduce these carbon-related outcomes.

I predict that forest plots characterized by low environmental stress and higher phylogenetic distance among co-occurring species will have measurably higher AGC stocks and accumulation rates compared to plots with high environmental stress and lower phylogenetic distances.

Therefore, In the first chapter, I will focus on, delineating the relationship between phylogenetic diversity and structure of vertical forest strata (Liana, understory, subcanopy, canopy and emergent tree classes) including variations across biogeographic subregions, elevation, rainfall and climatic Water Deficit (CWD) gradients.

In the second chapter, I will focus on investigating spatial patterns of AGC stocks. I will analyse the relationships between AGC and functional and phylogenetic diversity across several study sites.

In the third chapter, I will focus on investigating the temporal patterns of AGC accumulation rates. I will analyse the relationships between AGC and functional and phylogenetic diversity of study sites over several census periods.

Chapter 1 - Phylogenetic Structure and Assembly of Woody Plant Communities Across Tropical Forest Strata

1.1 Introduction

The spatiotemporal diversity patterns of organisms in forests are determined by stochastic and deterministic community assembly processes, including dispersal, drift, speciation, selection, and environmental filtering (Vellend 2016) (Figure 1). Quantifying ecological adaptations that result from interspecific differences in functional traits is essential for understanding community assembly mechanisms (Cadotte et al. 2011). There are many morphological and physiological traits responsible for the establishment and survival of a species and quantifying all traits for every species is both time consuming and expensive. Ecological adaptations are shaped by abiotic and biotic interactions experienced by a species ancestor, as all organisms are products of their evolutionary history (Nawalage et al. 2025). Because of similar resource use, competition among closely related species is stronger than competition between distantly related species, which in turn influences species coexistence (Darwin 1859; Elton 1946; Williams 1964; Simberloff 1970; Enquist et al. 2002). Furthermore, phylogenetically closely related species have similar trait values due to a shared evolutionary history, often occupying similar ecological and environmental niches (MacArthur and Levins 1967). This pattern of closely related taxa sharing characteristics related to their environmental niche, is referred to as phylogenetic niche conservatism (Wiens and Graham 2005).

Therefore, assuming phylogenetic conservatism, phylogenetic relatedness among species within a community can serve as a proxy for dissimilarity in functional traits (Cadotte and Davies 2016; Webb, Ackerly, Mcpeck, et al. 2002). Additionally, phylogenetic niche conservatism implies that functional traits of species are evolutionarily conserved between ancestors and descendants, and are thus correlated with their phylogenetic relationships (Webb 2000). In cases of phylogenetic clustering, species within a community are more closely related than would be expected by chance. Such communities are expected to consist of species with analogous ecological niches that have been selected through environmental filtering (Nawalage et al. 2025; Divya and Karanth 2018). This process occurs when the environment selects or filters species from a larger regional pool, allowing only those with appropriate traits to establish and persists (Webb, Ackerly, Mcpeck, et al. 2002). In contrast, phylogenetic overdispersion refers to communities where species are more distantly related than expected by chance, suggesting that they occupy distinct ecological niches and may have diverged due to competitive exclusion or other limiting similarity mechanisms (Webb, Ackerly, Mcpeck, et al. 2002). Therefore, analysing the phylogenetic relationships of species in a community provides valuable insight not only into the processes driving community assembly but also into the relative contributions of stochastic and deterministic mechanisms that shape observed species composition (Nawalage et al. 2025; Divya and Karanth 2018).

Large-scale topographical and latitudinal heterogeneity which generate environmental gradients at local and regional scales are considered major drivers shaping species diversity and distribution

patterns (Condit et al. 2002; Pascal 1988). According to the stress gradient hypothesis (SGH), environmental stress limits the range of ecological adaptations in more extreme conditions, thereby exerting a filtering effect on the functional and phylogenetic composition of communities (Kraft et al. 2015) (Figure 2). For example, high temperature and pronounced rainfall seasonality may represent key ecophysiological constraints. Under such conditions strong environmental filtering in combination with phylogenetic niche conservatism is expected to favour a subset of lineages that are preadapted to harsh environments. As a result, communities in abiotically stressful environments are hypothesized to exhibit phylogenetic clustering, characterized by the cooccurrence of closely related species (Grant et al. 2023; Nawalage et al. 2025; Divya and Karanth 2018). In contrast, environments with stable climates, high seasonality, and greater resource diversity are expected to support broader ecological niches and promote competitive exclusion based on limiting similarity (Grant et al. 2023; Nawalage et al. 2025; Divya and Karanth 2018). These conditions favour niche differentiation and trait divergence, leading to the cooccurrence of distantly related species and resulting in phylogenetically overdispersed communities. Accordingly, it has been hypothesised that greater lineage diversity is associated with a wider range of ecological adaptations, particularly in adiabatic, stable and low stress environments (Grant et al. 2023).

Several studies support these expectations. In the Western Ghats biodiversity hotspot, increasing phylogenetic clustering has been observed along gradients of increasing rainfall seasonality and decreasing mean annual rainfall, particularly from south to north and west to east (Shivaprakash et al. 2018; Bose et al. 2019; Divya et al. 2020). Similarly, studies in the Himalayan region have reported that increasing elevation, associated with declining temperature and harsher abiotic conditions, leads to phylogenetic clustering in plant communities, highlighting environmental filtering as a dominant assembly mechanism (Manish and Pandit 2018; Shooner et al. 2018).

The existence of habitats situated in extremely stable climatic conditions, often found in topographically complex areas for example high elevation zones with high rainfall and short dry seasons, may reflect remnants of paleoenvironmental stability (Gunatilleke et al. 2017). These regions act as refugia, serving as climatic shelters that enable species persistence during unfavourable conditions across evolutionary or geological time scales (Willis and Whittaker 2000). As climates became more favourable, maladapted species may have retreated to, persisted in, or later expanded from such refugial habitats (Keppel et al. 2012). Refugia is characterised not only by high species richness and environmental stability relative to surrounding ecosystems but also by the presence of relict taxa indicative of longterm evolutionary processes. Furthermore, relict taxa are often phylogenetically distinct, owing to their unique evolutionary histories, which may include a mixture of both ancient and recent diverged lineages. These taxa can contribute disproportionately to community level phylogenetic diversity and structure (Shooner et al. 2018; Grant et al. 2023). Therefore, it is hypothesized that climatically unstable regions may support assemblages composed of survivor lineages or recolonizing species following local extinctions, leading to phylogenetic clustering. Conversely, climatically stable regions are more likely to

support distantly related lineages that have persisted over evolutionary timescales and diversified across a broad range of ecological niches, thereby promoting phylogenetic overdispersion.

While numerous studies have examined woody plant community assembly in forest ecosystems using phylogenetic diversity metrics to highlight the role of environmental filtering (Shooner et al. 2018; Shivaprakash et al. 2018; Manish and Pandit 2018; Bose et al. 2019; Divya et al. 2020; Grant et al. 2023), and although species composition varies significantly across different forest vertical strata or layers, comparatively little attention has been given to how species composition and phylogenetic structure vary across distinct vertical strata within forests. These strata comprising lianas or woody climbers, understory, subcanopy, canopy and emergent trees are structured by variable light regimes, which in turn shape species distributions via environmental filtering. Each vertical strata harbours a distinct species pool (Draper et al. 2021), driven by regional differences in forest structure and turnover rates (Pascal 1990; 1986).

Based on this framework, I hypothesize that canopy and emergent species which are known to accumulate and store substantial amounts of carbon, are phylogenetically clustered. This is because the maximum potential tree size exhibits a strong phylogenetic signal (Shivaprakash et al. 2018), indicating that species capable of reaching canopy or emergent layers are often concentrated within particular lineages, especially deep clades such as *Dipterocarpaceae* (Pascal 1990; 1988; Pascal et al., n.d.). These above canopy species are exposed to intense solar radiation, elevated temperatures, high rainfall and low humidity. Such environmental extremes likely constrain the available niche space and act as filters that select for a specific suite of functional traits, which have evolved in a limited number of lineages (Draper et al. 2021). Dispersal mechanisms also support this pattern. For instance, tall canopy trees such as Dipterocarps produce winged seeds, while others produce fruits that attract large birds and arboreal mammals, facilitating broader dispersal compared to understory woody plants. Some dominant lineages may have maintained their ecological dominance over evolutionary timescales due to their superior dispersal abilities. These dispersal traits, in conjunction with competitive superiority in occupying upper canopy space, may have enabled such lineages to spread widely and become dominant (Thomson et al. 2018; Bansal et al. 2022).

Conversely, I hypothesize that understory species are phylogenetically distantly related due to stronger dispersal limitations (Draper et al. 2021; Thomson et al. 2018; Givnish 1999). Understory species often exhibit high local abundance, rapid regeneration capabilities (Ganesan and Davidar 2003), and are subject to negative density dependent mortality (Comita et al. 2014). Additionally, they must compete with saplings and juveniles of canopy species, further intensifying biotic interactions. The understory environment is spatially heterogeneous, shaped by variable forest structure, the frequency and size of canopy gaps, and disturbance regimes such as forest fires. This heterogeneity likely promotes niche partitioning and ecological specialization in understory communities.

Leaf phenology, which reflects adaptation to climatic stress, also varies across forest strata. In wet, high elevation tropical forests with low climatic stress, both canopy and understory species tend to

be evergreen. In contrast, in drier, low elevation forests experiencing higher climatic stress, both strata predominantly exhibit deciduous leaf phenology. Interestingly, in semievergreen forests, a discrepancy is observed, canopy species tend to be deciduous, whereas understory species remain evergreen (Pascal 1990; 1986; 1988).

Taken together, these abiotic and biotic filters acting differently across space and strata may drive greater local specialisation in understory species, resulting in the evolution of a more diverse set of functional traits. Therefore, I predict that understory species from different regions will be phylogenetically distant from one another compared to canopy or emergent species, reflecting increased overdispersion due to regional and microhabitat level environmental heterogeneity.

Building on the stress gradient hypothesis and refugia theory, the phylogenetic structure of woody plant communities in different vertical strata is also expected to vary predictably along environmental stress gradients. In climatically stable refugial environments, often associated with high rainfall, complex topography, and low seasonality both canopy and understory strata may exhibit greater phylogenetic overdispersion, reflecting the long-term persistence and diversification of distantly related lineages. Such conditions favour niche differentiation, allowing the coexistence of ecologically disparate species within the same stratum. In contrast, in abiotically stressful environments characterized by low rainfall, high temperature variability or pronounced seasonality, phylogenetic clustering is expected to dominate, particularly in the upper canopy and emergent strata where exposure extreme microclimatic conditions intensify environmental filtering. Understory communities in these stressful contexts may still retain some degree of overdispersion due to microhabitat heterogeneity, but their composition may shift toward closely related stress tolerant lineages. Consequently, analysing how phylogenetic structure across forest strata changes along gradients of environmental stress and climatic stability can provide novel insights into the interplay between deterministic and stochastic assembly processes, the persistence of relict lineages and the resilience of tropical forest biodiversity in a changing climate.

In this chapter, I will focus on delineating the relationship between phylogenetic diversity and structure of vertical forest strata (Liana, understory, subcanopy, canopy and emergent tree classes) including variations across biogeographic subregions, elevation, rainfall and climatic Water Deficit (CWD) gradients.

I hypothesize that vertical forest strata specifically liana, understory, subcanopy, canopy, and emergent layers in tropical forests will exhibit distinct and systematic patterns of phylogenetic community structure influenced by biogeographic subregions and environmental gradients, such as elevation, rainfall, and climatic water deficit (CWD). I expect canopy and emergent strata to predominantly exhibit phylogenetic clustering, reflecting strong environmental filtering selecting for specific functional traits adapted to intense solar radiation, elevated temperatures, higher rainfall exposure, and limited humidity traits commonly conserved within evolutionary lineages. Conversely, I expect that the understory and liana strata will demonstrate phylogenetic overdispersion due to enhanced niche differentiation driven by spatially heterogeneous

environments, variable light availability, frequent disturbances, and intense interspecific competition, resulting in coexistence among evolutionarily distantly related species possessing diverse adaptive traits. Furthermore, I predict significant variation in these phylogenetic patterns across different biogeographic subregions. Regions characterized by stable climates with consistent moisture availability are hypothesized to exhibit greater overall phylogenetic overdispersion, particularly in the understory and liana strata, due to conditions favoring niche diversification and reduced environmental stress. Conversely, regions characterized by pronounced climatic stress, seasonal rainfall, or drought conditions are expected to show strong phylogenetic clustering across all vertical forest layers. Additionally, along elevational gradients, an increase in phylogenetic clustering is expected at higher elevations, particularly within canopy and emergent strata, reflecting intensified selective pressures favoring traits adapted to cooler temperatures and harsher climatic conditions. Similarly, regions with lower rainfall and higher climatic water deficit are expected to exhibit stronger phylogenetic clustering, whereas areas with higher rainfall and lower climatic water deficit should promote phylogenetic overdispersion, particularly in understory and liana strata. Finally, the interactions between vertical forest strata and these environmental gradients are expected to vary systematically, with canopy and emergent strata consistently showing stronger phylogenetic clustering under stressful conditions, while understory and liana strata demonstrate greater diversification under favorable environmental conditions.

1.2 Methods

1.2.1 Data description

The Western Ghats biodiversity hotspot, a mountain chain along the western coast of peninsular India, is characterised by substantial latitudinal and topographic induced climatic heterogeneity, including increasing climatic water deficit (CWD) and dry months from south to north, decreasing rainfall from west to east, and a decline in temperature with increasing elevation (Figure 3). The southern region exhibits greater topographic complexity than the northern region and receive both the Southwest and Northeast monsoons (Divya et al. 2020) (Figure 4). Dry and moist deciduous forests are mostly at rain shadow eastern slopes (Figure 4).

The Western Ghats, biodiversity hotspot, is divided into four major biogeographic subregions Northern, Central, Nilgiris, and Southern based on latitudinal position, elevation, climate, and vegetation patterns (Davidar et al. 2005) (Figure 4). These subregions span a latitudinal range from approximately 8° to 20°N and exhibit pronounced ecological gradients that influence community composition and evolutionary history (Page and Shanker 2018). The Northern Western Ghats (approximately 16° to 20°N) are situated in the relatively drier and lower-elevation part of the range, dominated by moist and dry deciduous forests and subject to greater seasonal variability including 6-8 dry months. The Central Western Ghats (approximately 13° to 16°N) represent a transitional zone with moderate rainfall including 4-6 dry months, complex terrain, and a mix of vegetation types. The Nilgiris zone (around 11° to 13°N) comprises a high-elevation plateau and functions as a key ecological and climatic transition area, marked by montane forests and grassland

mosaics. The Southern Western Ghats (below 11°N) are topographically rugged and climatically stable, receiving high rainfall from both Southwest and Northeast monsoons, and supporting extensive tropical evergreen forests and high levels of species endemism. These latitudinally defined biogeographic subregions encapsulate the environmental heterogeneity and historical biogeography of the Western Ghats, offering a robust framework for examining spatial variation in woody plant diversity, community assembly processes, and conservation priorities.

I have estimated community-level phylogenetic diversity metrics from 1280 (25 x 25 m - 0.06 ha) plant inventory plots in the Western Ghats biodiversity hotspot in southern India (Figure 3) documented by (Roy et al. 2015). Since initial goal of (Roy et al. 2015) was classification of forest types supplementing with remote sensing data, they have only documented plant composition and abundance but did not measure diameter at breast height (DBH) of all the individual woody plants within the plots. The 925 woody plant species belonging to 102 families documented in tropical forest sites are classified into vertical strata including Liana, Understory, Subcanopy, Canopy, Emergent woody plants based on their maximum attainable height information from (Pascal 1988; Gamble 1928; Nayar et al. 2015; Vattakaven et al. 2016) including (biotik.org ; indiabiobiodiversity.org ; powo.science.kew.org) (Table 1).

1.2.2 Environmental variables

I have used the “*sp*” and “*raster*” packages in R to obtain annual rainfall, mean annual temperature, climatic water deficit (CWD) and elevation for each plot from the *WorldClim* data set (<https://www.worldclim.org>).

1.2.3 Phylogeny reconstruction

Using the “*phylo.maker*” function of the R package “*VPhyloMaker2*”, (Jin and Qian 2019) I have been able to create a species-level phylogeny of all species found in 1280 plots. GBOTB extended.tre, a time-calibrated mega tree, is used in this package with phylogeny of seed plants as a foundation for phylogenetic reconstruction (Smith and Brown 2018). On the backbone tree, all families and genera from this study were present. By binding phylogenetically uncertain species to the crown node of their corresponding genus (the node that unites all members of the clade), the default scenario (Scenario 1) of the “*phylo.maker*” function for producing phylogenetic hypotheses introduces them as polytomies to the tree. Since this analysis depends on relative comparisons of phylogenetic structure among regional assemblages, unresolved phylogenetic relationships may not have as much of an impact on phylogenetic structure metrics as they would have otherwise (Molina-Venegas and Roquet 2014). Nevertheless, such polytomies may provide a bias towards type II errors in general (Figure 5).

1.2.4 Phylogenetic diversity metrics

Using the R package “*picante*”, I have computed several indices to measure the phylogenetic structure of assemblages (Kembel et al. 2010). Mean Pairwise Distance (MPD) is a measure of the average phylogenetic distance between all pairs of species in an assemblage, giving insight into how evolutionarily distant species are from each other within the community (Webb, Ackerly,

McPeck, et al. 2002). Mean Nearest Taxon Distance (MNTD), on the other hand, calculates the average phylogenetic distance between each species and its closest relative in the assemblage, highlighting the fine-scale evolutionary relationships among species (Webb, Ackerly, McPeck, et al. 2002). Both MPD and MNTD provide valuable information on the degree of phylogenetic relatedness within a community, with MPD capturing overall divergence and MNTD emphasizing the nearest evolutionary neighbours (Nawalage et al. 2025). I have included abundance weighted MPD and MNTD - adjusted by the proportional product of the abundance of species making that distance (Cadotte and Davies 2016).

I have used the standardised effect size (SES MPD) because there is a strong correlation between MPD and species richness (Tucker and Cadotte 2013). To determine the standardized effect size of MPD (SES MPD), I have used the function “*ses.mpd*”, and “*ses.mntd*” with the number of runs set to 999 randomizations and the “*null.model*” argument set to “*taxa.labels*”(Nawalage et al. 2025). This function creates a z-score by comparing MPD and MNTD with a null distribution that is produced by randomly rearranging the phylogenetic tips of taxa from the regional species pool, which is defined by all species found in plots (Kembel et al. 2010). Furthermore, I have employed the mean pairwise distance's standardized effect size (SES MPD) and the mean nearest taxon distance (SES MNTD) as measures of phylogenetic divergence at the plot level (Kembel et al. 2010; Webb, Ackerly, McPeck, et al. 2002). Deeper evolutionary divergences in the phylogeny are captured by SES MPD, which calculates the mean phylogenetic distance between all species in an assemblage while by calculating the average of the phylogenetic distances between each taxon and its closest neighbour in the phylogeny, SES MNTD calculates the degree of terminal evolutionary divergences (Webb, Ackerly, McPeck, et al. 2002). Thus, SES MNTD can offer distinct but complementary insights into the phylogenetic structure of assemblages, aiding in the identification of ecological processes functioning at terminal evolutionary depth (Mazel et al. 2016). Each phylogenetic divergence metric (SES MPD, SES MNTD) is expressed as a standardized effect size relative to a null distribution generated using the same arguments as specified for SES MPD (Nawalage et al. 2025). Positive z-scores indicate community assemblages that are phylogenetically overdispersed relative to null expectations, meaning phylogenetically distantly related species coexisting together in a community and negative z-scores indicate phylogenetically clustered assemblages, meaning phylogenetically close related species coexisting together in a community (Nawalage et al. 2025; Divya and Karanth 2018) (Figures 6 & 7).

1.2.5 Statistical analysis

I have used to generalize least square (GLS) models using “*gls*” function in “*nlme*” R package accounting for spatial autocorrelation structure to predict the relationship between phylogenetic structure of forest strata along the gradients of elevation, rainfall and climatic water deficit. Extreme outliers identified from boxplots in the phylogenetic divergence response variables were excluded from the analyses. Models were run both with and without outliers, and their diagnostic plots were examined, as the inclusion of outliers often leads to violations of the normality assumptions. Environmental variables with differing units of measurement were standardized using

the “scale” function, which centers and scales the data to produce uniform values ranging from -1 to +1. To avoid multicollinearity among variables in the model, Pearson correlation coefficients (maintained below $R = 0.7$) and variance inflation factors ($VIF < 5$) were examined for all explanatory variables (Figure 8 & Table 2). I detected spatial autocorrelation using Moran’s I test and Moran’s scatter plot. To account for spatial autocorrelation in the analyses, I employed generalized least squares (GLS) models incorporating spatial correlation structures that were consistent with the shapes of the empirical semi-variograms across the network of plots (Figure 9). Model selection among spherical, exponential, Gaussian, and rational spatial correlation structures was based on Akaike Information Criterion (AIC) values, with lower AIC scores indicating better model fit (Table 3).

1.3 Results

Species richness and Shannon’s alpha diversity varied markedly across strata and biogeographic subregions of the western ghats (Figure 10 & Table 4). Among strata the understory consistently exhibited the highest richness and diversity, with values peaking in the southern WG and remaining high in the Nilgiris WG. In contrast, the liana and emergent strata supported the lowest richness particularly in the Nilgiris and northern WG. The subcanopy and canopy strata displayed intermediate values. When all strata were combined the southern WG emerged as the most diverse subregion followed by the Nilgiris. The northern WG consistently has lowest diversity across strata and overall.

1.3.1 Phylogenetic Structure Across Biogeographic subregions of the Western Ghats

The phylogenetic community structure, evaluated using standardized effect sizes of mean pairwise distance (SESMPD) and mean nearest taxon distance (SESMNTD), exhibited unique patterns of phylogenetic structure among the Western Ghats Forest layers and biogeographic subregions (Figure 11, Tables 5 - 7). The SESMPD provide insight into deep evolutionary divergence, while the SESMNTD highlight divergence at the tips of the phylogeny. Negative standardized values indicate phylogenetic clustering (closely related taxa co-occurring more than expected by chance), while near-zero or positive values indicate weak structure or overdispersion (distantly related taxa co-occurring more than expected by chance).

Lianas showed generally weak and inconsistent phylogenetic structure across both metrics. Significant basal clustering was detected in the Central WG (SESMPD: unweighted -1.16, $p = 0.02$; abundance -0.98, $p = 0.02$) and Nilgiris WG (SESMPD: unweighted -0.99, $p = 0.05$; abundance -0.90, $p = 0.02$). On the other hand, southern and northern zones were not statistically significant. The SESMNTD results confirmed this weak pattern: the unweighted values were close to zero and not statistically significant in all zones, but I detect clustering with the abundance-weighted metric in the Nilgiris (-1.07, $p = 0.15$) but not statistically significant. It seems lianas thus only filtered by their evolutionary history, with the basal clustering patterns being largely confined to the Central and Nilgiris zones.

The understorey showed the strongest and most consistent clustering across the Western Ghats. For SESMPD unweighted metric, estimates were significantly negative across all zones (Central -1.76, Southern -1.72, Nilgiris -2.27, Northern -2.30; $p \leq 0.01$), and remained significant under abundance weight metric, particularly in the Central (-2.11, $p < 0.001$) and Nilgiris (-1.92, $p < 0.001$). SESMNTD values also indicated strong terminal clustering, especially under unweighted estimates (Southern -4.79, Northern -3.02, Nilgiris -2.73, Central -2.20; $p \leq 0.01$). However, abundance weighted estimates reduced, with only the Nilgiris retaining significance (-1.72, $p = 0.02$). Together, these results suggest that understorey assembly is strongly shaped by evolutionary filtering, particularly at the tip level in unweighted analyses, and that rare species disproportionately drive these clustering patterns.

Subcanopy assemblages comparatively showed slight clustering with stronger signals at the terminal than basal level. In the SESMPD, the unweighted clustering was significant in the central (-1.37, $p = 0.01$) and northern (-1.12, $p = 0.04$) zones but decreased with the abundance weighted estimates. The SESMNTD showed more pronounced clustering: the unweighted estimates were negative in all zones, significant in the southern zone (-2.76, $p < 0.001$) and Northern zone (-1.85, $p = 0.03$), with a marginal clustering in nilgiris zone (-1.59, $p = 0.06$). The abundance weight-based clustering was reduced, limited to Central zone with a significant clustering (-1.54, $p = 0.04$). This pattern suggests that subcanopy clustering are more pronounced at terminal clustering and is mainly driven by rare taxa.

At the deep evolutionary scales, canopy communities were shown reduced clustering (more overdispersion or neutral) but showed significant terminal clustering. SESMPD values were low and not significant in all zones, suggesting a low basal level filtering. In contrast, the SESMNTD unweighted metric estimates showed a significant clustering in Central WG (-2.91, $p < 0.001$), Nilgiris WG (-1.79, $p = 0.03$), and Southern WG (-1.94, $p = 0.02$), with weaker signals in Northern WG (-1.44, $p = 0.08$). The abundance weight estimates find reduced clustering but remained significant in Central (-1.65, $p = 0.02$) and in Nilgiris (-1.46, $p = 0.03$). Thus, canopy structure appears to be shaped by the most recent evolutionary lineages at the tip of the phylogenetic tree, with dominance-driven effects reducing overall clustering.

The emergent trees showed strong and consistent clustering across both basal and terminal metrics. unweighted SESMPD estimates were significantly negative in all zones (Central -1.16, Southern -2.20, Northern -1.67, Nilgiris -1.79; $p \leq 0.03$), and abundance weight estimates often remained significant (e.g., Southern -1.10, $p = 0.01$; Central -0.92, $p = 0.04$). The SESMNTD reinforced these findings, by showing highly significant clustering across all zones under unweighted metrics (Central -3.22, Southern -3.18, Nilgiris -2.71, Northern -2.49; $p < 0.001$), and persistence of significant clustering under abundance weighted metrics (Central -2.28, $p < 0.001$; Nilgiris -1.84, $p = 0.02$). Emergent communities therefore represent a prominently filtered stratum, shaped by both deep and terminal evolutionary clustering.

When all strata were pooled, the SESMPD showed strongly significant clustering in all zones in the unweighted metrics (Central -2.80, Southern -2.76, Northern -2.97, Nilgiris -2.60; $p < 0.01$).

Under the abundance weight metrics clustering reduced, leaving weaker but significant clustering in the Central (-1.35 , $p = 0.02$), Northern (-1.31 , $p < 0.001$), and Nilgiris (-1.03 , $p = 0.03$), while Southern WG became not statistically significant. The results of the SESMNTD were more variable. The unweighted metric-based clustering was weak (Southern -1.84 , $p = 0.04$), with not statistically significant estimates in other zones. Abundance-weighted estimates showed moderate clustering only in the Central WG (-1.43 , $p = 0.03$). These contrasts suggest that while deep evolutionary filtering is evident when taxa are pooled, tip-level clustering is more variable and strongly influenced by the relative abundance of dominant against rare lineages.

1.3.2 Environmental Drivers of Phylogenetic Structure

The effect of environmental gradient on the phylogenetic community structure, expressed in standardized effect sizes of mean pairwise distance (SESMPD) and the mean nearest taxon distance (SESMNTD) including both presence and abundance-weighted versions, was evaluated using generalized least squares (GLS) models for all woody species and for each forest strata (Figure 12, Tables 8–11).

The environmental gradients in the Western Ghats are shaped by a strong interaction between latitude, elevation, and climate, producing two overlapping axes that jointly influence woody plant distribution and phylogenetic structure (Figure 8). From south to north, rainfall declines sharply ($r = -0.7$) and climatic water deficit (CWD) increases ($r = 0.8$), reflecting a transition from moist, aseasonal forests in the southern WG to drier, more seasonal forests in the north. Elevation is strongly negatively correlated with latitude ($r = -0.8$) and perfectly negatively correlated with temperature ($r = -1.0$), indicating that high-elevation, cooler zones are concentrated in the southern WG, while low-elevation, warmer areas dominate in the north (Figure 8). This overlap means that the moist, high-elevation habitats of the south also coincide with low CWD, fostering phylogenetic overdispersion through competitive interactions among diverse lineages, whereas the lower, drier northern forests are more prone to phylogenetic clustering under strong environmental filtering. However, the correlation matrix reveals substantial multicollinearity among predictors, particularly between elevation and temperature, latitude and CWD, and latitude and rainfall, making their simultaneous inclusion in generalized least squares (GLS) models problematic. To avoid inflated variance estimates and unreliable parameter significance, one variable should be selected from each highly collinear group for example, representing either elevation or temperature, while latitude should only be included when spatial effects are explicitly tested and not alongside its climatic proxies.

At the community level, SESMPD was significantly and positively related to elevation ($\beta = 0.068$, $p < 0.001$) and rainfall ($\beta = 0.185$, $p < 0.001$), indicating an increase in phylogenetic divergence (reduced clustering) in wetter and higher-elevation sites, but no effect of climatic water deficit (CWD) was found (Figure 12, Tables 8–11). Response at the stratum level was more variable. Lianas showed a significant divergence with rainfall ($\beta = 0.042$, $p = 0.039$) but a strong clustering with increasing CWD ($\beta = -0.165$, $p < 0.001$). Understorey strata showed consistent divergence with rainfall ($\beta = 0.080$, $p < 0.001$) but clustering with CWD ($\beta = -0.091$, $p < 0.001$). Subcanopy

and canopy strata showed consistent divergence with both elevation and rainfall but clustering with CWD, while emergent strata were strongly showed divergence with elevation alone ($\beta = 0.107$, $p < 0.001$). With abundance estimates, the SESMPD relationship for the whole community was maintained like unweighted estimates particularly with rainfall ($\beta = 0.196$, $p < 0.001$) and became significantly negative with CWD ($\beta = -0.126$, $p = 0.046$), indicating that dominant taxa in water-stressed sites are more phylogenetically clustered. The understorey and canopy strata again showed strong divergence with rainfall ($\beta = 0.064$ and $\beta = 0.052$, respectively; $p < 0.01$) and clustering with the CWD. The subcanopy showed weaker clustering with CWD ($\beta = -0.033$, $p = 0.025$). The emergent strata showed significant and strong divergence with elevation ($\beta = 0.085$, $p < 0.001$) and relatively weaker clustering with CWD ($\beta = -0.061$, $p = 0.020$). In contrast, lianas showed significant divergence only with rainfall ($\beta = 0.109$, $p = 0.013$), while no effects were observed with CWD.

The SESMNTD, which emphasize tip-level divergence or clustering, are generally in line with the SESMPD but are interesting with additional strata-specific variation. At community level, rainfall was the only significant driver of divergence ($\beta = 0.235$, $p < 0.001$) (Figure 12, Tables 8–11). Lianas and understorey again diverged with rainfall, but clustered strongly with increasing CWD ($\beta = -0.126$ and -0.136 , respectively; $p < 0.01$). In contrast, the subcanopy showed significant tip-level clustering with rainfall ($\beta = -0.088$, $p = 0.011$), while the canopy strata clustered with elevation ($\beta = -0.089$, $p = 0.003$). The emergent taxa diverged significantly with elevation ($\beta = 0.098$, $p = 0.009$). With abundance weight SESMNTD, the rainfall increased divergence at the community level ($\beta = 0.165$, $p < 0.001$), while both the elevation ($\beta = -0.081$, $p = 0.009$) and the CWD ($\beta = -0.167$, $p < 0.001$) increased clustering, highlighting the stronger role of environmental stress when dominant taxa are emphasized. Lianas and understorey again reflected the responses of the entire community, diverging with rainfall and clustering with CWD. The responses of subcanopy and canopy strata was weaker; neither showed strong rainfall effects, but canopy tended toward clustering with elevation ($\beta = -0.052$, $p = 0.065$). The emergent strata showed a strong divergence with elevation ($\beta = 0.098$, $p = 0.004$) but clustering with CWD ($\beta = -0.080$, $p = 0.037$).

Together, these results show that rainfall consistently promotes phylogenetic divergence across strata, while climatic water deficit strongly predict clustering, particularly in the understorey and liana strata. The effects of elevation vary, favouring divergence in emergent strata but clustering in the canopy strata. Importantly, abundance-weighted models reveal a stronger clustering under environmental stress, suggesting that dominant taxa drive community level clustering in harsher environments, whereas rare taxa contribute disproportionately to divergence patterns under the presence-absence models.

1.4 Discussion

1.4.1 Phylogenetic Structure Across Biogeographic subregions of the Western Ghats

Although a few studies have explored differences in species diversity (Bohlman 2015) and functional trait diversity (do Vale et al. 2014; Santiago and Wright 2007) between canopy and

understory layers in a local scale neotropical tropical forests, there remains a notable gap in understanding phylogenetic diversity across vertical strata. Aside from the regional scale study by (Draper et al. 2021) in the Amazon, there are currently no comprehensive investigations that examine phylogenetic diversity differences between canopy and understory layers in tropical forests. The phylogenetic structure of forest strata and biogeographic subregions in the western Ghats exhibits significant variation (Figure 11, Tables 5 - 7). Contrary to our hypothesis, the understory layer showed consistent phylogenetic clustering across both SESMPD and SESMNTD metrics, indicating strong evolutionary filtering. This is in contrast to our expectations but aligns with clustering patterns observed in the emergent layer, which behaved as predicted. Both shade tolerant and stress tolerant emergent trees appear to represent evolutionarily conserved clades in the tropical forests of the western ghats. In contrast, the canopy and liana layers exhibited weak or inconsistent phylogenetic structure, with significant clustering evident only at the tip level in certain zones. These results are broadly consistent with findings from Amazonian tropical forests (Draper et al. 2021), where vertical stratification has also been shown to differently influence lineage assembly across forest layers. However, despite similar hypothesis, our findings differ in key aspects. Draper et al (2021) reported phylogenetic overdispersion in the understory layers of the amazon, whereas I have observed clustering in the western ghats. Methodological differences may partially explain this discrepancy. For instance, Draper's classification of vertical strata was based on diameter at breast height (DBH), potentially including saplings and juveniles from canopy strata and lianas. Moreover, their analysis was primarily conducted at the genus level and focused on hyper dominant species.

The understory exhibited the strongest and most consistent phylogenetic clustering across the biogeographic subregions of the western ghats. Both unweighted SESMPD and SESMNTD metrics indicated significant clustering, with particularly strong tip level clustering in the southern western ghats (Figure 11, Tables 5 - 7). This pattern can largely be attributed to the high abundance of species from phylogenetically conserved families such as *Rubiaceae* and *Lauraceae* (Pascal et al., n.d.). These results support the hypothesis that strong environmental filtering operates in the shaded understory, where intense competition for limited light favours lineages with deeply conserved traits including high shade and herbivore tolerance, slow growth rates, high survival and conservative leaf traits which enable persistence under such conditions (Santiago and Wright 2007; Swenson and Rubio 2025). The observed reduction in clustering estimates when using abundance weighting metrics further suggests that rare species play a disproportionate role in shaping understory community structure. Notably, many previous studies have focused only on trees with a diameter at breast height (DBH) greater than 10cm, thereby excluding a significant portion of understory species. This has led to an underestimation of the diversity and distribution patterns of rare species in the understory layer. In the context of the western ghats, these findings highlight the critical importance of conserving and restoring rare understory species to sustain evolutionary diversity within tropical forest ecosystems.

The emergent trees exhibited consistent phylogenetic clustering across both basal and terminal metrics in all biogeographic subregions even when abundance was considered (Figure 11, Tables

5 - 7). This contrasts with canopy, subcanopy and liana strata, where clustering was reduced under abundance weighted metrics. The persistence of clustering in the emergent layer under both weighting schemes suggest that dominant emergent taxa belong to lineages that have long endured the selective pressures of high light exposure and wind (Bastin et al. 2018; Draper et al. 2021; Lutz et al. 2018; Bastin et al. 2015a). Emergent trees often evolve traits like large crowns, tall boles, large buttress, dense wood and resistance to wind exposure. Emergent species often produce large seeds with high energy reserves that are primarily dispersed over long distances by winged Dipterocarps seeds, large birds and arboreal mammals, facilitating successful seedling establishment in light gaps (Ganesh and Davidar 2001). These lineages often include functional and structural keystone species belonging to genera like *Dipterocarpus*, *Cullenia*, *Durio*, *Terminalia*, and *Palaquium* that play a critical role in maintaining forest architecture, enhancing carbon storage (Souza et al. 2019; Draper et al. 2021), and providing essential habitat for arboreal fauna and flora. Indeed, canopy and emergent trees sometimes described as the sixth continent of the planet harbour remarkable biodiversity with new species and ecological niches continuing to be discovered (Devy and Ganesh 2021). The establishment and dominance of emergent trees typically require extended periods of forest recovery after disturbance, as these species depend on long term growth and stable conditions to reach maturity. Their loss would therefore not only erode phylogenetic diversity but also compromise essential ecosystem functions.

By contrast the absence of strong basal clustering in subcanopy and canopy strata across all zones indicates a greater presence of evolutionarily distant lineages with more flexible trait syndromes (Figure 11, Tables 5 - 7). This suggest that diverse lineages may converge functionally to exploit semi shaded and light rich environments resulting in weaker phylogenetic clustering despite ecological similarities. Trait based and phylogenetic studies show emergent are more evolutionarily conserved, while canopy trees allow more functional convergence in the French Guiana (Baraloto et al. 2012). In the subcanopy, clustering is more pronounced at the terminal level and is primarily driven by rare taxa. Consequently, canopy structure appears to be shaped largely by recent evolutionary lineages at the tips of the phylogenetic tree, where dominance driven effects reduce the extent of phylogenetic clustering.

The liana growth form has evolved independently across multiple angiosperm lineages including *Fabaceae*, *Bignoniaceae*, *Rubiaceae* and *Vitaceae*. This strategy is considered an adaptation to maximize light capture while minimizing investment in self-supporting tissue. Lianas have developed multiple climbing mechanisms such as tendrils, twining stems, hooks and adhesive roots that allow them to colonise a wide range of habitats. These climbing strategies represent key ecological innovations that underpin their evolutionary success. In the Western ghats, lianas exhibited the weakest and most spatially inconsistent phylogenetic clustering, with significant signals restricted primarily to central and Nilgiris zones. This pattern is consistent with broader findings that the climbing growth form enables lianas to evade strong environmental and evolutionary filters (Schnitzer and Bongers 2011). Unlike trees, which are more strongly constrained by niche conservatism and functional trait filtering, lianas display greater ecological flexibility and opportunism (Rios et al. 2014). Their community assembly appears to be shaped

more by dispersal limitation, stochastic colonisation, local ecological opportunities than by shared evolutionary history (Lai et al. 2017). Lianas are particularly abundant and diverse in tropical dry forests compared to evergreen or wet forests. In dry forests, they exhibit more acquisitive traits such as lower leaf mass per area and higher foliar nutrient concentrations that enhance performance under drought prone conditions (Medina-Vega et al. 2021). In the tropical dry forests of southern India, (Vivek and Parthasarathy 2015) reported high functional richness linked to dispersal modes, leaf traits and climbing strategies. Classic studies in both Amazon and the western ghats (Gentry 1992; Ramesh et al. 2010) similarly noted that lianas are disproportionately dominant in dry forests, often contributing up to 25% of woody stems. Evidence from Biligiri Rangan hills further shows that liana richness and abundance increase during successional recovery from disturbance in dry forests (Ticktin et al. 2012). In contrast, lianas in evergreen or wet forests are generally less diverse both phylogenetically and functionally. (Rocha et al. 2022) demonstrated in the amazon that lianas assemble functionally along hydrological gradients, but their functional diversity peaks in drier environments. Importantly lianas play a major role in shaping forest dynamics by reducing host tree growth and survival, thereby influencing community assembly processes. Their evolutionary success reinforces the repeated selection of climbing strategies across lineages. As lianas are phylogenetically diverse and occupy multiple ecological niches they represent vital repositories of evolutionary history. Their loss would therefore erode both functional and phylogenetic diversity in tropical forests.

When strata were pooled, whole-community SESMPD revealed strong basal clustering in all zones under unweighted analyses, but clustering weakened under abundance weights, particularly in the Southern western ghats highlighting that southern WG is a museum and cradle of evolutionary diversity (Gopal et al. 2023; Bose et al. 2019; Divya et al. 2020; Page and Shanker 2018) (Figure 11, Tables 5 - 7). Variation among zones further reflects the interplay of climate and historical biogeography in shaping assembly. Stronger clustering in the Nilgiris and Northern WG likely reflects the role of seasonality and montane climates as filters that restrict communities to stress-tolerant lineages (Bose et al. 2019; Divya et al. 2020; Shivaprakash et al. 2018). In contrast, the Southern and Central WG-characterized by wetter and more aseasonal conditions-displayed stronger tip-level clustering, suggesting that recent diversification within certain lineages has been more influential in these stable environments (Gopal et al. 2023; Bose et al. 2019).

The observation that abundance weighted phylogenetic metrics reduced clustering estimated across forest strata underscores the disproportionate role of rare species in maintaining evolutionary diversity. This finding highlights a critical limitation in many previous studies of the western ghats, which have typically relied exclusively on either presence-absence based metrics (Bose et al. 2019; Divya et al. 2020) or solely on abundance-weighted phylogenetic metrics (Shivaprakash et al. 2018) to infer community assembly mechanisms. Such approaches risk overlooking key contrasts that emerge when the distinct contributions of rare versus dominant species are explicitly considered. By integrating both types of metrics, our analysis reveals how rare species contribute significantly to phylogenetic clustering and community structure, offering a more nuanced understanding of the mechanisms shaping biodiversity patterns in tropical forests.

1.4.2 Environmental Drivers of Phylogenetic Structure

Across both basal and terminal phylogenetic scales, rainfall consistently promoted phylogenetic divergence at the whole-community scale and within most strata (Figure 12, Tables 8–11). This suggests that wetter environments support a broader array of lineages with differing ecological strategies, thereby reducing phylogenetic clustering and increasing overdispersion. Such patterns are consistent with the hypothesis that high water availability relaxes abiotic constraints, permitting the coexistence of distantly related taxa through niche differentiation. (Shivaprakash et al. 2018). In the understory, where light is a primary limiting factor, the positive association between rainfall and phylogenetic divergence likely reflects the buffering effect of mesic conditions, which support the persistence of shade tolerant lineages from diverse evolutionary origins. Similarly, the positive effect of rainfall on liana diversity suggests that increased water availability facilitates the coexistence of multiple climbing lineages consistent with studies showing higher liana abundance and diversity in wetter tropical forests (Rios et al. 2014). However, the evolutionary diversity of understory communities may be particularly vulnerable to increasing dry periods associated with El Nino events intensified by anthropogenic climate change. These droughts can reintroduce strong abiotic filtering, favouring drought adapted clades and leading to reduced phylogenetic diversity. The impact is further exacerbated by anthropogenic disturbance, where medium to large tree fall gaps increase canopy openness, altering the understory microclimate and exposing the soil to greater desiccation and thermal fluctuations. Such conditions can significantly affect the composition and diversity of shade adapted understorey communities. Lianas, in contrast, are often more abundant in ecotones between wet and dry forests, including riparian zones, where increased canopy openness promoted light availability. These conditions enhance liana diversity and abundance, particularly in areas subject to natural or human induced canopy disturbance.

In contrast to rainfall, climatic water deficit (CWD) emerged as a strong predictor of phylogenetic clustering, particularly within the understory and liana strata (Figure 12, Tables 8–11). This pattern suggests that increasing drought stress acts as a potent environmental filter, excluding drought sensitive taxa and favouring the persistence of a narrow suite of lineages with conserved stress tolerance traits. Notably, the intensification of clustering under high CWD even within canopy and emergent layers underscores the pervasive constraint that water limitation places on evolutionary diversity in the western ghats. When species abundance was incorporated into the analysis, CWD driven clustering became even more pronounced, indicating the numerical dominance of a few stress adapted clades under water limited conditions. These findings align with growing evidence that dominant taxa in stressful habitats tend to be phylogenetically clustered and functionally convergent (Shivaprakash et al. 2018), thereby increasing evolutionary distinctiveness (Grant et al. 2023). In addition, deciduous leaf phenology imposes a strong additional filter, intensifying phylogenetic clustering across all strata, especially at deeper phylogenetic scales, favouring ancient drought-adapted lineages (Figure 13 & 14). This reflects the prevalence of ancient drought adapted lineages such as *Terminalia* and *Anogeissus* that exhibit traits like seasonal leaf shedding and physiological drought avoidance. Moreover, the increasing frequency of natural and anthropogenic forest fires, especially in drier forest types, further promoted phylogenetic clustering by selecting

for fire tolerant lineages. These include species with thick bark (e.g., *Terminalia chebula*) and strong resprouting abilities (e.g., *Anogeissus latifolia*), both of which confer resilience to fire disturbance. Anthropogenic climate change characterised by rising mean annual temperature, extended dry seasons, and increased climatic seasonality is expected to shift the current boundaries of wet forests, reducing the extent of wet evergreen forest habitats. These climatic pressures are compounded by habitat fragmentation and land use change, including the expansion of tea, coffee and eucalyptus plantations, forest to agriculture conversion, and infrastructure development (e.g., roads and railways) to meet the demands of a growing population. Such disturbances not only reduce habitat continuity but also impair regeneration dynamics and elevate edge effects. Finally, the proliferation of the invasive species *Lantana camara* originating from South America poses an additional ecological filter in the understories of dry and moist deciduous forests. Intense competition by *Lantana* for light and nutrients, exert strong selection pressure on native species. The long-term effects are yet to be explored.

For emergent and canopy strata the observed positive relationship with elevation suggests that montane habitats support distinct and evolutionarily distant lineages adapted to less stressful climatic conditions (Bose et al. 2019; Gopal et al. 2023; Draper et al. 2021). Historically, these montane forests have functioned as climatic refugia during periods of extreme environmental change, including last Glacial maxima and Last interglacial periods in the western ghats (Bose et al. 2016; Grant et al. 2023). In particular, the southern western ghats montane forests are well known for their high levels of endemism and are often referred to as both evolutionary museums and cradles of speciation. These high elevation forests also play a critical role in carbon storage, harbouring large emergent and canopy tree species such as *Cullenia exarillata* and *Palaquium ellipticum*, which contribute significantly to above ground biomass (Ganesh et al. 1996). Beyond tree diversity, these montane forest emergent trees support exceptional diversity for epiphytes and provide critical habitat for a wide range of arboreal fauna. For instance, in the southern western ghats, large emergent trees are essential habitat for the endemic and endangers Lion tailed macaque (*Macaca silenus*), which depends on complex forest structure for foraging and movement (Ganesh 1995). However, these biodiversity rich montane habitats are increasingly threatened by land use change, particularly the expansion of tea, coffee and eucalyptus plantations that fragment native forests and alter local microclimates and takes years for recovery (Mohandass et al. 2016; Chetan et al. 2019; Nerlekar et al. 2019). Additionally, these high elevation forests face potential risks from increasing dry days and climate variability driven by anthropogenic climate change, which may undermine their long term resilience and ecological stability.

The comparative analysis of SESMPD (basal divergence) and SESMNTD (terminal divergence) revealed that environmental gradients act differently across deep versus tip-level evolutionary scales (Figure 12, Tables 8–11). Rainfall consistently promoted divergence in both metrics, with stronger effects at the basal level, indicating that humid conditions facilitate the coexistence of distantly related lineages rather than simply enabling recent diversification within clades. In contrast, climatic water deficit (CWD) often induced stronger clustering at both deep and tip levels, particularly in lianas and understory strata, suggesting that drought stress not only filters lineages

but also promotes convergence within closely related, stress tolerant clades. These patterns reinforce the scale dependence of community assembly: deep time filtering dominates under favourable environments, while tip-level convergence emerges under stress conditions (Tucker et al. 2017; Kraft et al. 2015). Taken together, these results demonstrate that rainfall promotes evolutionary diversification across forest strata, whereas CWD consistently enforces clustering through phylogenetic conservatism of stress adapted lineages. Elevation effects were stratum specific, with emergent and canopy trees exhibiting stronger divergence at higher altitudes. Importantly the distinction between basal and terminal divergence underscores that assembly mechanisms operate at different evolutionary scales, consistent with previous studies. Furthermore the comparison of unweighted versus abundance weighted models highlights the critical role of rare taxa in maintaining phylogenetic diversity a dimension largely overlooked in earlier studies of the western ghats. In the context of ongoing climate change, increasing drought intensity and altered rainfall regimes in the western ghats may lead to stronger phylogenetic clustering, thereby reducing evolutionary distinctiveness and potentially eroding ecosystem resilience. These findings have direct implications for conservation practice, providing insights that can help forests and policymakers mitigate forest degradation and carbon losses while maximizing biodiversity conservation and ecological restoration efforts.

1.5 Conclusion

The phylogenetic structure of woody plant communities in the western ghats shows strong stratification and clear environmental filtering. Consistent clustering in the understory and emergent layers reflect strong environmental filtering. Shade tolerant understory species often from conserved clades such as *Rubiaceae* and *Lauraceae*, persist through traits like slow growth and high survival. Emergent trees represented by keystone lineages such as *Cullenia*, *Dipterocarpus*, and *Palaquium* exhibit persistent clustering under both unweighted and abundance weighted metrics. Their conserved traits including tall boles, and large seeds support forest architecture, carbon storage and arboreal biodiversity.

In contrast, canopy, subcanopy and liana strata displayed weaker or inconsistent clustering. Lianas which have evolved multiple climbing strategies across independent lineages showed the weakest and most variable structure reflecting their ecological flexibility and opportunism particularly in drier or disturbed forests.

Environmental gradients strongly influenced assembly processes. Rainfall promoted phylogenetic divergence, allowing coexistence of distantly related lineages under humid conditions. CWD imposed strong evolutionary filtering especially in understory and liana strata, driving convergence toward drought tolerant clades. Elevation enhanced divergence in emergent and canopy strata where montane forests harbour distinct evolutionary lineages adapted to cooler less stressful climates. These habitats function as biodiversity refugia and store substantial above ground carbon.

Comparisons of unweighted and abundance weighted metrics underscore the disproportionate role of rare species in sustaining evolutionary diversity. Presence absence metrics revealed strong

clustering across regions whereas abundance weighting reduced clustering estimates, showing that dominant taxa may obscure the contribution of rare lineages.

Overall, these findings demonstrate that community assembly in the western ghats is strata and scale dependent and shaped by both evolutionary history and environmental stress. Conserving rare understory taxa and dominant emergent lineages is essential for maintaining evolutionary diversity, carbon storage, and long term forest resilience under climate and land use change.

1.6 Figures and Tables

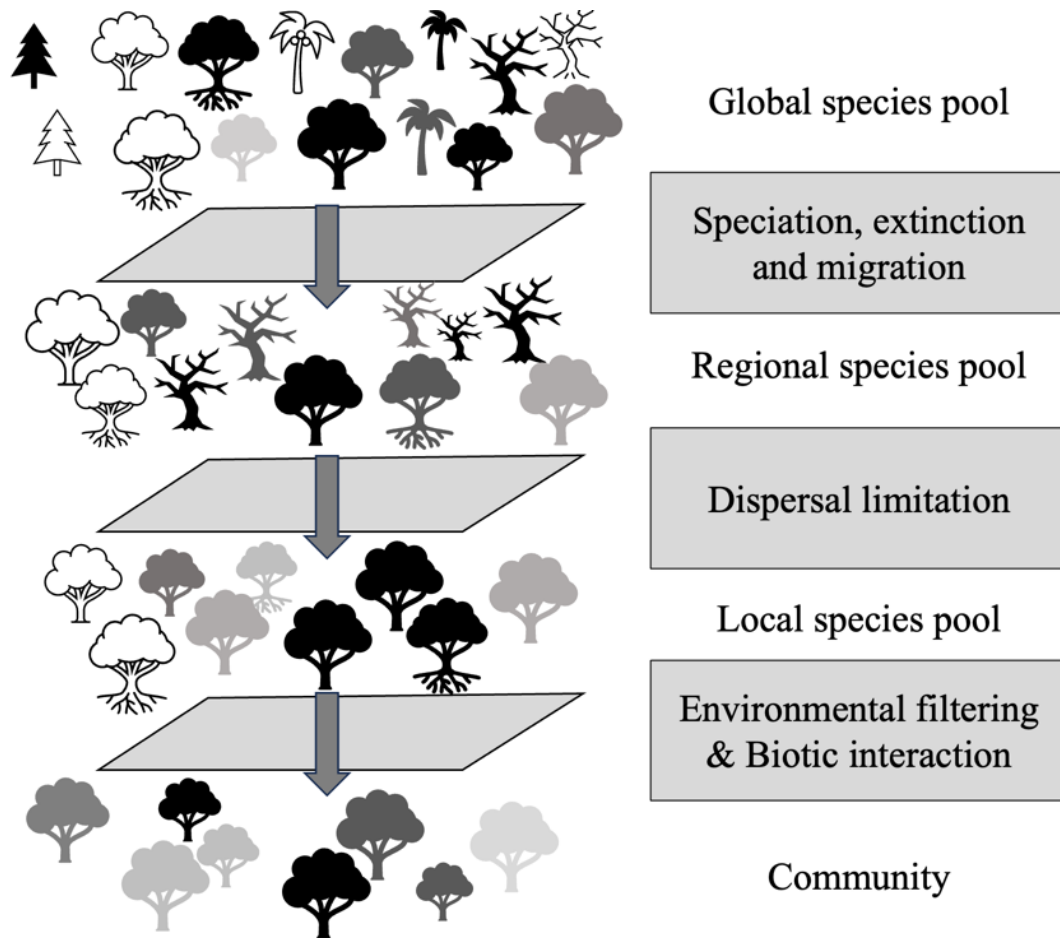


Figure 1: Conceptual representation of the community assembly processes of woody plants, shaped by stochastic processes including dispersal and deterministic processes including competition, environmental filtering.

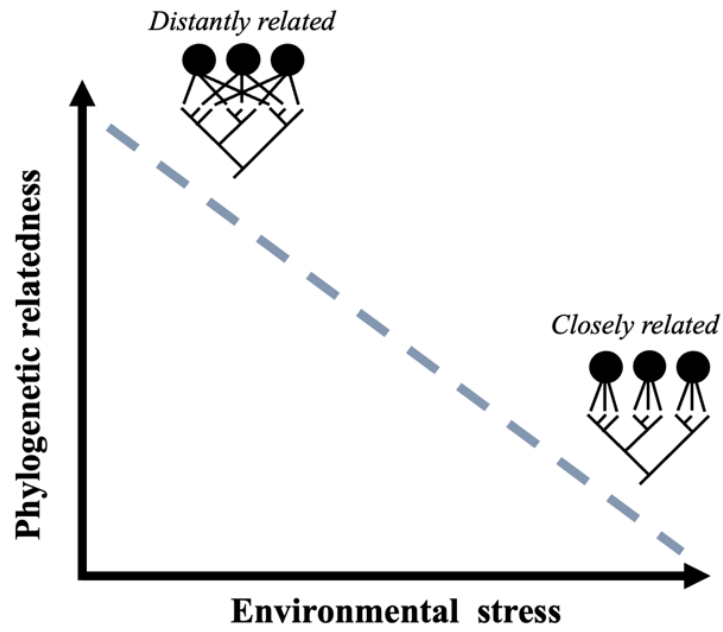


Figure 2: Conceptual illustration of stress gradient hypothesis (SGH).

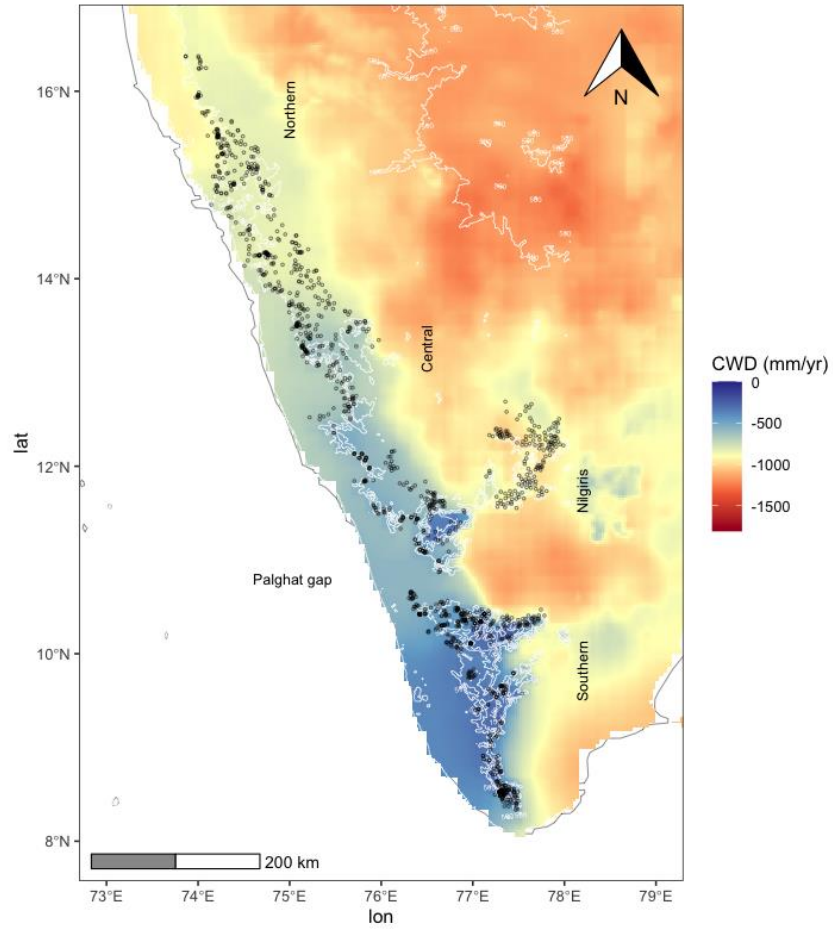


Figure 3: Spatial distribution of 1280 (25 x 25 m - 0.06 ha) forest plots (indicated with black dots) across the Western Ghats biodiversity hotspot overlaid on a climate water deficit (CWD) gradient (mm/yr) , ranging from higher moisture availability (blue) to greater water deficit (red).

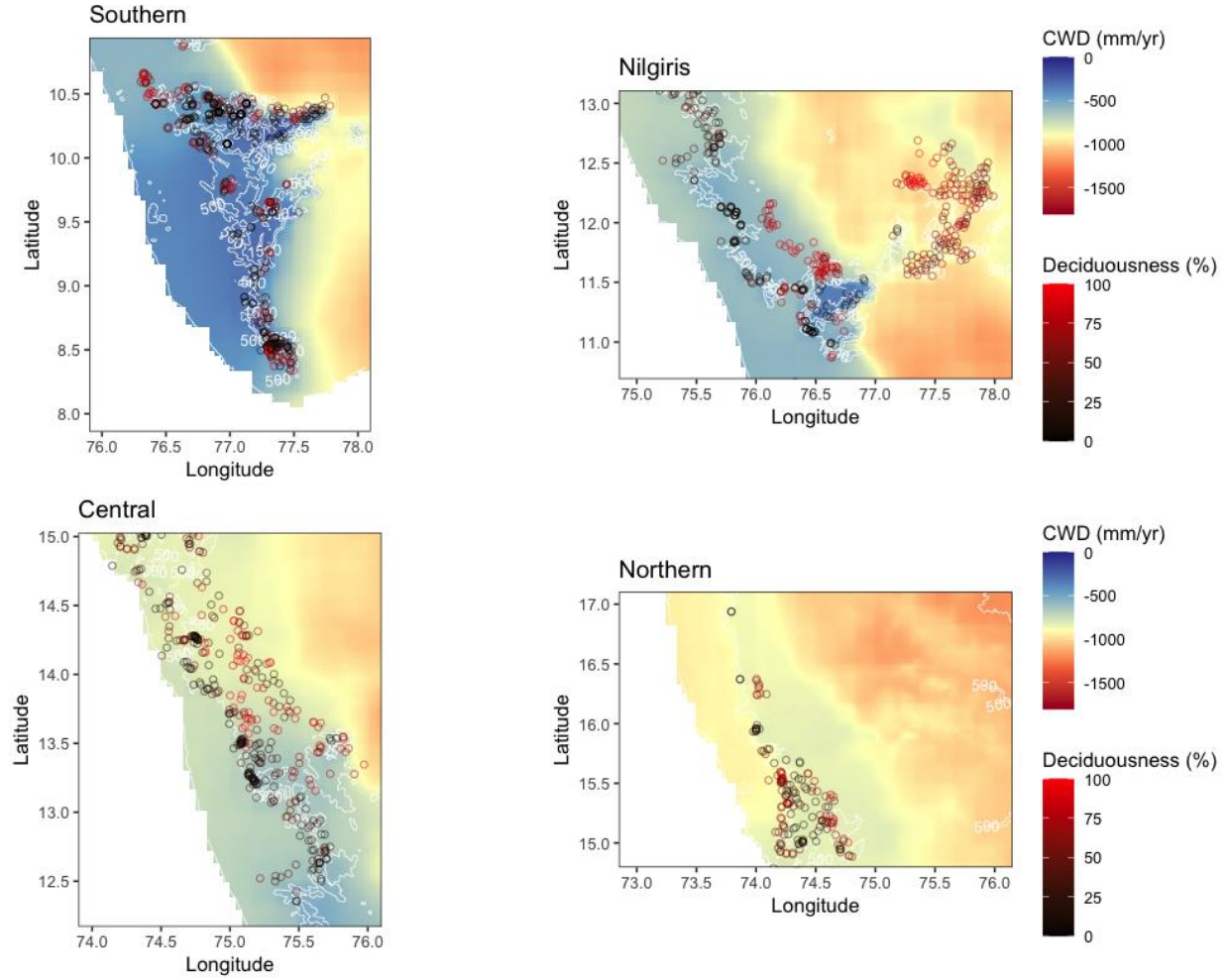
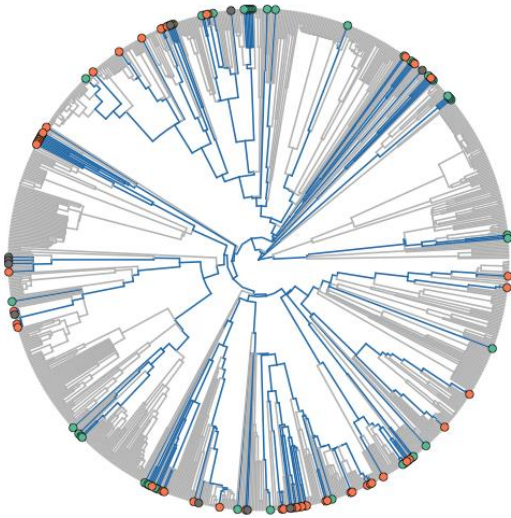


Figure 4: Spatial distribution of 1280 (25 x 25 m - 0.06 ha) forest plots across the Western Ghats biodiversity hotspot categorized into Northern, Central, and Southern biogeographic subregions, separated by the Palghat Gap. Circles represent proportion of deciduous species in a plot distinguishing dry forest (red) to wet (black) forests Overlaid on a climate water deficit (CWD) gradient (mm/yr) gradient ranging from higher moisture availability (blue) to greater water deficit (red).

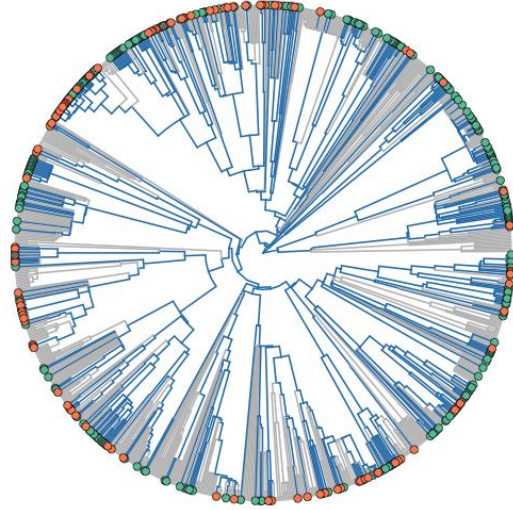
Table 1: Species richness distribution between deciduous and evergreen phenology among tropical forest plots within Western ghats.

Habit	Deciduous	Evergreen	Total
Liana	49	55	113
Understorey	103	274	381
Subcanopy	59	130	189
Canopy	45	86	131
Emergent	26	85	111

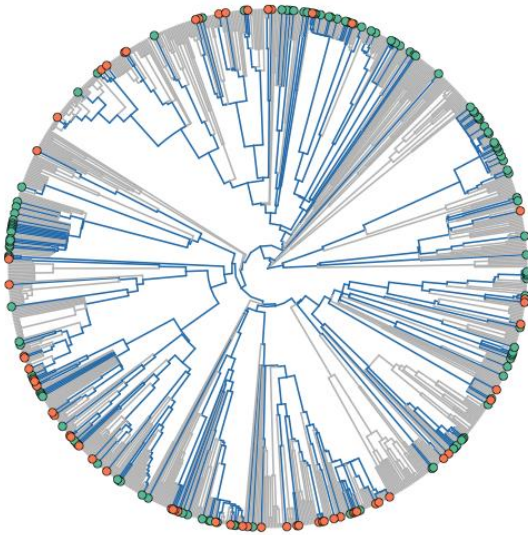
LIANA



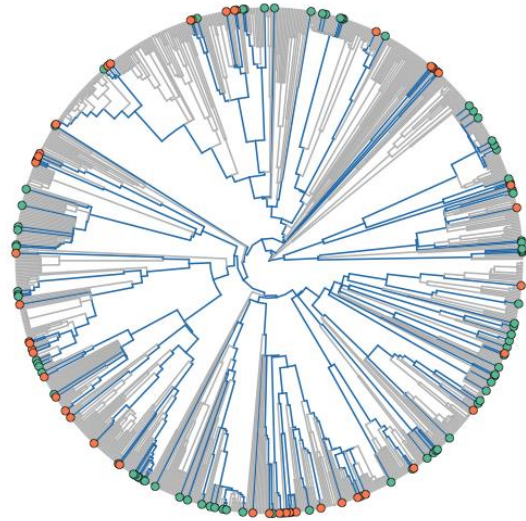
UNDERSTORY



SUBCANOPY



CANOPY



Continue to next page

EMERGENT

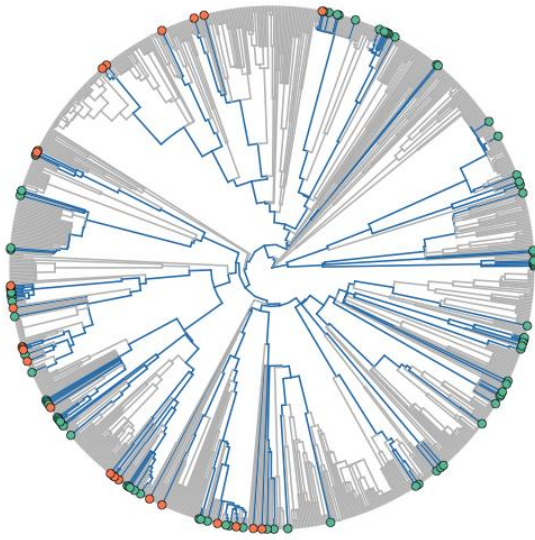


Figure 5: Phylogenetic tree of 925 woody plants species highlighted by Liana, Understory, Subcanopy, Canopy and Emergent strata species including deciduous (orange circles) and evergreen species (green circles).

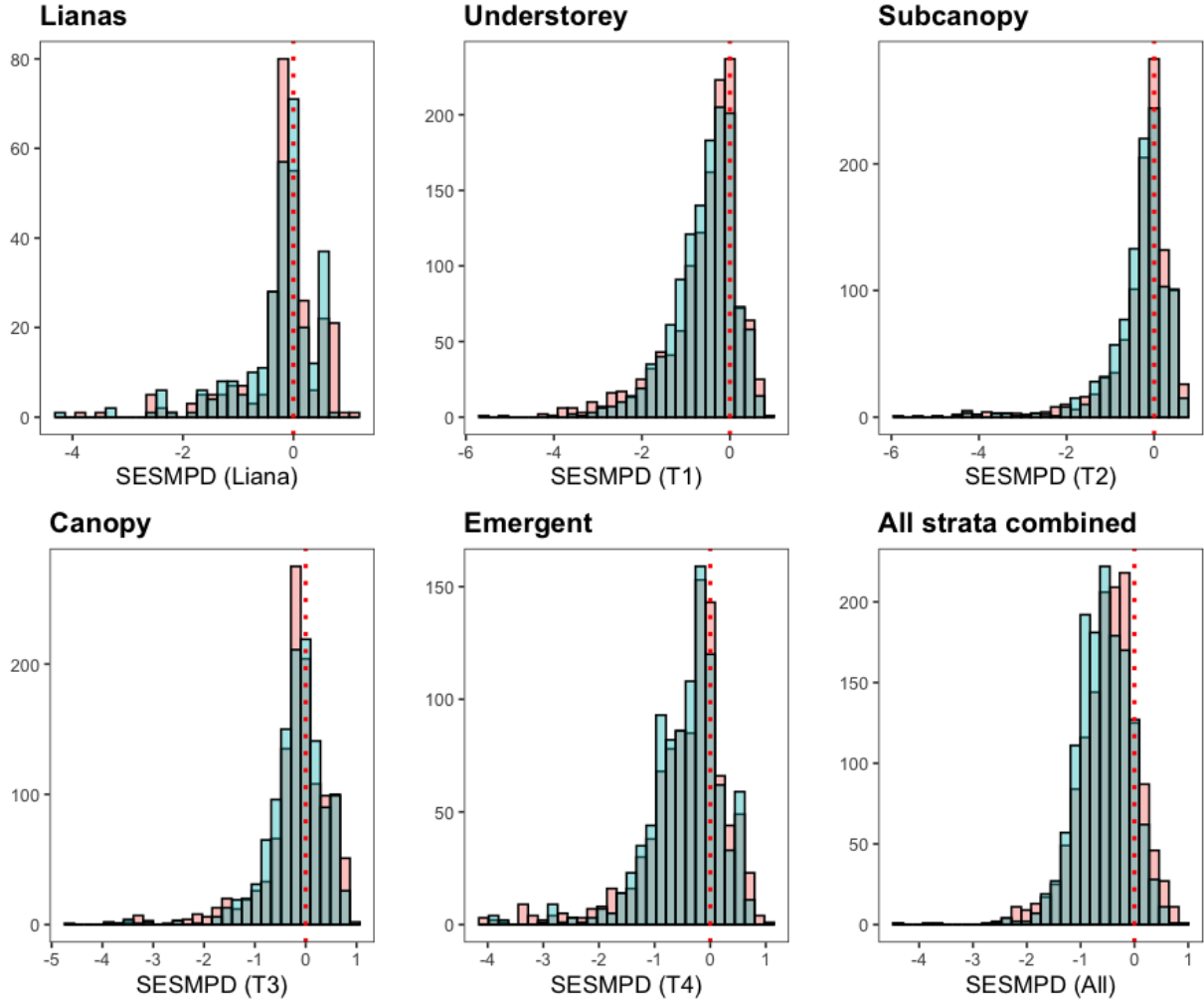


Figure 6: Histograms of standardised effect sizes of mean pairwise distance (SESMPD) across forest strata in the western ghats. Blue bars represent unweighted SESMPD, while red bars represent abundance weighted SESMPD. Vertical red dashed lines indicate $SESMPD = 0$. Negative SESMPD values reflect phylogenetic clustering, whereas positive values indicate phylogenetic overdispersion.

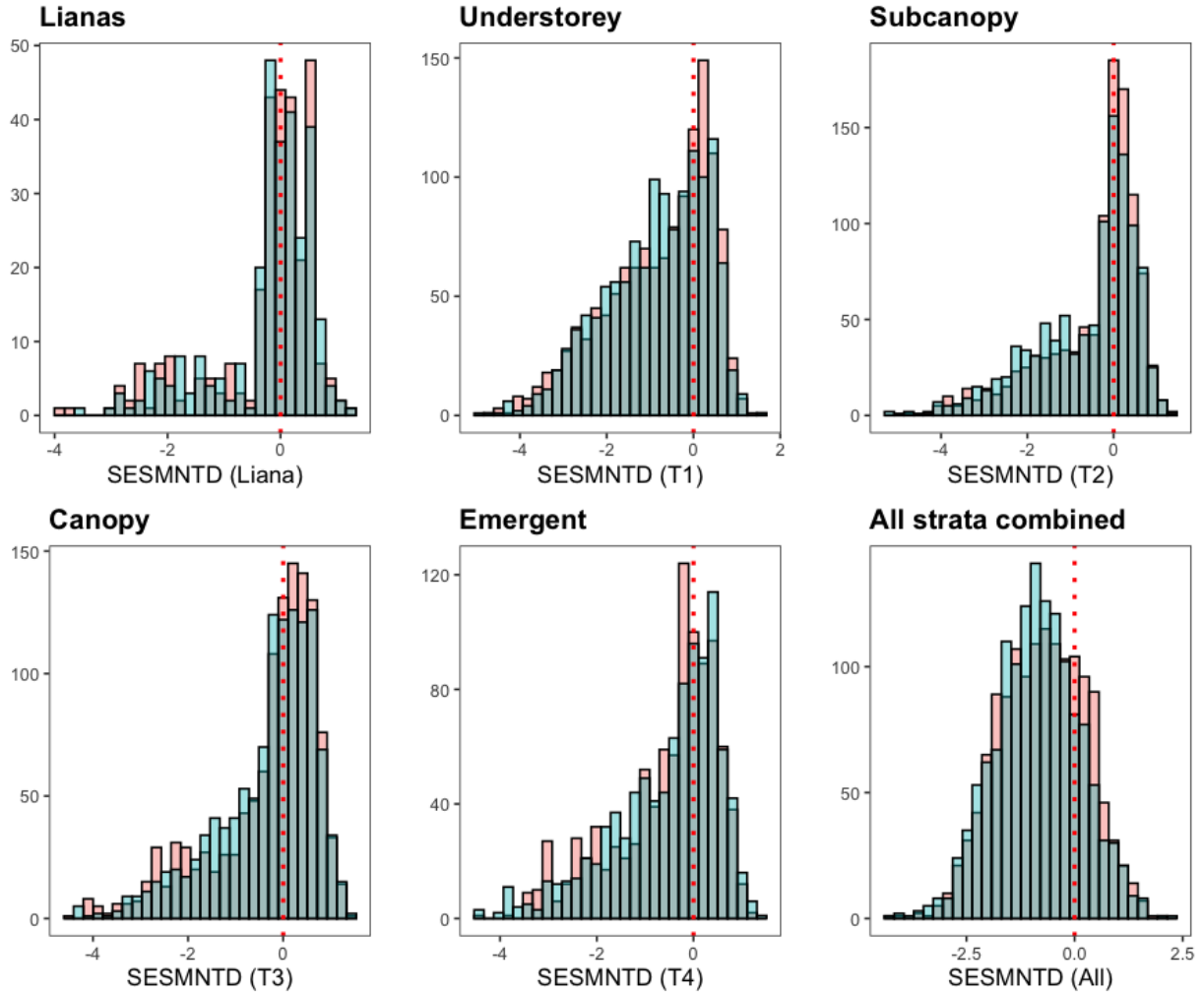


Figure 7: Histograms of standardised effect sizes of mean nearest taxon distance (SESMNTD) across forest strata in the western ghats. Blue bars represent unweighted SESMNTD, while red bars represent abundance weighted SESMNTD. Vertical red dashed lines indicate $SESMNTD = 0$. Negative SESMNTD values reflect phylogenetic clustering, whereas positive values indicate phylogenetic overdispersion.

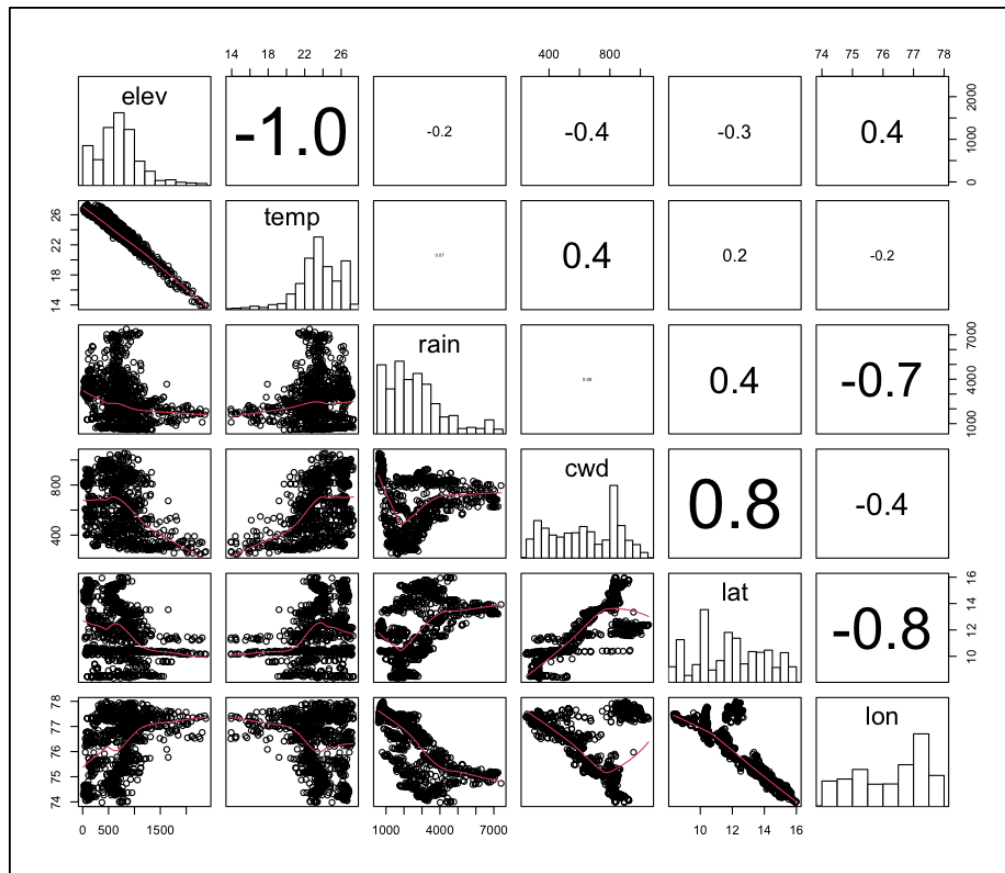


Figure 8: Correlation among environmental variables measured across forest sites in the Western Ghats. Variables include elevation (elev), mean annual temperature (temp), annual rainfall (rain), climatic water deficit (cwd), latitude (lat), and longitude (lon).

Table 2: Variation inflation factor (VIF) among environmental variables measured across forest sites in the Western Ghats.

	VIF	
Elevation	25.31	1.21
Temperature	25.48	-
Rainfall	1.53	1.04
Climatic water deficit (CWD)	1.28	1.16

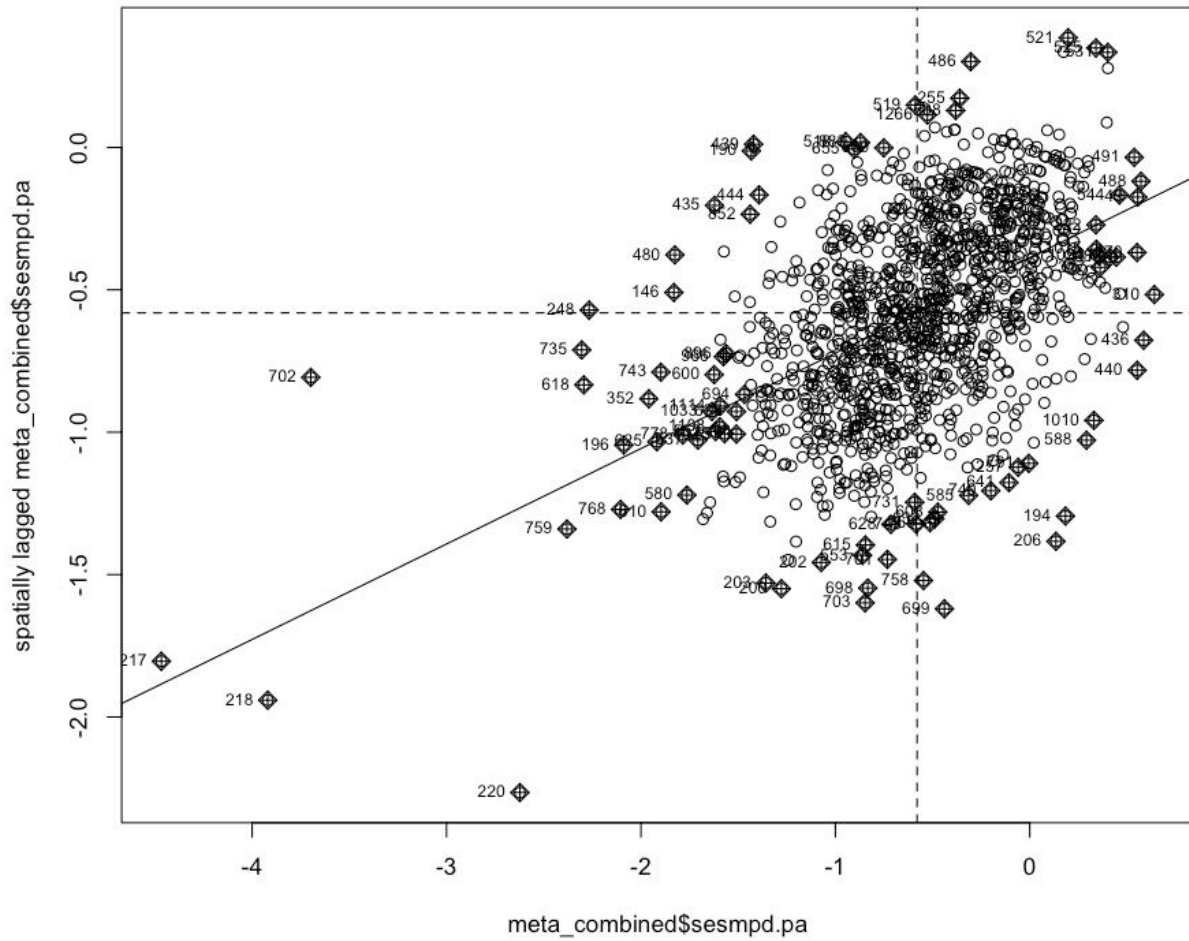


Figure 9: Moran's scatter plot illustrating spatial autocorrelation in SESMPD (unweighted) across study plots in the western ghats. The plot shows positive autocorrelation pattern, with a Moran's I statistic of 0.33, indicating that sites with similar SESMPD values are spatially clustered rather than randomly distributed.

Table 3: Model selection results from generalized least squares (GLS) analyses testing spherical, exponential, Gaussian, and rational spatial correlation structures to account for spatial autocorrelation in phylogenetic community structure across forest strata of the Western Ghats. Values represent Akaike Information Criterion (AIC) scores, with lower values indicating better model fit.

Strata	Metrics	Weights	Spherical	Exponential	Gaussian	Rational
ALL	SESMPD	Unweighted	1267.57	1257.55	1277.75	1267.57
ALL	SESMPD	Abundance	1514.14	1491.47	1505.29	1488.77
ALL	SESMNTD	Unweighted	3348.97	3343.10	3352.24	3346.23
ALL	SESMNTD	Abundance	3503.16	3471.40	3503.03	3472.86
Liana	SESMPD	Unweighted	149.80	149.80	149.80	149.80
Liana	SESMPD	Abundance	51.06	50.07	82.64	68.19
Liana	SESMNTD	Unweighted	283.69	283.69	283.69	283.69
Liana	SESMNTD	Abundance	271.02	271.02	271.02	271.02
Understory	SESMPD	Unweighted	2130.94	2092.75	2112.90	2093.09
Understory	SESMPD	Abundance	2065.61	2000.47	2007.92	2003.45
Understory	SESMNTD	Unweighted	3702.14	3624.76	3702.15	3627.19
Understory	SESMNTD	Abundance	3820.58	3729.96	3738.13	3732.99
Subcanopy	SESMPD	Unweighted	1094.65	1094.65	1094.65	1072.29
Subcanopy	SESMPD	Abundance	820.37	820.80	820.31	819.88
Subcanopy	SESMNTD	Unweighted	2882.50	2846.03	2851.12	2848.78
Subcanopy	SESMNTD	Abundance	2343.23	2324.14	2343.23	2323.39
Canopy	SESMPD	Unweighted	1315.71	1207.97	1315.71	1212.70
Canopy	SESMPD	Abundance	1110.00	1032.73	1110.04	1037.96
Canopy	SESMNTD	Unweighted	2816.78	2790.83	2816.78	2786.96
Canopy	SESMNTD	Abundance	2574.42	2542.88	2574.42	2539.94
Emergent	SESMPD	Unweighted	1295.55	1296.17	1295.64	1283.12
Emergent	SESMPD	Abundance	1400.52	1377.15	1399.76	1378.34
Emergent	SESMNTD	Unweighted	2267.89	2268.24	2267.84	2267.67
Emergent	SESMNTD	Abundance	2014.95	2003.37	2008.21	2003.32

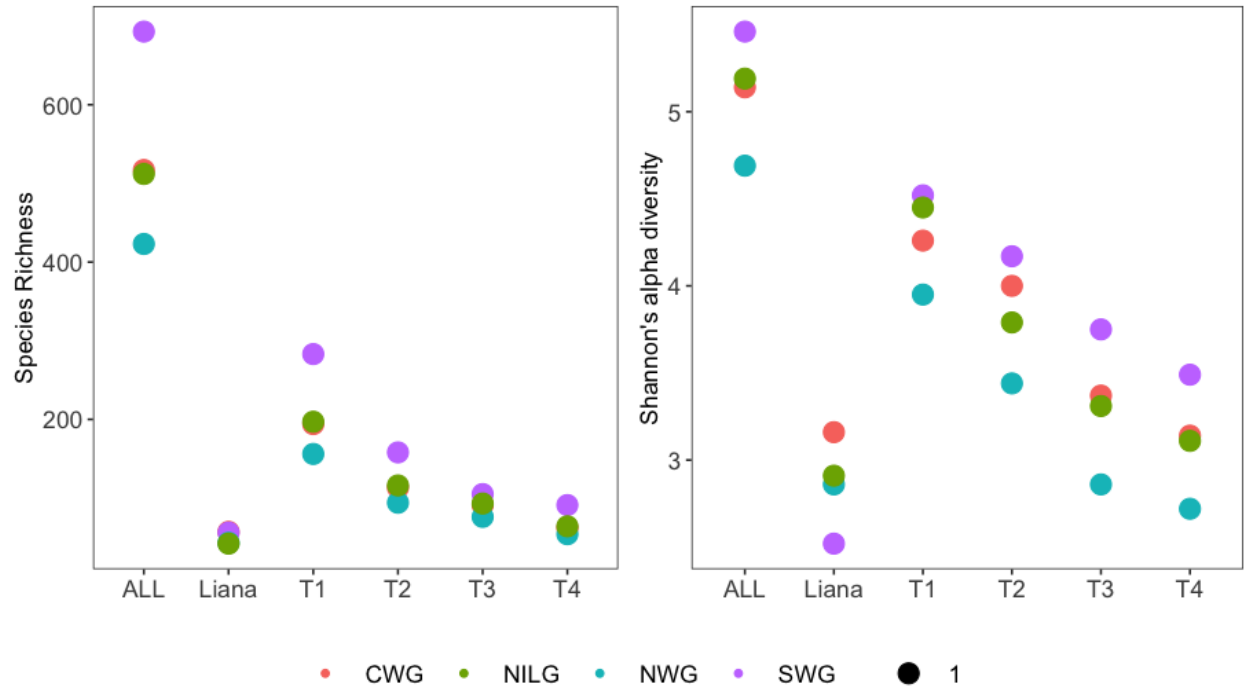


Figure 10: Species richness and Shannon's alpha diversity among tropical forest plots within Western ghats. Colors represent biogeographic subregions: Central WG (red), Nilgiris (green), Northern WG (blue), and Southern WG (purple).

Table 4: Species richness and Shannon's alpha diversity among tropical forest plots within Western ghats.

Strata	Biogeographic subregions	Species richness	Shannon's alpha diversity
Liana	Central WG	57	3.16
Liana	Southern WG	56	2.52
Liana	Northern WG	43	2.86
Liana	Nilgiris WG	42	2.91
Understory	Central WG	194	4.26
Understory	Southern WG	283	4.52
Understory	Northern WG	156	3.95
Understory	Nilgiris WG	197	4.45
Subcanopy	Central WG	113	4.00
Subcanopy	Southern WG	158	4.17
Subcanopy	Northern WG	94	3.44
Subcanopy	Nilgiris WG	116	3.79
Canopy	Central WG	91	3.37
Canopy	Southern WG	105	3.75
Canopy	Northern WG	76	2.86
Canopy	Nilgiris WG	93	3.31
Emergent	Central WG	62	3.14
Emergent	Southern WG	91	3.49
Emergent	Northern WG	54	2.72
Emergent	Nilgiris WG	64	3.11
ALL	Central WG	517	5.14
ALL	Southern WG	693	5.46
ALL	Northern WG	423	4.69
ALL	Nilgiris WG	512	5.19

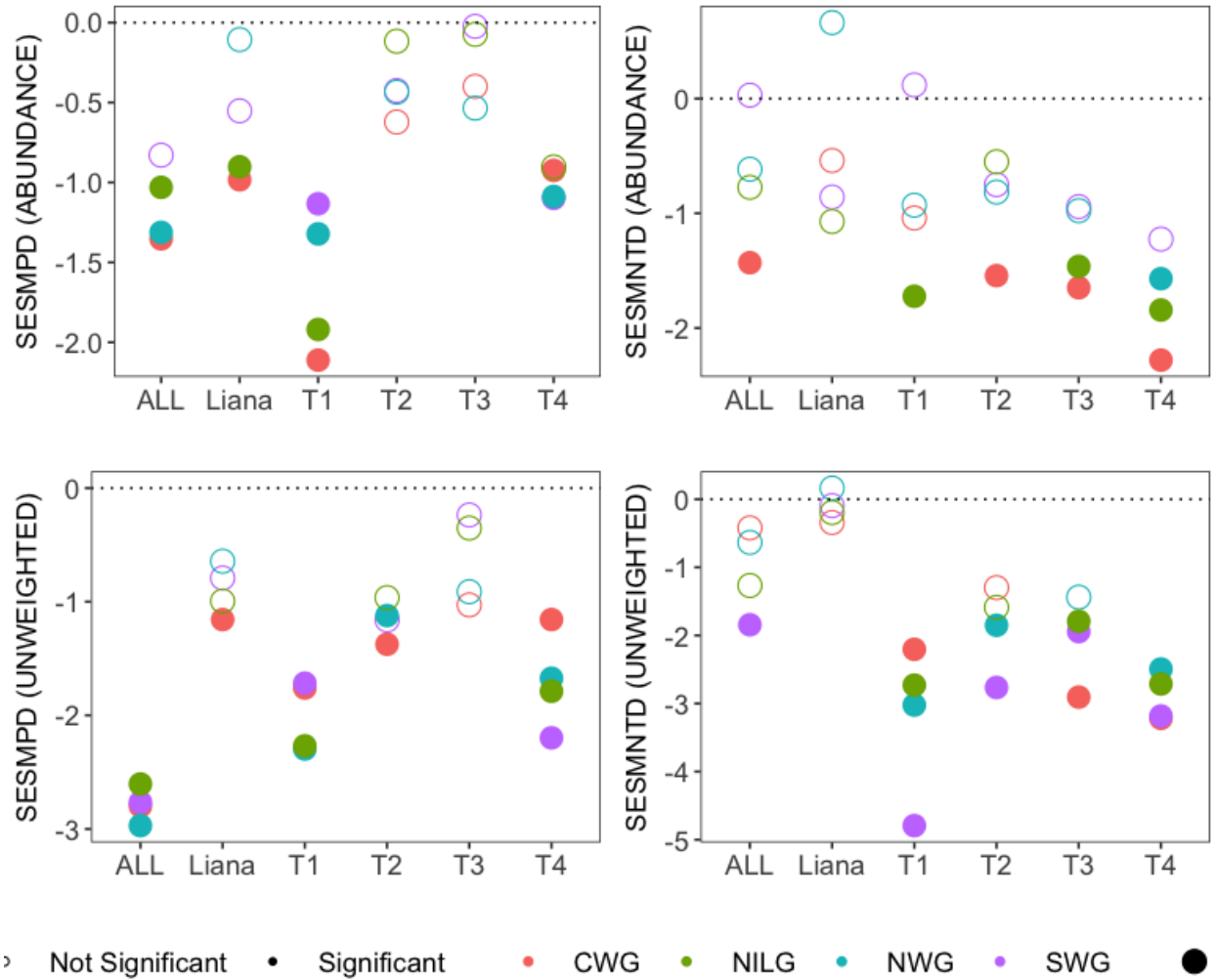


Figure 11: Standardized effect sizes of mean pairwise phylogenetic distance (SESMPD) and mean nearest taxon distance (SESMNTD) across forest communities including Liana, T1 -Understory, T2 -Subcanopy, T3 -Canopy and T4 -Emergent strata in the Western Ghats, showing divergence from null model expectations. Filled circles indicate statistically significant values ($p < 0.05$). Colors represent biogeographic subregions: Central WG (red), Nilgiris (green), Northern WG (blue), and Southern WG (purple).

Table 5: Mean pairwise phylogenetic distance (MPD) and mean nearest taxon distance (MNTD) across forest strata and biogeographic subregions of the Western Ghats. Both unweighted (presence–absence) and abundance-weighted values are presented for each stratum (liana, understory, subcanopy, canopy, and emergent) and for all woody plants combined. MPD reflects average evolutionary distances among all co-occurring taxa (basal divergence), whereas MNTD emphasizes the mean phylogenetic distance to each species closest relative (terminal divergence). Higher values denote greater phylogenetic divergence among co-occurring species, while lower values indicate stronger evolutionary relatedness.

Strata	Biogeographic subregions	MPD (unweighted)	MPD (abundance)	MNTD (unweighted)	MNTD (abundance)
Liana	Central WG	233.25	210.27	100.08	91.96
Liana	Southern WG	236.08	198.29	103.36	80.04
Liana	Northern WG	236.32	218.17	118.16	131.56
Liana	Nilgiris WG	233.33	203.79	112.92	88.41
Understory	Central WG	235.13	215.50	55.76	55.35
Understory	Southern WG	236.88	227.74	42.49	60.26
Understory	Northern WG	231.51	219.71	55.58	60.12
Understory	Nilgiris WG	233.59	221.66	53.47	49.91
Subcanopy	Central WG	234.64	229.31	71.92	61.60
Subcanopy	Southern WG	237.05	232.78	57.24	63.13
Subcanopy	Northern WG	235.51	223.87	71.83	72.87
Subcanopy	Nilgiris WG	237.24	228.41	69.45	70.72
Canopy	Central WG	236.05	224.83	63.13	57.47
Canopy	Southern WG	240.78	233.00	68.10	68.55
Canopy	Northern WG	236.01	208.50	79.84	68.90
Canopy	Nilgiris WG	240.21	223.03	71.71	53.15
Emergent	Central WG	234.13	215.41	64.56	51.64
Emergent	Southern WG	229.68	215.15	59.91	59.80
Emergent	Northern WG	229.37	193.85	75.12	58.43
Emergent	Nilgiris WG	230.04	214.20	69.31	57.60
ALL	Central WG	237.03	231.91	47.31	40.04
ALL	Southern WG	238.90	236.36	42.00	44.90
ALL	Northern WG	235.58	226.73	49.86	46.47
ALL	Nilgiris WG	237.67	233.07	45.95	43.74

Table 6: Results of standardized effect sizes of mean pairwise distance (SESMPD), representing basal phylogenetic structure, across biogeographic subregions of the Western Ghats. Values are shown for both unweighted (presence–absence) and abundance-weighted versions, separately for each forest stratum (liana, understory, subcanopy, canopy, and emergent) and for all woody plants combined. Negative SESMPD values indicate phylogenetic clustering (co-occurrence of more closely related species than expected by chance), whereas positive values indicate phylogenetic overdispersion. Associated p-values denote the significance of deviation from null expectations.

Strata	Biogeographic subregions	SESMPD (unweighted)	p-value	SESMPD (abundance)	p-value
Liana	Central WG	-1.16	0.02	-0.98	0.02
Liana	Southern WG	-0.79	0.14	-0.55	0.14
Liana	Northern WG	-0.64	0.17	-0.11	0.51
Liana	Nilgiris WG	-0.99	0.05	-0.90	0.02
Understory	Central WG	-1.76	0.00	-2.11	0.00
Understory	Southern WG	-1.72	0.01	-1.13	0.01
Understory	Northern WG	-2.30	0.00	-1.32	0.00
Understory	Nilgiris WG	-2.27	0.00	-1.92	0.00
Subcanopy	Central WG	-1.37	0.01	-0.62	0.16
Subcanopy	Southern WG	-1.16	0.08	-0.43	0.34
Subcanopy	Northern WG	-1.12	0.04	-0.44	0.26
Subcanopy	Nilgiris WG	-0.96	0.12	-0.12	0.54
Canopy	Central WG	-1.03	0.08	-0.40	0.30
Canopy	Southern WG	-0.24	0.56	-0.02	0.64
Canopy	Northern WG	-0.91	0.10	-0.54	0.17
Canopy	Nilgiris WG	-0.35	0.52	-0.07	0.58
Emergent	Central WG	-1.16	0.03	-0.92	0.04
Emergent	Southern WG	-2.20	0.00	-1.10	0.01
Emergent	Northern WG	-1.67	0.00	-1.09	0.05
Emergent	Nilgiris WG	-1.79	0.00	-0.90	0.07
ALL	Central WG	-2.80	0.00	-1.35	0.02
ALL	Southern WG	-2.76	0.01	-0.83	0.12
ALL	Northern WG	-2.97	0.00	-1.31	0.00
ALL	Nilgiris WG	-2.60	0.00	-1.03	0.03

Table 7: Results of standardized effect sizes of mean nearest taxon distance (SESMNTD), representing terminal phylogenetic structure, across biogeographic subregions of the Western Ghats. Values are presented for both unweighted (presence–absence) and abundance-weighted versions, separately for each forest stratum (liana, understory, subcanopy, canopy, and emergent) and for all woody plants combined. Negative SESMNTD values indicate phylogenetic clustering (closely related species co-occurring more than expected by chance), whereas positive values reflect phylogenetic overdispersion. Associated p-values indicate the significance of departure from null expectations.

Strata	Biogeographic subregions	SESMNTD (unweighted)	p-value	SESMNTD (abundance)	p-value
Liana	Central WG	-0.34	0.38	-0.54	0.30
Liana	Southern WG	-0.09	0.47	-0.86	0.20
Liana	Northern WG	0.16	0.58	0.66	0.79
Liana	Nilgiris WG	-0.20	0.44	-1.07	0.15
Understory	Central WG	-2.20	0.01	-1.04	0.13
Understory	Southern WG	-4.79	0.00	0.12	0.64
Understory	Northern WG	-3.02	0.00	-0.93	0.16
Understory	Nilgiris WG	-2.73	0.00	-1.72	0.02
Subcanopy	Central WG	-1.30	0.10	-1.54	0.04
Subcanopy	Southern WG	-2.76	0.00	-0.75	0.24
Subcanopy	Northern WG	-1.85	0.03	-0.81	0.22
Subcanopy	Nilgiris WG	-1.59	0.06	-0.55	0.31
Canopy	Central WG	-2.91	0.00	-1.65	0.02
Canopy	Southern WG	-1.94	0.02	-0.94	0.17
Canopy	Northern WG	-1.44	0.08	-0.98	0.16
Canopy	Nilgiris WG	-1.79	0.03	-1.46	0.03
Emergent	Central WG	-3.22	0.00	-2.28	0.00
Emergent	Southern WG	-3.18	0.00	-1.22	0.05
Emergent	Northern WG	-2.49	0.00	-1.57	0.03
Emergent	Nilgiris WG	-2.71	0.00	-1.84	0.02
ALL	Central WG	-0.42	0.33	-1.43	0.03
ALL	Southern WG	-1.84	0.04	0.03	0.58
ALL	Northern WG	-0.63	0.26	-0.62	0.30
ALL	Nilgiris WG	-1.27	0.11	-0.77	0.21

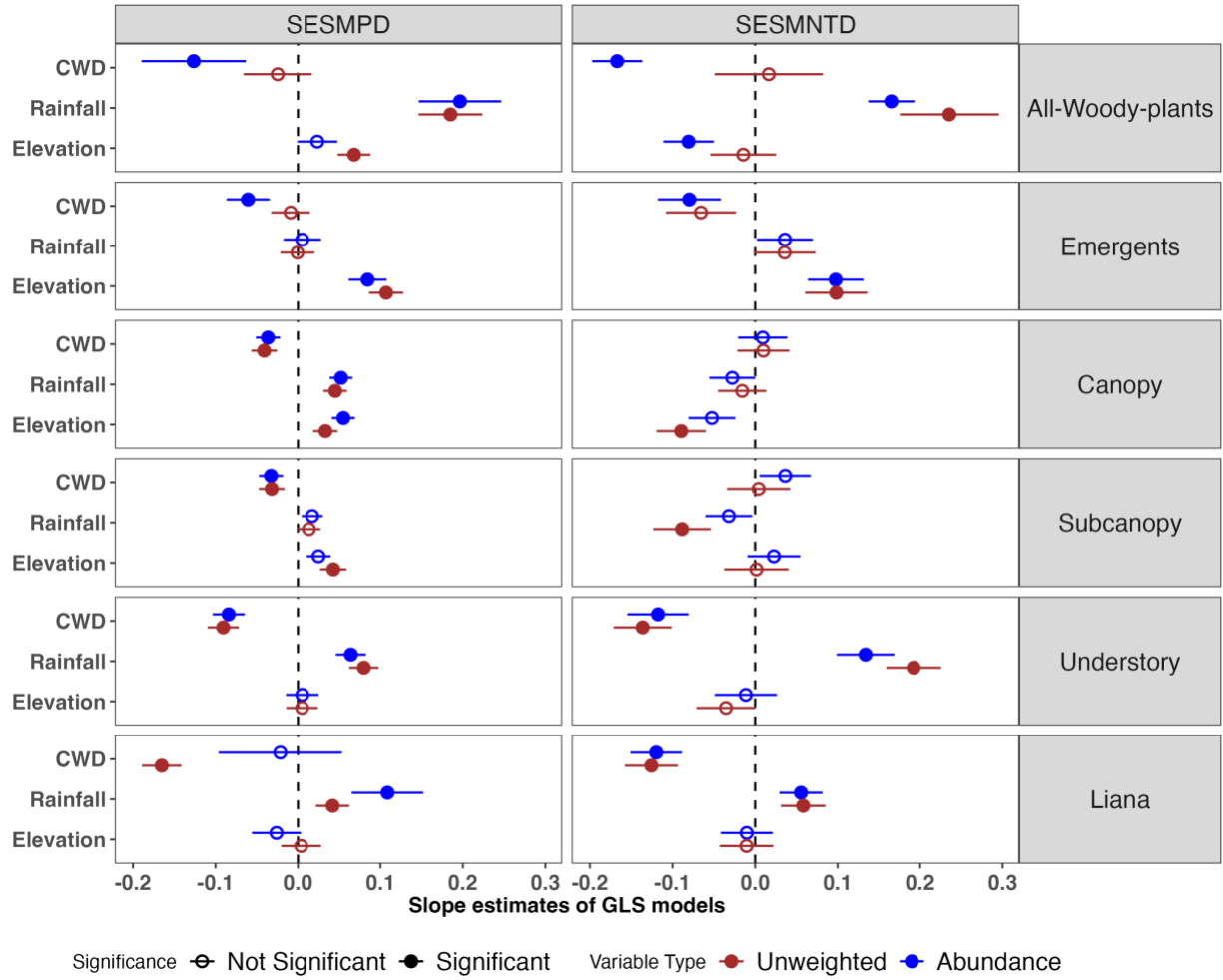


Figure 12: Results of stratum-specific and scale-dependent environmental drivers of phylogenetic clustering and divergence with slope estimates ($\pm$ SE) of generalized least squares (GLS) models particularly testing the influence of climatic water deficit (CWD), rainfall, and elevation on phylogenetic community structure across vertical forest strata of the Western Ghats. Phylogenetic structure is quantified as standardized effect sizes of mean pairwise distance (SESMPD; basal divergence) and mean nearest taxon distance (SESMNTD; terminal divergence) with unweighted (red) and abundance-weighted (blue) versions. Filled symbols indicate significant relationships ($p < 0.05$), while open symbols denote non-significant results.

Table 8: Results of generalized least squares (GLS) models examining the influence of environmental gradients on phylogenetic community structure, expressed as standardized effect sizes of mean pairwise distance (SESMPD), with unweighted (presence–absence) version across all woody plants and individual forest strata. Reported values include regression estimates, standard errors (SE), t-values, and p-values for each predictor including Elevation, Rainfall, and Climatic Water Deficit (CWD). Significant positive coefficients indicate increased phylogenetic divergence (reduced clustering) with increasing predictor values, whereas significant negative coefficients reflect stronger phylogenetic clustering.

GLS model	Response	weight	predictors	Estimate	SE	t-value	p-value
ALL	SESMPD	Unweighted	intercept	-0.547	0.05	-10.937	<0.001
			Elevation	0.068	0.02	3.421	<0.001
			Rainfall	0.185	0.039	4.781	<0.001
			CWD	-0.025	0.041	-0.593	0.553
Liana	SESMPD	Unweighted	intercept	0.051	0.022	2.374	0.018
			Elevation	0.004	0.024	0.162	0.871
			Rainfall	0.042	0.02	2.079	0.039
			CWD	-0.165	0.024	-6.921	<0.001
Understorey	SESMPD	Unweighted	intercept	-0.534	0.017	-30.592	<0.001
			Elevation	0.005	0.019	0.261	0.794
			Rainfall	0.08	0.018	4.503	<0.001
			CWD	-0.091	0.019	-4.792	<0.001
Subcanopy	SESMPD	Unweighted	intercept	-0.213	0.014	-14.737	<0.001
			Elevation	0.043	0.016	2.68	0.008
			Rainfall	0.013	0.014	0.953	0.341
			CWD	-0.032	0.016	-2.045	0.041
Canopy	SESMPD	Unweighted	intercept	-0.14	0.014	-10.182	<0.001
			Elevation	0.033	0.015	2.252	0.025
			Rainfall	0.045	0.014	3.161	0.002
			CWD	-0.041	0.016	-2.635	0.009
Emergent	SESMPD	Unweighted	intercept	-0.357	0.02	-17.665	<0.001
			Elevation	0.107	0.021	5.153	<0.001
			Rainfall	-0.001	0.021	-0.031	0.975
			CWD	-0.009	0.024	-0.377	0.706

Table 9: Results of generalized least squares (GLS) models examining the influence of environmental gradients on phylogenetic community structure, expressed as standardized effect sizes of mean pairwise distance (SESMPD), with abundance weights across all woody plants and individual forest strata.

Model	Response	weight	predictors	Estimate	SE	t-value	p-value
ALL	SESMPD	Abundance	intercept	-0.05	3.529	-0.014	0.989
			Elevation	0.024	0.024	0.971	0.332
			Rainfall	0.196	0.05	3.933	<0.001
			CWD	-0.126	0.063	-1.999	0.046
Liana	SESMPD	Abundance	intercept	0.021	0.183	0.117	0.907
			Elevation	-0.026	0.03	-0.879	0.38
			Rainfall	0.109	0.043	2.505	0.013
			CWD	-0.021	0.075	-0.287	0.775
Understorey	SESMPD	Abundance	intercept	-0.453	0.018	-25.352	<0.001
			Elevation	0.005	0.02	0.265	0.791
			Rainfall	0.064	0.018	3.527	<0.001
			CWD	-0.084	0.019	-4.329	<0.001
Subcanopy	SESMPD	Abundance	intercept	-0.111	0.013	-8.331	<0.001
			Elevation	0.025	0.015	1.71	0.088
			Rainfall	0.017	0.013	1.355	0.176
			CWD	-0.033	0.015	-2.24	0.025
Canopy	SESMPD	Abundance	intercept	-0.063	0.013	-4.875	<0.001
			Elevation	0.055	0.014	3.941	0.001
			Rainfall	0.052	0.014	3.792	<0.001
			CWD	-0.036	0.015	-2.48	0.013
Emergent	SESMPD	Abundance	intercept	-0.337	0.022	-15.138	<0.001
			Elevation	0.085	0.023	3.678	<0.001
			Rainfall	0.005	0.023	0.228	0.82
			CWD	-0.061	0.026	-2.326	0.02

Table 10: Results of generalized least squares (GLS) models examining the influence of environmental gradients on phylogenetic community structure, expressed as standardized effect sizes of mean nearest taxon distance (SESMNTD), with unweighted (presence–absence) version across all woody plants and individual forest strata.

GLS model	Response	weight	predictors	Estimate	SE	t-value	p-value
ALL	SESMNTD	Unweighted	intercept	-0.835	0.067	-12.42	<0.001
			Elevation	-0.014	0.04	-0.361	0.718
			Rainfall	0.235	0.06	3.917	<0.001
			CWD	0.017	0.066	0.252	0.801
Liana	SESMNTD	Unweighted	intercept	0.152	0.029	5.268	<0.001
			Elevation	-0.01	0.033	-0.32	0.749
			Rainfall	0.058	0.027	2.154	0.032
			CWD	-0.126	0.032	-3.907	<0.001
Understorey	SESMNTD	Unweighted	intercept	-0.866	0.033	-26.523	0.001
			Elevation	-0.035	0.036	-0.986	0.325
			Rainfall	0.192	0.033	5.79	0.001
			CWD	-0.136	0.035	-3.87	<0.001
Subcanopy	SESMNTD	Unweighted	intercept	-0.561	0.036	-15.695	0.001
			Elevation	0.002	0.039	0.041	0.968
			Rainfall	-0.088	0.035	-2.54	0.011
			CWD	0.004	0.038	0.11	0.912
Canopy	SESMNTD	Unweighted	intercept	-0.242	0.028	-8.689	<0.001
			Elevation	-0.089	0.03	-2.999	0.003
			Rainfall	-0.016	0.029	-0.537	0.592
			CWD	0.01	0.032	0.314	0.754
Emergent	SESMNTD	Unweighted	intercept	-0.433	0.036	-11.927	<0.001
			Elevation	0.098	0.038	2.609	0.009
			Rainfall	0.036	0.037	0.955	0.34
			CWD	-0.066	0.042	-1.547	0.122

Table 11: Results of generalized least squares (GLS) models examining the influence of environmental gradients on phylogenetic community structure, expressed as standardized effect sizes of mean nearest taxon (SESMNTD), with abundance weight version across all woody plants and individual forest strata.

Model	Response	weight	predictors	Estimate	SE	t-value	p-value
ALL	SESMNTD	Abundance	Intercept	-0.743	0.028	-26.999	<0.001
			Elevation	-0.081	0.031	-2.635	0.009
			Rainfall	0.165	0.028	5.889	0.001
			CWD	-0.167	0.03	-5.509	0.001
Liana	SESMNTD	Abundance	Intercept	0.154	0.028	5.489	<0.001
			Elevation	-0.01	0.031	-0.323	0.747
			Rainfall	0.055	0.026	2.125	0.035
			CWD	-0.12	0.031	-3.844	0.001
Understorey	SESMNTD	Abundance	Intercept	-0.817	0.034	-23.771	<0.001
			Elevation	-0.011	0.038	-0.3	0.764
			Rainfall	0.134	0.035	3.827	0.001
			CWD	-0.118	0.037	-3.172	0.002
Subcanopy	SESMNTD	Abundance	intercept	-0.289	0.029	-9.989	<0.001
			Elevation	0.023	0.032	0.71	0.478
			Rainfall	-0.032	0.028	-1.127	0.26
			CWD	0.036	0.031	1.172	0.241
Canopy	SESMNTD	Abundance	intercept	-0.13	0.026	-4.928	<0.001
			Elevation	-0.052	0.028	-1.849	0.065
			Rainfall	-0.028	0.028	-1	0.317
			CWD	0.009	0.03	0.307	0.759
Emergent	SESMNTD	Abundance	intercept	-0.378	0.033	-11.514	<0.001
			Elevation	0.098	0.034	2.894	0.004
			Rainfall	0.036	0.034	1.064	0.288
			CWD	-0.08	0.038	-2.092	0.037

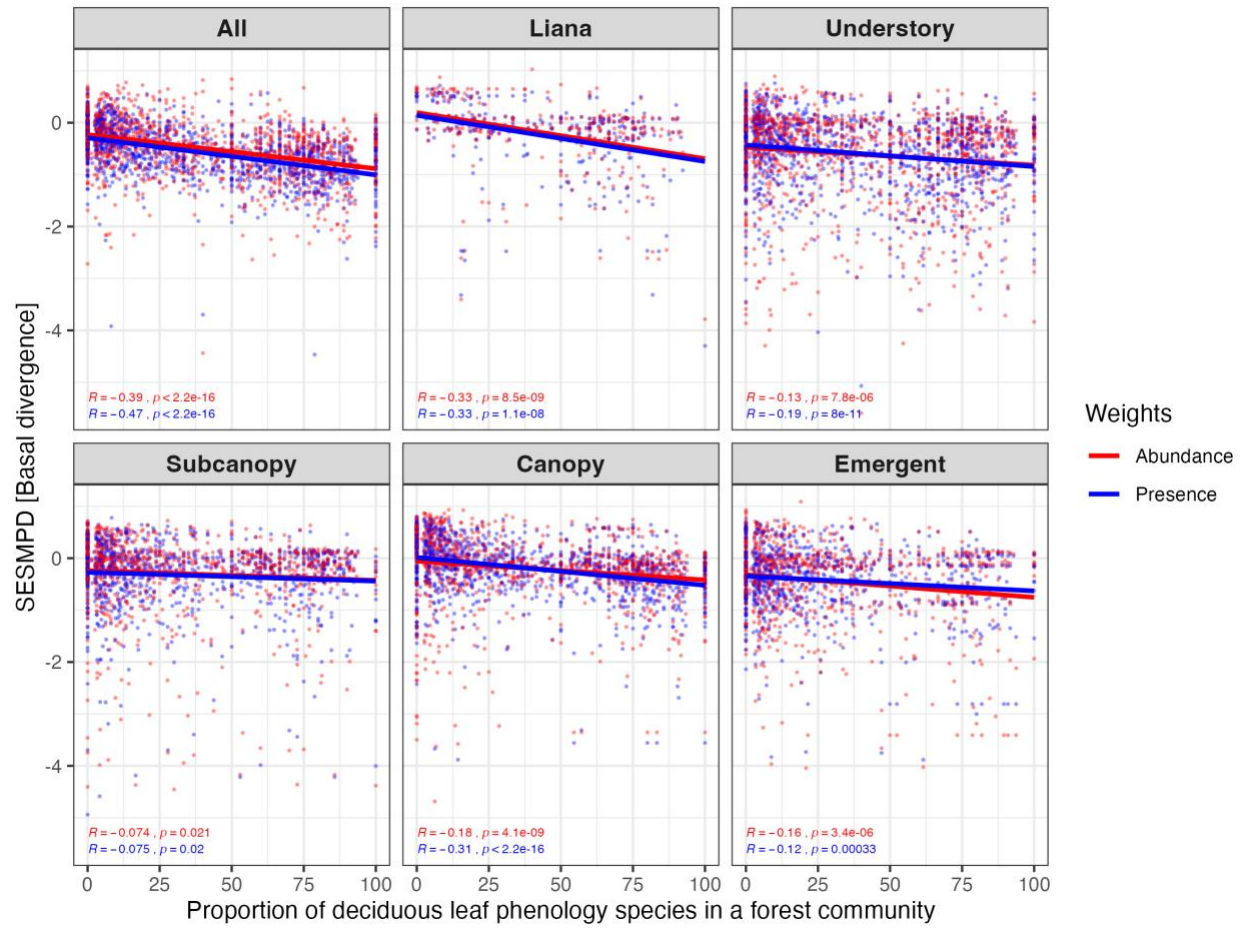


Figure 13: Relationship between deciduousness and the standardized effect size of mean pairwise distance (SESMPD) for a different forest stratum, including all strata combined (All), Liana, Understory, Subcanopy, Canopy, and Emergent. The blue and red lines represent results from models without weights presence and weighted by abundance respectively.

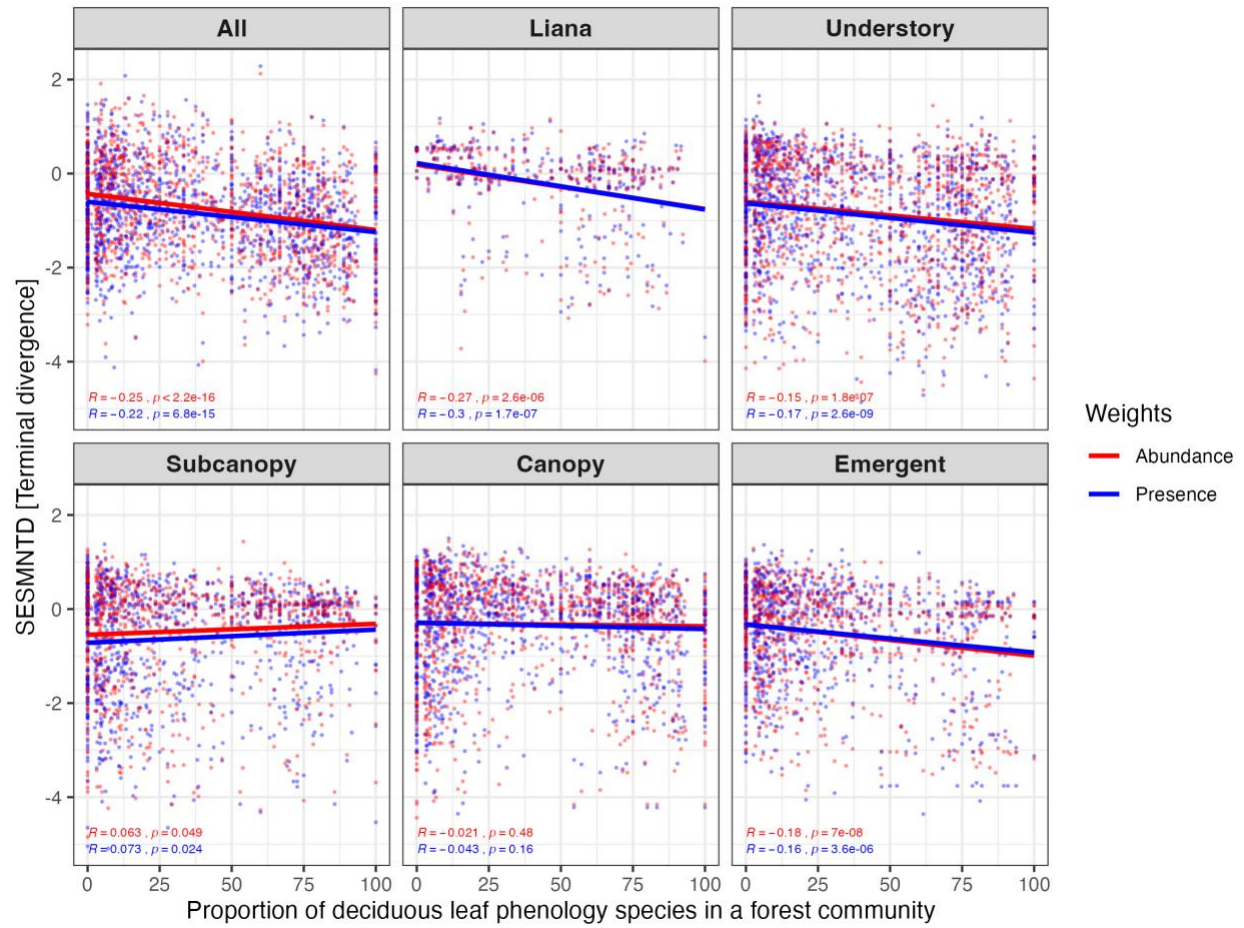


Figure 14: Relationship between deciduousness and the standardized effect size of mean nearest taxon distance (SESMNTD) for a different forest stratum, including all strata combined (All), Liana, Understory, Subcanopy, Canopy, and Emergent. The blue and red lines represent results from models without weights presence and weighted by abundance respectively.

Chapter 2 - Structurally Dominant Tree Species and Their Evolutionary Diversity Drive Aboveground Carbon Storage in Tropical Forests

2.1 Introduction

Woody plants in the tropical forest ecosystem due to equatorial climate including warmer temperature and higher precipitation, are rich in taxonomic, functional and evolutionary diversity (Slik et al. 2015; 2018). But also play a crucial role in regulating the global carbon cycle by sequestering more than 40% of atmospheric carbon through higher rates of plant productivity acting as a largest atmospheric carbon sink (Joseph Wright 2013; Phillips and Lewis 2014; Pan et al. 2011; Hubau, Lewis, Phillips, Affum-Baffoe, Zemagho, et al. 2020). However, within equatorial climates, temperature and precipitation seasonality, induced by the effects of latitude and topography also known as climatic or environmental stress determine the spatial distribution of diversity and carbon stocks by influencing growing conditions of woody plants (Jucker et al. 2018; Shen et al. 2016; Shivaprakash et al. 2018; Bose et al. 2019). The article 2.1 of the Kyoto Protocol addressed the rising concerns of global warming and assigned responsibility to signatory countries to protect sinks and reservoirs of greenhouse gases, increase afforestation, reforestation, and promote sustainable forest management. However, an understanding of the spatial distribution and temporal dynamics of above ground carbon (AGC) is a prerequisite for determining the sources and sinks of carbon, and few studies have examined forest biomass and carbon dynamics. Precise assessments of CO₂ emissions at the species level resulting from land-use changes, forest fire, degradation, and other anthropogenic activities are difficult to accomplish through remote sensing techniques. Therefore, ground data is needed to obtain a detailed understanding of regional carbon cycles and to enact related policies. International climate change mitigation initiatives such as Reducing Emissions from Deforestation and Forest degradation (REDD+) aim to strengthen terrestrial carbon storage by incentivizing forest conservation and restoration. These climate-focused measures have the potential to provide additional co-benefits for carbon stocks and biodiversity conservation in tropical forests through detailed understanding of underlying biotic and abiotic ecological processes. Therefore, this study focuses on understanding the role of biodiversity on above ground carbon accumulation by woody plants in tropical forest communities.

Taxonomic diversity metrics alone have limited ability to explain the spatial distribution patterns of aboveground biomass and carbon in tropical forests because they often do not account for functional diversity, which directly impacts biomass accumulation and carbon storage through variations in traits such as wood density and leaf area, which directly affect survival and growth rates by occupying a unique ecological niche in the tropical forest ecosystem (Cadotte and Davies 2016). For example, within tropical forests, species individuals with larger leaf area and lower wood density tend to grow faster and live for only a short time, thus accumulating less AGC, whereas species individuals with smaller leaf area and higher wood density tend to grow slower and live longer, thereby accumulating higher levels of (Cadotte et al. 2011). Niche complementarity hypothesis suggests that different species occupying distinct ecological niches can more efficiently utilize resources, thereby leading to higher productivity and improved carbon sequestration

(Cadotte et al. 2008). In addition, the sampling or selection or mass ratio hypothesis postulates that variation of ecosystem functions including above ground carbon storage is mainly determined by few dominant species with particularly distinctive functional traits, such as high growth rates or efficient carbon storage (Cadotte et al. 2008). However, identifying and determining all relevant functional traits responsible for woody plants survival and growth and subsequently defining above ground carbon dynamics including influencing the spatial distribution patterns in tropical forest are difficult, time consuming and expensive (Cadotte and Davies 2016). However, ecological adaptations are shaped by the environment and biological interactions experienced by the ancestors of modern taxa, as all organisms are products of their evolutionary history. Because of similar resource use by common ancestors, competition within closely related species is stronger than competition between distantly related species, which in turn influence species coexistence (Darwin 1859; Elton 1946; Williams 1964; Simberloff 1970; Enquist et al. 2002). Basically, the idea is that closely related species have similar trait values due to a shared evolutionary history, making them similar ecologically and in their niche preferences (Macarthur and Levins 1967). This pattern of shared niche preferences and characteristics of closely related taxa is called phylogenetic conservatism (Wiens and Graham 2005). Therefore, first, assuming phylogenetic conservatism, the phylogenetic relatedness of species in a community can be used as a proxy for functional trait relationships. Second, phylogenetic niche conservatism assumes that functional traits of species are conserved between ancestors and descendants and are therefore linked with phylogeny. Based on this link, species in a community can be either phylogenetically clustered or overdispersed (Webb, Ackerly, McPeck, et al. 2002). In phylogenetic clustering, species present in a community are more closely related to each other than would be expected by chance. Therefore, they are expected to consist of closely related species with similar niche preferences and to arise primarily through environmental filtering, whereby the environment selects species from a larger species pool or filters them into the observed community based on whether species possess suitable characteristics to establish and survive in an environment (Webb, Ackerly, McPeck, et al. 2002). In contrast, species in a phylogenetically overdispersed community are more distantly related to each other by chance and are therefore expected to have different niche preferences, primarily due to limited similarity, with closely related species tending to be mutually exclusive because they occupy similar niches (Webb, Ackerly, McPeck, et al. 2002). The phylogenetic relationships of species in communities can provide insights not only into the processes that structure community assembly, but also the relative contribution of stochastic and deterministic mechanisms in determining the observed pattern of species composition (Webb, Ackerly, McPeck, et al. 2002; Tucker et al. 2017).

Incorporating abundance and structural dominance-weighted measures aligns with the selection and mass-ratio hypotheses by highlighting the role of dominant species in ecosystem processes like carbon storage (Tucker et al., 2017). The selection hypothesis suggests biodiverse communities likely include species with beneficial traits, while abundance-weighted measures focus on how prevalent species with traits enhancing carbon sequestration drive ecosystem functions. Structurally dominant metrics, emphasizing tree size and biomass, complement this by showing

how the traits of larger trees influence carbon storage, reflecting the mass-ratio hypothesis. This combined approach offers a comprehensive view of biodiversity's role in ecosystem functioning, particularly in mature forests where large trees are vital (Lutz et al., 2018). Integrating these metrics bridges theoretical and empirical insights into how biodiversity shapes ecosystem processes.

Carbon-biodiversity co-benefits can occur in areas where priority locations for carbon storage overlap with locations of high biodiversity and human dominated landscapes including biodiversity hotspots (Osuri et al. 2020). Therefore, analysing the relationship between above ground biomass carbon stocks and diversity metrics at taxonomic, functional and phylogenetic levels is not only important to understanding spatial distribution patterns of above ground carbon but also crucial for predicting consequences of natural and anthropogenic induced changing climate on above ground carbon stocks in biodiversity hotspots (Chisholm and Dutta Gupta 2023).

Although there are many studies explaining the biotic and abiotic mechanisms determining distribution and abundance of deciduous and evergreen trees (Shivaprakash et al. 2018) there is a lack of empirical evidence on how above-ground carbon relationships differ across forest types. Moreover, the contributions of niche complementarity and the selection or mass-ratio hypotheses to biodiversity effects on carbon are not yet fully understood.

However, environmental variables such as altitude, temperature, and precipitation seasonality can obscure or distort these relationships between biodiversity and carbon. At higher altitudes, lower temperatures may limit plant growth and carbon storage, even in areas with high biodiversity, while lower altitudes with more favourable growing conditions might store more carbon despite lower biodiversity. Likewise, temperature fluctuations can affect species growth rates, and rainfall seasonality can influence water availability, which in turn impacts carbon storage potential. These environmental factors create variations in how biodiversity affects carbon storage, emphasizing the importance of incorporating such variables into models of carbon storage and biodiversity to develop more effective climate change mitigation strategies (Chisholm and Dutta Gupta 2023).

I hypothesize that lower environmental stress and increased co-occurrence of evolutionarily distantly related woody plant species enhance above-ground carbon stocks and carbon accumulation rates in forest communities. Conversely, higher environmental stress and increased co-occurrence of evolutionarily closely related woody plant species reduce these carbon-related outcomes (Figure 15).

I predict that forest plots characterized by low environmental stress and higher phylogenetic distance among co-occurring species will have measurably higher AGC stocks and accumulation rates compared to plots with high environmental stress and lower phylogenetic distances (Figure 15).

2.2 Methods

2.2.1 Data description

I have estimated community-level above-ground carbon stocks (AGC) and taxonomic, functional and phylogenetic diversity metrics from 111 1-ha undisturbed inventory plots in the Western Ghats biodiversity hotspot in southern India (Figure 16). Within 1 ha of inventory plots, (Ramesh et al. 2010; Ganesh et al. 1996; Ayyappan and Parthasarathy, n.d.; 2004; Péliissier et al. 2011), R Ganesan (Unpublished) and Soundarpandian (Unpublished) documented diameter at breast height (DBH) including the species names of all tree individuals with a diameter of at least 10 cm DBH.

2.2.2 Estimation of above ground biomass and carbon

Above-ground biomass (AGC_{est} , in mega grams Mg) was estimated using the following general equations (Chave et al. 2014) that have been commonly used for tropical forest trees :

$$AGB_{est} = 0.0673(\rho D^2 H)^{0.976}$$

where D is the tree diameter at breast height (DBH cm), ρ is the wood density (g/cm^3) and H is the tree height in (m). Carbon stocks were assumed to account 47.78% of above ground biomass, which is consistent with stem carbon content estimates of evergreen trees (Ma et al. 2018). AGB was estimated using the functions available in the *BIOMASS* R package (Réjou-Méchain et al. 2017).

2.2.3 Environmental variables

I have used the *sp* and *raster* packages in R to obtain mean annual temperature and precipitation data for each plot from the *WorldClim* data set (<https://www.worldclim.org>) and elevation from *elevatr* r package. I have estimated Chave's Environmental stress using the *computeE* function in the *BIOMASS* r package. (Chave et al. 2014) developed the Environmental Stress (CES) framework to explain how environmental factors, particularly climatic water deficit (CWD) and temperature and precipitation seasonality extremes, shape tree growth and survival.

$$E = 1.e - 3 * (0.178 * TS - 0.938 * CWD - 6.61 * PS)$$

Here environmental stress that compounds temperature seasonality (TS), climate water deficit (CWD) and precipitation seasonality (PS), as defined in the *WorldClim* data set (<https://www.worldclim.org>).

2.2.4 Functional traits diversity

I have collected functional trait values for maximum attainable diameter and height, wood density, leaf area, leaf nitrate mass, leaf mass area and seed diaspore mass. I have estimated the maximum attainable diameter and height from the dataset. Wood density, leaf area, leaf nitrate mass, leaf mass area and seed diaspore mass were determined from (Díaz et al. 2022). The dataset on functional traits of tree species reveals the extent of data availability at both species and genus levels for various ecological traits. For traits like Leaf Area, Leaf Nitrogen Mass, and Leaf Mass per Area, a

substantial portion of the data is available at the species level, covering 82%, 78%, and 79% of species respectively, highlighting the need for further data at the species level (Table 12).

I have estimated community weighted mean of functional traits including the weights of presence (unweighted), abundance and carbon (instead of basal area) using “*weighted.mean*” function from “*dplyr*” R package. I used abundance and carbon weights as an indicator of plants performance. Because I found species like *Terminalia anogeiessiana* in dry forests and *Agrostistachys boornensis* are highly abundant but structurally smaller in size but accumulate and stock large quantities of AGC with their sheer abundance. However, species like *Cullenia exarillata* and *Vateria indica* are as large statured trees stocking large proportions of AGC. I found variations among unweighted; abundance and size weighted community means (CWM) (Figure 17 & 18).

I have also estimated unweighted, abundance and carbon weighted functional richness, divergence, evenness and dispersion metrics using “*dbFD*” function from “*FD*” R package. I found variations among unweighted; abundance and size weighted functional diversity metrics (Figure 19 & 20).

2.2.5 Phylogeny reconstruction

Same as section 1.2.3 (Figure 20 & 21)

2.2.6 Phylogenetic signal

Phylogenetic signal quantifies the extent to which phylogeny predicts ecological similarity between species. This signal is measured using the K statistic, which compares the observed trait signal with that expected under a Brownian motion model of trait evolution in a phylogeny (Blomberg et al. 2003). A “K” value of 1 indicates some degree of phylogenetic signal or conservatism, values greater than 1 indicate strong phylogenetic signal and trait conservatism, while values closer to zero indicate a random or convergent evolutionary pattern. The statistical significance of the phylogenetic signal is assessed by comparing the observed variance in independent contrasts of the trait with a null model that includes taxonomic marker change across phylogeny tips. This evaluation is implemented using the “*phylosignal*” function from “*picante*” R package.

2.2.7 Phylogenetic diversity metrics

It is similar to section 1.2.4. However, I have included abundance and carbon-based size weights in estimations of functional traits community weighted mean (CWM), and phylogenetic (mean pairwise distance (MPD) and mean nearest taxon distance (MNTD)) diversity metrics. The difference between abundance and size weighted and unweighted standardized effect size (MPD and MNTD) metrics, lies in how they account for species abundance and size in their calculations. Unweighted MPD and MNTD based on presence-based distance matrix reflects the overall phylogenetic structure of a community. In contrast, abundance-weighted MPD and MNTD modify these calculations by weighting the distances by the relative abundance of each species, meaning that more abundant species have a greater influence on the overall metric. When incorporating carbon-based size weights into these metrics, the focus shifts to the stand structural dominance of species. AGC-weighted MPD and MNTD account for the carbon stored in the above-ground parts

of each woody plant or tree species, thereby adjusting the metric to reflect the influence of species with greater structural dominance (size) on the phylogenetic structure (Figure 22 & 23). This approach highlights how dominant species in terms of both abundance and size shape the community's phylogenetic diversity. Essentially, unweighted metrics provide a comprehensive overview of phylogenetic diversity, while abundance-weighted and size weighted metrics offer deeper insights into how species abundance and size influence phylogenetic composition of a community.

2.2.8 Statistical analysis

To examine the strength of the relationship between above ground carbon (AGC) and functional and phylogenetic diversity metrics, I conducted generalized least squares modelling (GLS) using functions from “*nlme*” R package (Pinheiro et al. 2017). Environmental variables also influence ecosystem's diversity and carbon regulation and therefore obscure relationships between diversity and ecosystem function. To account for the effects of environmental variables, I constructed GLS models in which AGC was modelled as a function of Chave's environmental stress (CES) and elevation as base model accounting for confounding effects of environment and then CWM, functional and phylogenetic diversity metrics were added. All environmental and diversity variables with differing units of measurement were standardized using the “scale” function, which centers and scales the data to produce uniform values ranging from -1 to +1. To avoid multicollinearity among variables in the model, Pearson correlation coefficients (maintained below $R = 0.7$) and variance inflation factors ($VIF < 5$) were examined for all explanatory variables (Figures 24-26 & Table 13). I detected spatial autocorrelation by Moran's I test, Moran's scatter plot and variogram, and accounted for spatial autocorrelation in the GLS analyses by specifying a “Rational” spatial correlation structure, consistent with the shape of the semi-variograms for AGC across network of plots (Figures 27 & 28, Table 14).

2.3 Results

Above-ground carbon (AGC) stocks, species richness, functional richness and phylogenetic diversity were significantly higher in evergreen forests than in deciduous forests (Figure 29 and Table 15).

2.3.1 Phylogenetic Signal

Phylogenetic signal, assessed using Bloomberg's K statistic, revealed the degree to which phylogeny predicts ecological similarity among species. Several functional traits, including maximum DBH, maximum height, wood density, leaf area, leaf nitrate mass, seed diaspore mass, and AGC, exhibited significant phylogenetic signals ($K > 0$, $P < 0.05$) (Table 16). This indicates phylogenetic conservatism, where closely related species share similar traits. For instance, species with shared evolutionary ancestry tended to have similar maximum DBH and wood density, reflecting the evolutionary constraints on growth and carbon storage potential. Conversely, traits like leaf mass per area (LMA) displayed no significant phylogenetic signal, suggesting these traits are shaped more by environmental factors or convergent evolution than by phylogenetic lineage.

2.3.2 Independent effects of functional and phylogenetic diversity on AGC

Generalized least squares analysis was used to disentangle the independent effects of functional, and phylogenetic diversity metrics on AGC storage while accounting for elevation and Chave's Environmental Stress (CES) (Figure 30, Tables 17-20). The analysis incorporated spatial correlation structure to reduce the influence of spatial autocorrelation. The base model, incorporating only CES and elevation, explained 35.44% of the variation in AGC (Table 17). CES showed a significant negative effect on AGC stocks, reflecting the adverse impact of temperature and precipitation seasonality on carbon accumulation (Table 17). Community-weighted means revealed diverse effects on AGC. Wood density (abundance- and size -weighted) negatively influenced AGC, suggesting trade-offs between structural integrity and carbon storage in communities dominated by dense wood species (Table 18). In contrast, seed diaspore mass (unweighted and abundance-weighted) and maximum attainable height (size weighted) positively influenced AGC, emphasizing the role of reproductive and growth traits in carbon sequestration. I found variations among unweighted, abundance and carbon weighted functional diversity indices (Figure 17-20). Functional richness significantly enhanced AGC across all weighting schemes, demonstrating the importance of trait diversity in promoting ecosystem functioning (Table 19). However, size-weighted functional dispersion had a negative effect, indicating that excessive trait variability may not always optimize carbon sequestration (Table 19). I found variations among unweighted, abundance and carbon weighted phylogenetic diversity indices (Figures 22-23). SES MPD positively influenced AGC stocks across all models, particularly in the size-weighted model, highlighting the importance of phylogenetic relatedness and recognizing the breadth of functional traits in enhancing ecosystem function. SES MNTD showed no significant effects, suggesting that fine-scale phylogenetic relatedness may have limited relevance to AGC (Table 20).

2.3.3 Additive Effects of Diversity Metrics on AGC

The stepwise variance partitioning analysis shows the progressive contribution of environmental, functional, and phylogenetic diversity components to variation in above-ground carbon (AGC) storage, while accounting for the confounding effects of environmental variables on these metrics. Environmental variables alone explained 35.44% of the variance. Adding Community-Weighted Means (CWM) increased the explained variance to 48%, indicating that species' functional traits improve model performance beyond environmental effects. Unweighted and abundance-weighted functional diversity contributed modestly (5.55% and 5.76%), suggesting a limited yet distinct role of trait diversity in carbon storage. Phylogenetic diversity had a stronger effect: unweighted and abundance-weighted metrics raised the explained variance to 52.37% and 54.38%, respectively. The final model combining all predictors environmental, functional, and phylogenetic explained 58.55% of AGC variation. Models integrating both functional and phylogenetic diversity achieved the lowest AIC and highest R^2 values (Table 21). The abundance-weighted model reduced AIC by 20.63, and the size-weighted model by 22.76, highlighting the superior predictive performance of size-weighted models and the ecological importance of carbon allocation. Overall, while environmental factors dominate AGC variation, functional and phylogenetic diversity provide complementary insights, revealing how trait composition and evolutionary history together shape carbon storage in forest communities.

2.4 Discussion

The analysis reveals intricate relationships between Above-Ground Carbon (AGC) and various diversity metrics, with significant implications for understanding how functional and phylogenetic diversity and relatedness of abundant and structurally dominant species influence carbon storage in tropical forest ecosystems particularly in Western Ghats biodiversity hotspot. This study, employing generalized least squares (GLS) models and accounting for spatial autocorrelation, offers a comprehensive view of these relationships while controlling for the confounding effects of environmental variables such as Chave's Environmental Stress (CES) and elevation. The base model, incorporating only CES and elevation, explained 35.44% of the variation in AGC (Table 17). The significant negative effect of CES on AGC suggests that as environmental stress increases, the capacity of trees to store carbon diminishes. This can be attributed to the physiological strain that stress factors such as temperature and precipitation seasonality, climatic water deficit and prolonged dry periods place on trees, limiting their growing degrees days, growth rates, biomass production, and overall carbon sequestration potential (Hubau, Lewis, Phillips, Affum-Baffoe, Zemagho, et al. 2020; Meakem et al. 2018; Anderegg et al. 2013). On the other hand, the positive effect of elevation on AGC suggests that higher altitudes may provide more favourable conditions for carbon storage. This could be due to factors like historical stable climatic conditions, cooler temperature, higher rainfall and reduced human disturbance at higher elevations, which can promote increased tree growth and survival and thus biomass accumulation and overall carbon sequestration (Mani and Parthasarathy 2007; Jucker et al. 2018; Lee et al. 2015).

Taxonomic diversity metrics alone have limited ability to explain the spatial distribution patterns of aboveground biomass and carbon in tropical forests because they often do not account for phenotypic variations or functional diversity, which directly impacts biomass accumulation and carbon storage through variations in traits such as wood density and leaf area, which directly affect survival and growth rates by occupying a unique ecological niche in the tropical forest ecosystem (Cadotte et al. 2008). For example, within tropical forests, species individuals with larger leaf area and lower wood density tend to grow faster and live for only a short time, thus accumulating less aboveground carbon, whereas species individuals with smaller leaf area and higher wood density tend to grow slower and live longer, thereby accumulating higher levels of above ground carbon (Cadotte et al. 2011).

The community abundance and size weighted mean of wood density demonstrates significant negative effects on carbon stocks, aligning with the mass ratio hypothesis and also highlighting a critical trade-off (Table 18). Communities dominated by species with denser wood exhibit lower carbon stocks compared to those with softer wood. This dynamic is particularly evident across forest types, where denser wood is more prevalent in dry forests and softer wood in evergreen forests.

This pattern can be explained with three ecological mechanisms. First, in dry forests, climatic water deficit imposes significant hydraulic constraints on trees. To enhance survival under these conditions, species prioritize structural investment by producing denser wood, which confers

greater mechanical strength and drought resilience (Prado-Junior et al. 2016). However, this prioritization come at a cost of reduced biomass accumulation and consequently carbon stocks (Becknell et al. 2021; de Meira Junior et al. 2020). Second, high fire frequency in dry forests further amplifies the selection of denser wood. Denser wood is less flammable and contributes to post fire survival, yet this adaptation reduces the ability to sequester additional carbon, as slow growing, fire resistant species dominate (Kodandapani et al. 2008; Otterstrom et al. 2006; Pulla et al. 2015). Third, the intrinsic trade-off between structural investment and growth rate highlights the observed pattern. While denser wood enhances longevity and persistence, it limits the capacity for rapid biomass turnover and carbon uptake, contrasting sharply with the faster dynamics of softer wood species in evergreen forests.

Thus, have following implications for forest carbon storage. In evergreen forests, with lower water deficit and fire frequency, species in evergreen forests invest less in structural density, resulting in softer wood. This allows for faster growth and higher biomass turnover, leading to more rapid carbon accumulation. In contrast the dominance of dense wood species in dry forests contributes to slower carbon accumulation despite potentially longer-term carbon storage. This pattern reflects the ecological trade off imposed by environmental stressors such as water deficit and fire.

This hypothesis integrates the complex interplay of biotic traits and abiotic pressers in shaping forest carbon dynamics. It suggests that dense wood species while critical for ecosystem stability in stressful environments, constrain the pace of carbon sequestration, these findings underscore the need to consider trait environment interaction when evaluating forest carbon dynamics across biomes.

The community unweighted and community abundance weighted means of seed diaspore mass exhibited significant positive effects on AGC stocks, aligning with the mass ratio hypothesis (Table 18). This hypothesis suggests that dominant species with traits maximizing ecosystem functions disproportionately drive carbon stocks. Large seed diaspore mass is strongly linked with large stature trees, which are characterised by slow growth, long life spans, and substantial carbon accumulation capabilities (Lohbeck et al. 2015).

Large seed diaspores are linked with large stature, longevity and resilience and enhanced reproductive success (Nerlekar et al. 2019). Species with large seeds, like *Cullenia exarillata* and *Palaquium ellipticum*, grow into slow-growing long-living trees with substantial structural biomass (Ganesh et al. 1996). These species exhibit low mortality rates and contribute to stable carbon storage over extended periods. Larger seed provide nutrient reserves for seedling establishment, ensuring higher survival rated in competitive environments (Ganesan 2001; Selwyn and Ganesan 2009).

Larger seed diaspores are often dispersed by large mammals and birds, such as the endemic and endangered lion tailed macaques (Ganesh 1995; Ganesh and Davidar 2001; 1999). These dispersal agents facilitate long distance seed transport, reducing negative neighbourhood density effects of conspecifics on seedling survival and growth (Seidler and Plotkin 2006). This process helps

maintain forest genetic diversity by reducing the chances of inbreeding and, further enhancing AGC stocks.

Dominant tree species like *Cullenia exarillata* and *Palaquium ellipticum* play a pivotal role in AGC accumulation, storing significantly higher quantities of carbon per hectare per year compared to other tree species in the study. These trees, dispersed by lion tailed macaques, form a critical component of the forest carbon storage potential. Their contribution emphasizes the interconnectedness of biodiversity, species traits and ecosystem processes (Ganesh and Davidar 1999).

The resilience of large seed species on faunal dispersers underscores the importance of maintaining animal populations in tropical forests. Defaunation caused by habitat destruction, hunting and climate change can disrupt seed dispersal networks (Bello et al. 2015; Harrison et al. 2013). This in turn limits the recruitment of large seed species, reducing the forest's capacity for carbon storage and accumulation. studies have shown that forests with reduced densities of large seed dispersed exhibit shifts toward species with smaller seeds, which may store less carbon over time (Osuri et al. 2016). Protecting large arboreal mammals and birds is therefore essential for maintaining tropical forest carbon dynamics (Chanthorn et al. 2019).

The positive effects of seed diaspore mass on AGC accumulation underscore the critical role of large seed species in tropical forest carbon dynamics. Species like *Cullenia exarillata* and *Palaquium ellipticum* exemplify how ecological traits and faunal interactions drive carbon storage processes. However, the disruption of these interactions through defaunation threatens to undermine forest resilience and carbon sequestration (Chanthorn et al. 2019). Conservation strategies must prioritise protecting key dispersers, like lion tailed macaques, and their habitats to sustain the ecological and carbon storage functions of tropical forests (Devy and Ganesh 2021).

Functional diversity metrics had varied impacts on AGC stocks (Table 19). Functional richness emerged as a strong predictor. This suggests that greater functional diversity, indicating a wider range of functional traits, enhances carbon storage, potentially due to complementary resource use and niche differentiation among species (Mensah et al. 2016; Shen et al. 2016). On the other hand, functional diversity metrics such as functional evenness, divergence and dispersion did not significantly influence AGC, possibly due to their lesser direct role in influencing AGC storage compared to functional richness. Additionally, I documented lesser functional traits at the species level, which may be why I did not detect a significant impact of functional diversity metrics on AGC. However, identifying and determining all relevant functional traits responsible for woody plants survival and growth and subsequently defining above ground carbon storage in tropical forest are difficult, time consuming and expensive (Cadotte and Davies 2016). However, ecological adaptations are shaped by the environment and biological interactions experienced by the ancestors of modern taxa, as all organisms are products of their evolutionary history. Because of similar resource use by common ancestors, competition within closely related species is stronger than competition between distantly related species, which in turn influence species coexistence. Basically, the idea is that closely related species have similar trait values due to a shared

evolutionary history, making them similar ecologically and in their niche preferences (Macarthur and Levins 1967). Therefore, the total amount of phylogenetic diversity represented by species within a community is invaluable predictor of carbon storage capacity in tropical forest. This is because evolutionary relationships can capture information about multiple traits including those that are difficult to measure like root architecture and root morphology. Evolutionary diversity metrics that encompass the full breadth of functional diversity may be more informative about how much species contribute to carbon storage capacity, particularly in biodiversity hotspots including tropical forests where the links between soft functional traits including specific leaf area and wood density and ecosystem functions including carbon sequestration are typically weak (Fauset, Michelle O Johnson, et al. 2015; Bordin et al. 2023)

Standardized effect size (SES) phylogenetic mean pairwise distance (MPD) including unweighted, abundance and size weighted versions had significant positive effects on AGC storage within tropical forest of western ghats biodiversity hotspot (Figure 30 & Table 20). Meaning increasing co-occurrence of evolutionary distantly related species in a forest community are having higher above ground carbon stocks by efficient resource partitioning through meticulously occupying unique niche space (Souza et al. 2019). Thus, fulfilling the niche complementarity hypothesis. Furthermore, evolutionary distant, abundant and structurally dominant species in a tropical forest community acquire larger carbon stocks. Thus fulfilling mass ratio hypothesis (Aguiar-Campos et al. 2021; Kunwar et al. 2021; Mensah et al. 2024).

2.5 Conclusion

My study provides comprehensive evidence that functional traits, phylogenetic relatedness, and species dominance together shape the spatial patterns of above-ground carbon (AGC) storage in tropical forests of the Western Ghats. By integrating generalized least squares (GLS) models with spatial correlation structures, I demonstrate that both abiotic stress gradients and biotic diversity patterns strongly regulate carbon dynamics. Environmental stress, particularly climatic water deficit, constrains biomass accumulation and carbon storage, whereas elevation provides a buffering effect, likely due to historically stable climates, cooler conditions, and reduced anthropogenic disturbance.

Functional trait analyses underscore the dual roles of wood density and seed diaspore mass in shaping AGC. While communities dominated by dense-wood species exhibit resilience to drought and fire, their carbon accumulation is limited by slow growth rates, illustrating a key trade-off between survival under stress and carbon sequestration potential. In contrast, large-seeded species contribute disproportionately to long-term and stable carbon storage, not only because of their large structural biomass and longevity but also due to their reliance on animal-mediated dispersal, which enhances recruitment and resilience. These findings highlight the interdependence of plant functional traits and faunal dispersal networks in sustaining carbon storage potential, with defaunation posing a serious risk to long-term forest carbon dynamics.

Phylogenetic analyses further reveal that evolutionary diversity is a strong predictor of AGC. Communities with greater phylogenetic divergence store more carbon, consistent with the niche complementarity hypothesis, whereby distantly related species partition ecological resources more efficiently. At the same time, abundant and structurally dominant species disproportionately drive carbon stocks, providing support for the mass ratio hypothesis. Together, these results indicate that both the breadth of evolutionary lineages and the dominance of functionally important species must be considered when evaluating forest carbon storage potential.

In conclusion, my findings emphasize that conserving and restoring tropical forests requires a dual focus on maintaining functional and phylogenetic diversity as well as protecting keystone species and their faunal dispersers. These results have direct implications for climate mitigation and biodiversity conservation strategies in tropical forest biomes. By safeguarding the evolutionary and functional dimensions of biodiversity, particularly in biodiversity hotspots like the Western Ghats, the resilience and long-term carbon sequestration capacity of tropical forests under changing environmental conditions can be enhanced.

2.5 Figures and Tables

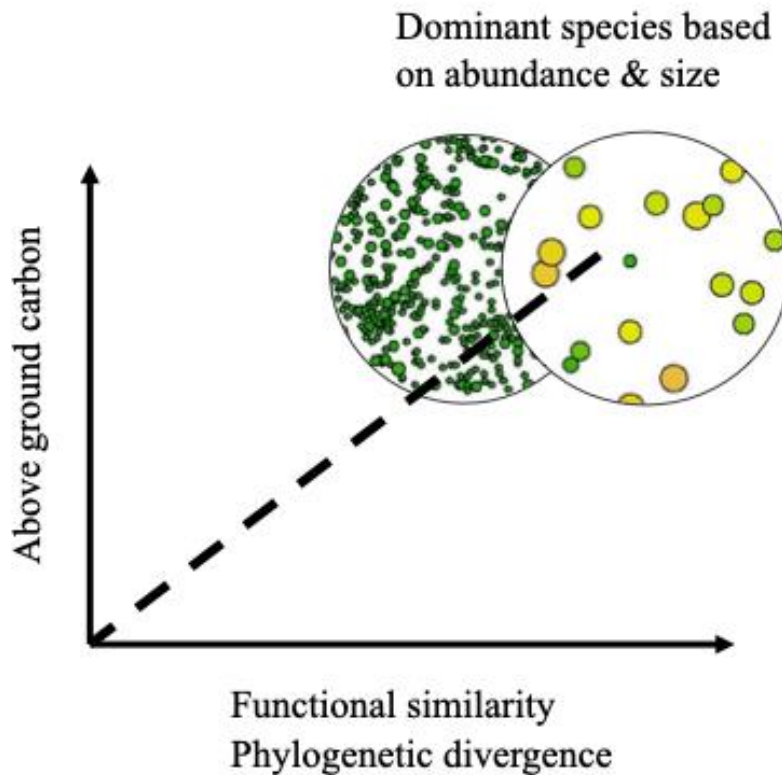


Figure 15: Conceptual framework linking functional and phylogenetic divergence, environmental stress, and above ground carbon dynamics. Forest sites experiencing lower environmental stress and greater co-occurrence of evolutionarily distant woody plant species are hypothesised to exhibit higher above ground carbon (AGC) stocks. In contrast, plots under higher environmental stress with greater co-occurrence of closely related species are predicted to show reduced AGC stocks.

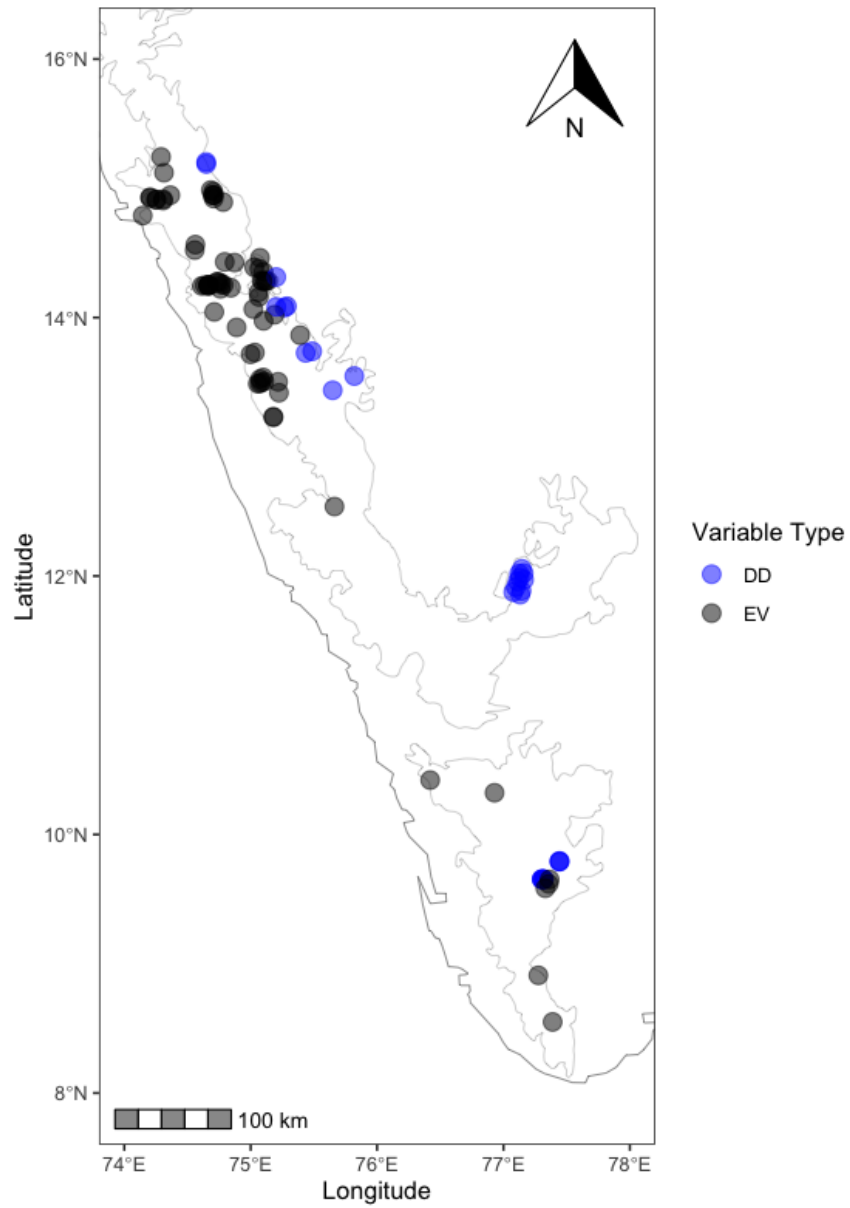


Figure 16: Map showing the locations of 111 one-hectare forest plots across the western ghats, India (gray boundary). Deciduous plots are indicated in blue and evergreen plots in black.

Table 12: Summary of functional trait data availability at the species level for 592 woody plant species across 111 one-hectare plots in the Western Ghats.

Functional traits	Species level	%
Maximum height (Max H)	592	100
Maximum diameter (Max DBH)	592	100
Wood density (WD)	592	100
Leaf area (LA)	121	20.43
Leaf nitrate mass (LNM)	105	17.73
Leaf mass area (LMA)	86	14.52
Seed Diaspore Mass (DM)	181	30.57

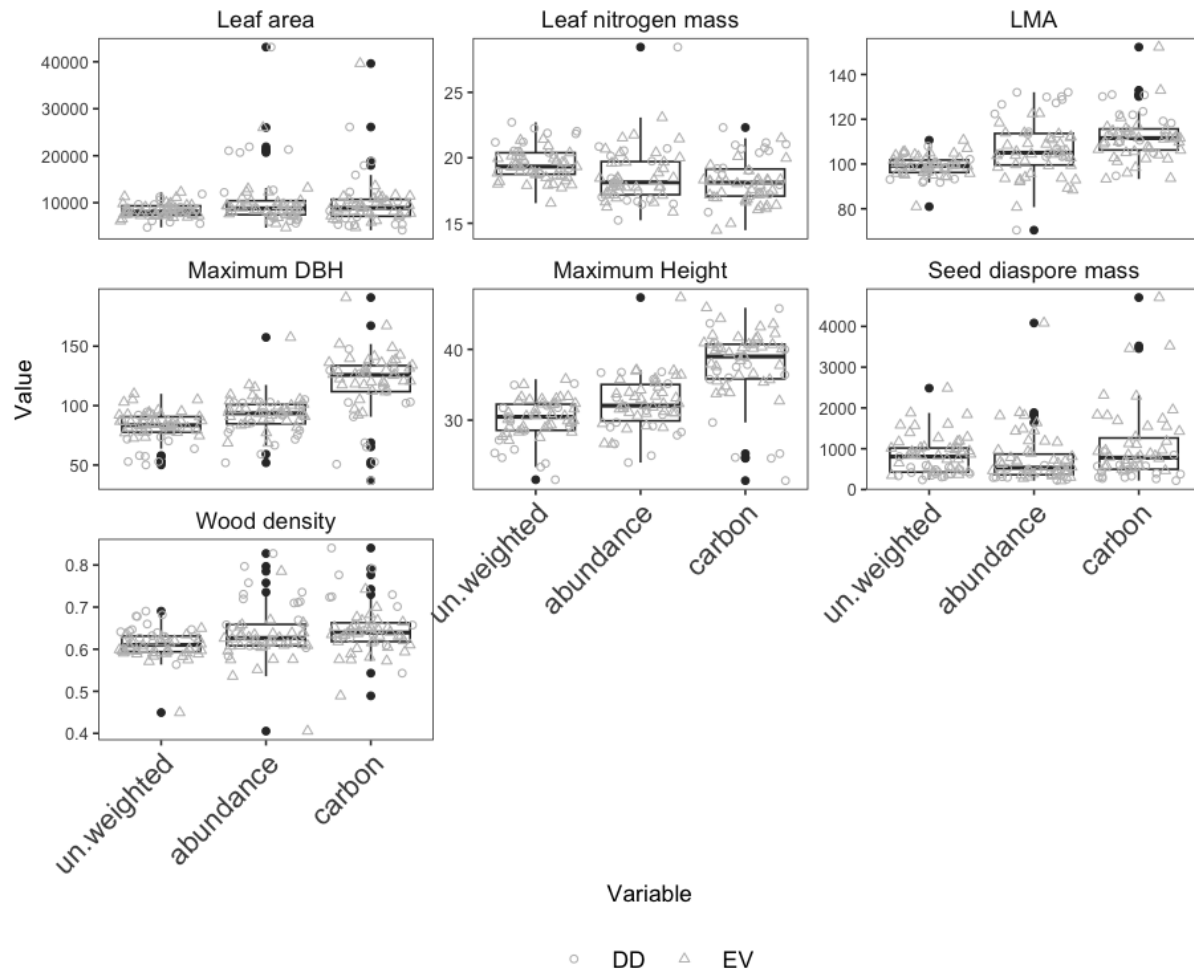


Figure 17: Boxplots showing variations in community-weighted means (CWMs) of functional traits under three weighting schemes: unweighted (presence-absence), abundance-weighted, and size-weighted. Traits include maximum height (Max H), maximum diameter (Max DBH), wood density (WD), leaf area (LA), leaf nitrate mass (LNM), leaf mass per area (LMA), and seed diaspore mass (DM).

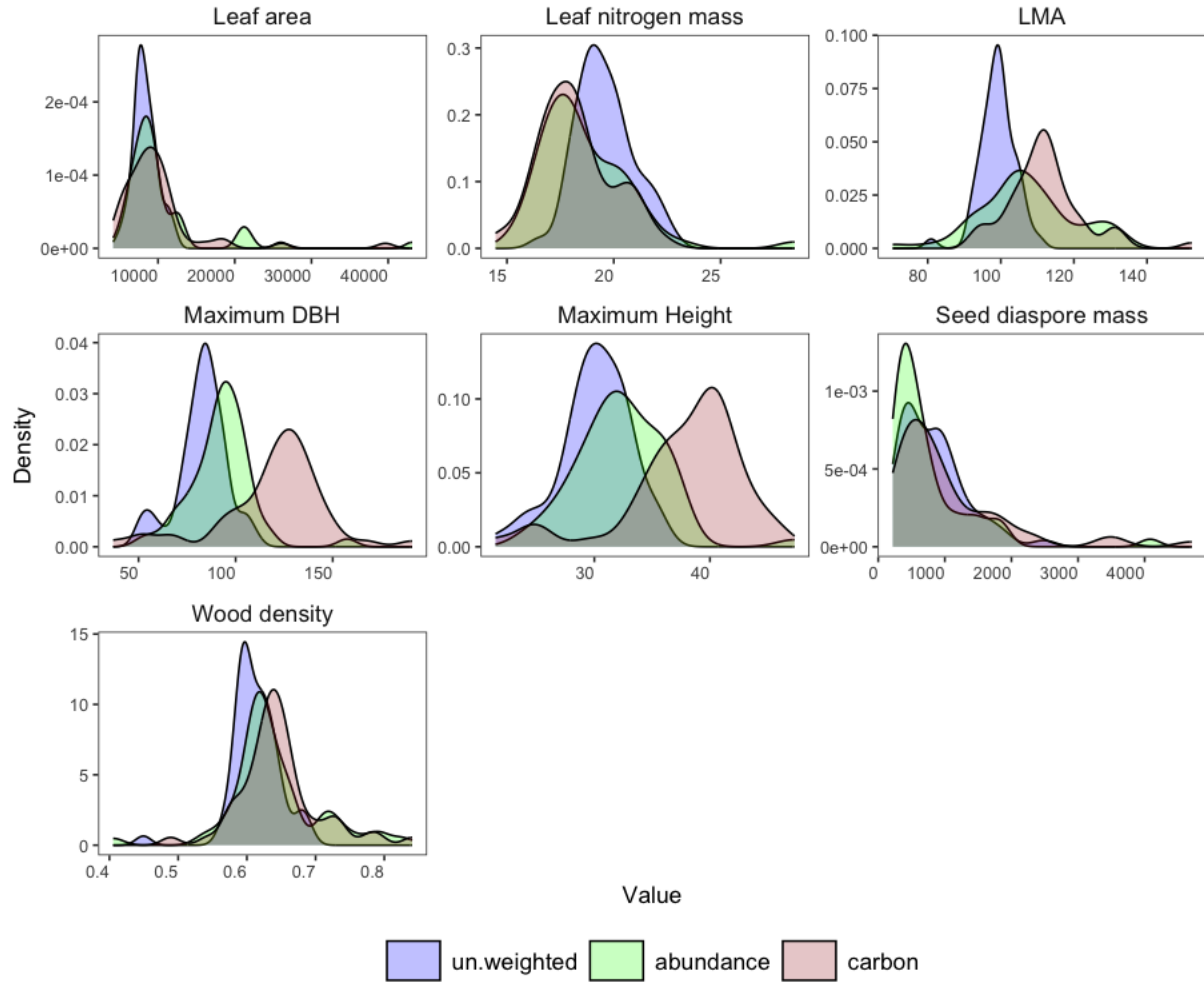


Figure 18: Density plots illustrating the distribution of community-weighted means (CWMs) of functional traits under unweighted (presence–absence), abundance-weighted, and size-weighted frameworks. Traits include maximum height (Max H), maximum diameter (Max DBH), wood density (WD), leaf area (LA), leaf nitrate mass (LNM), leaf mass per area (LMA), and seed diaspore mass (DM).

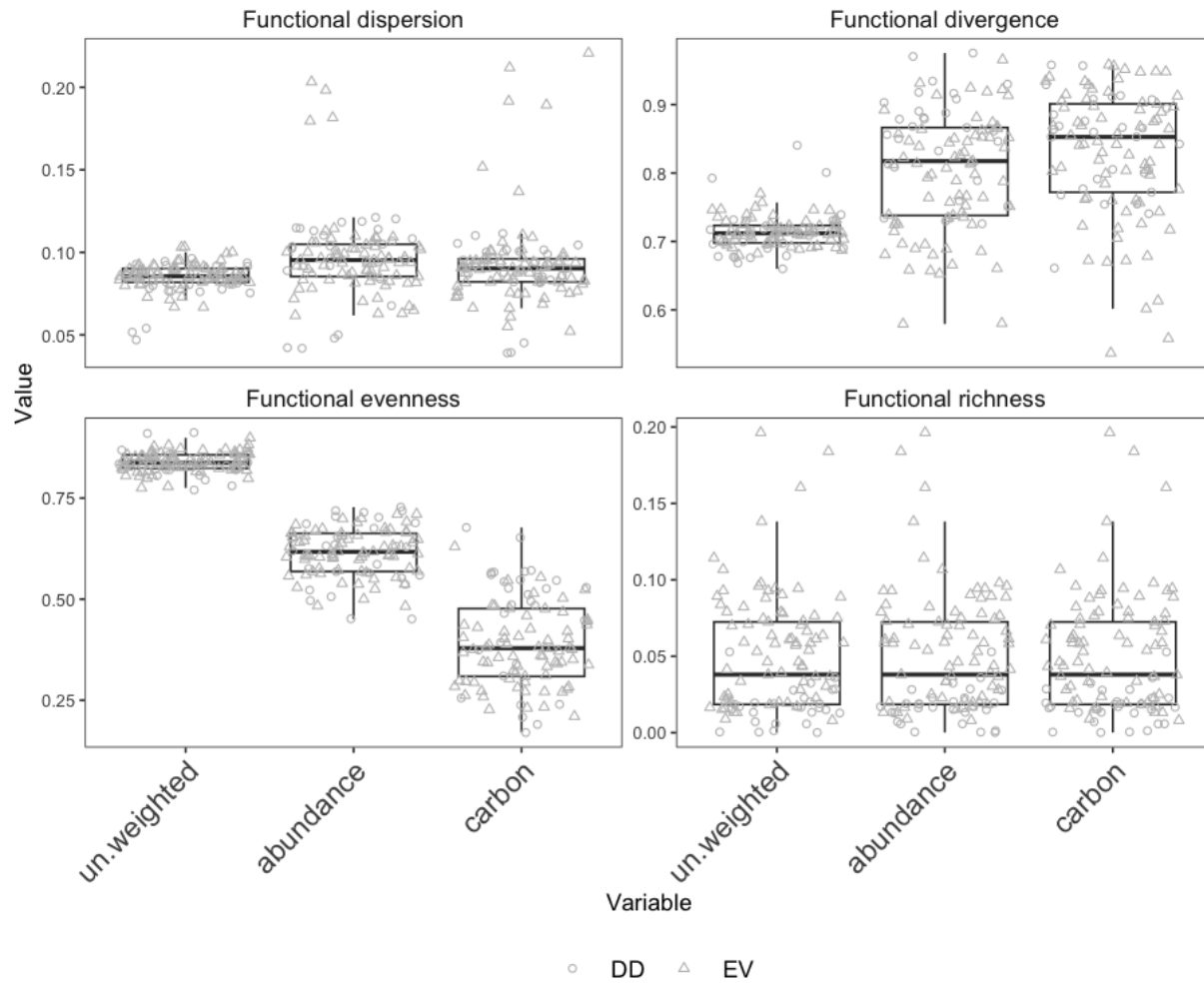


Figure 19: Boxplots showing variation in functional diversity metrics under unweighted (presence–absence), abundance-weighted, and size-weighted frameworks. Metrics include functional richness, functional evenness, functional divergence, and functional dispersion.

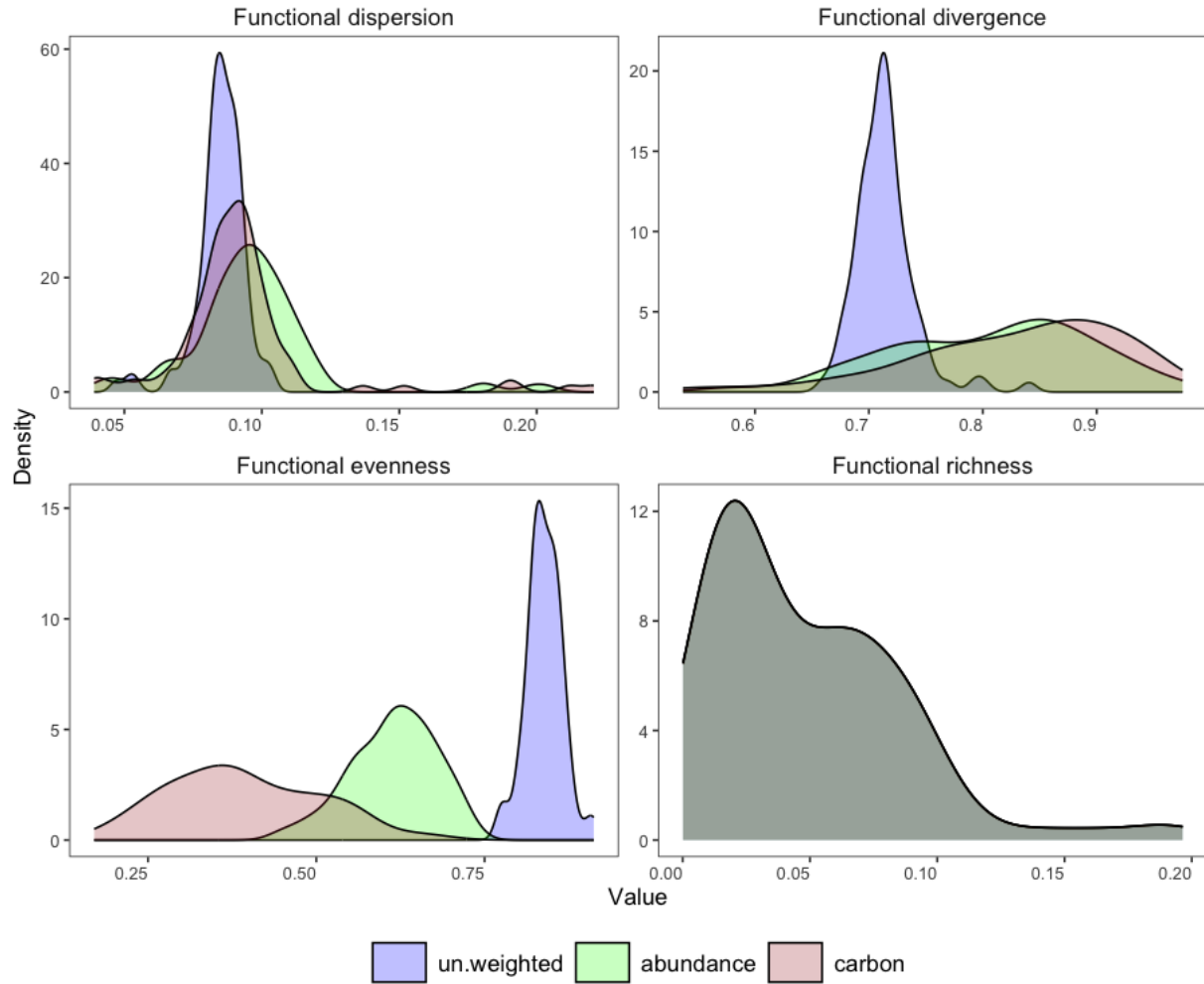
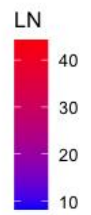
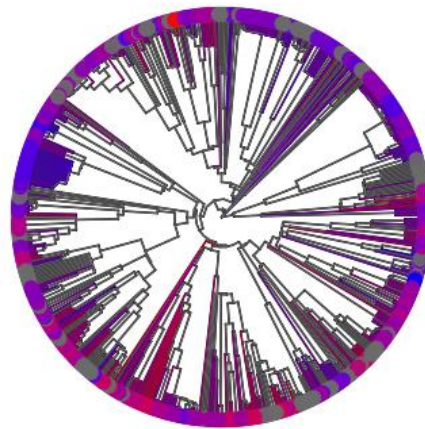
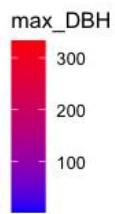
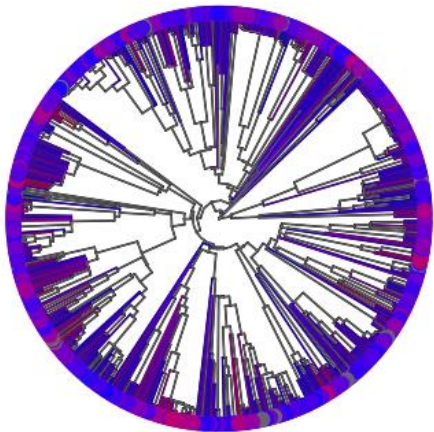
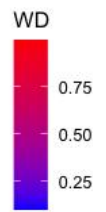
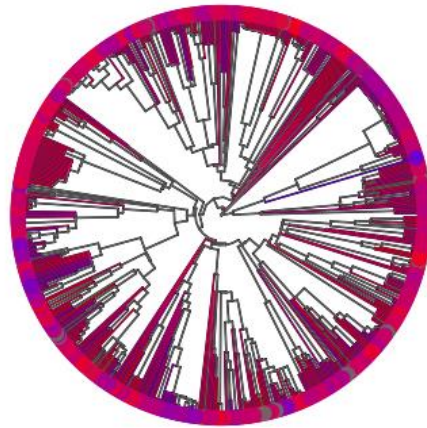
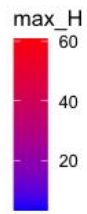
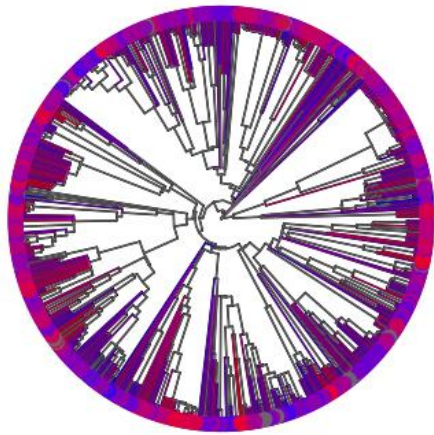


Figure 20: Density plots showing the distribution of functional diversity metrics under unweighted (presence–absence), abundance-weighted, and size-weighted frameworks. Metrics include functional richness, functional evenness, functional divergence, and functional dispersion.



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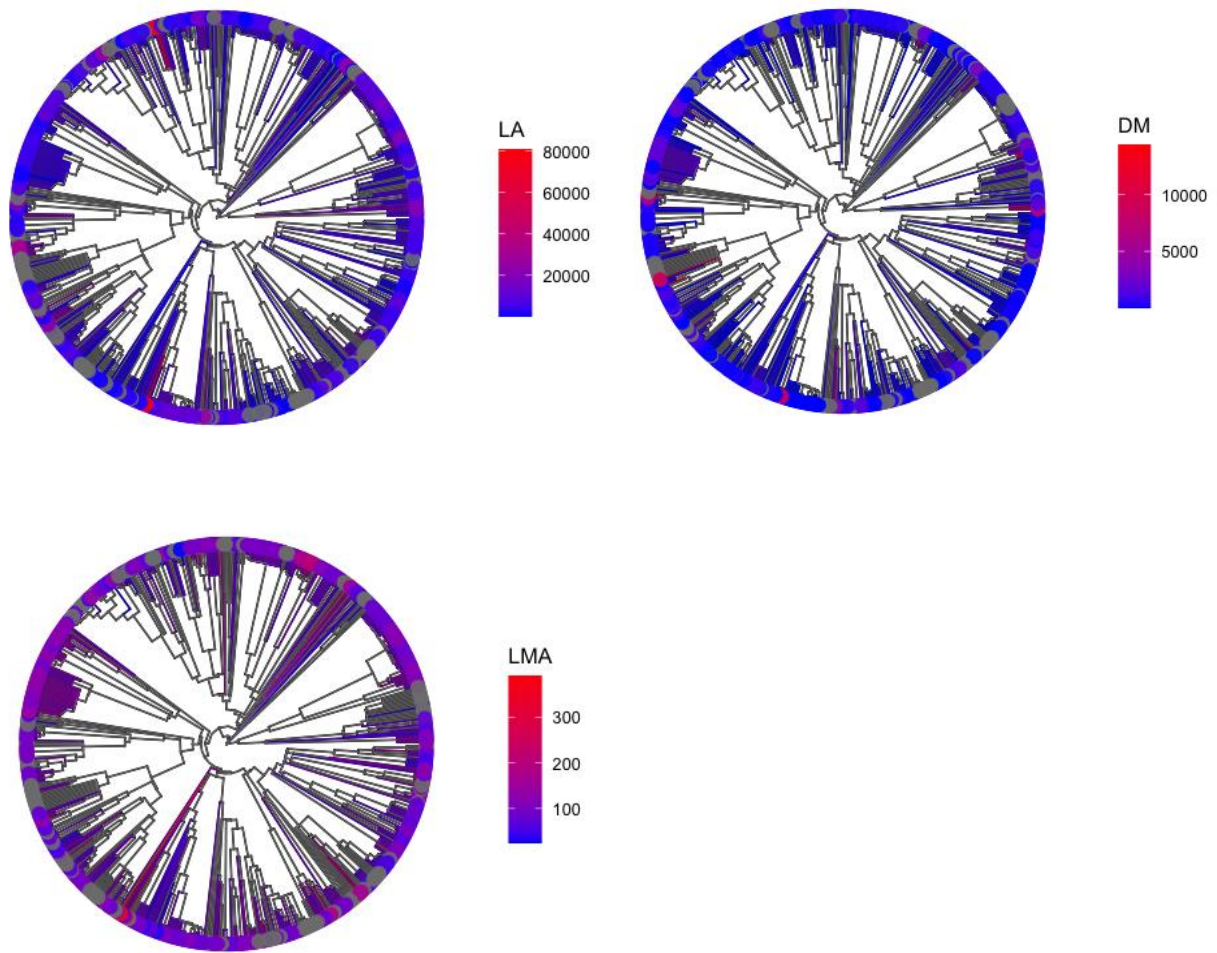


Figure 21: Phylogenetic tree of 592 woody plant species recorded across 111 one-hectare plots in the Western Ghats. Functional trait values are mapped onto the phylogenetic tree with gradients ranging from high (in red) to low (in blue). Traits include maximum attainable height (max H), maximum attainable diameter at breast height (max DBH), Wood density (WD), Seed diaspore mass (DM), Leaf Nitrogen (LN), Leaf mass per area (LMA), Leaf area (LA).

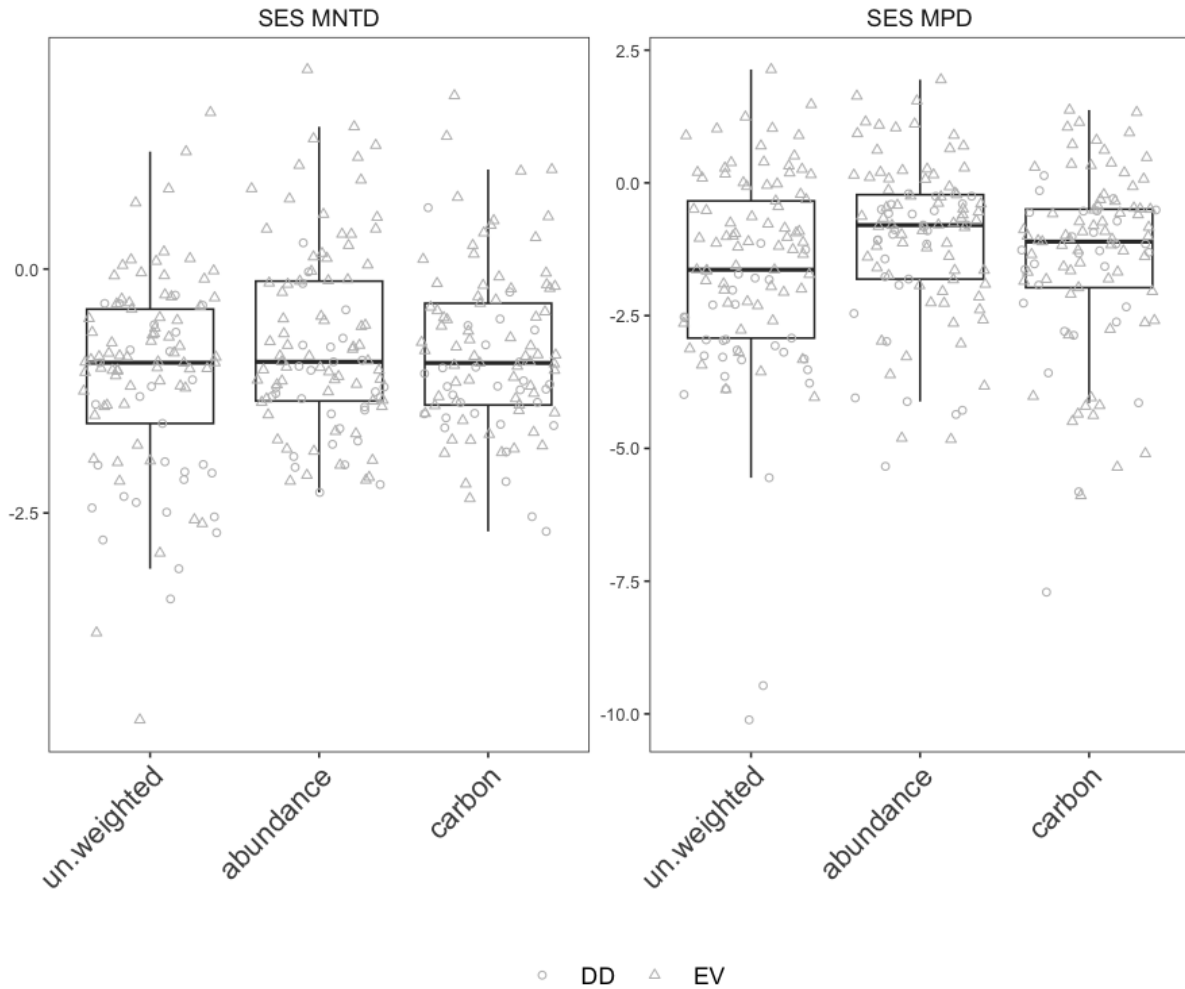


Figure 22: Boxplots showing variation in phylogenetic diversity metrics under unweighted (presence–absence), abundance-weighted, and size-weighted frameworks. Metrics include the standardized effect size of mean pairwise distance (SES MPD), reflecting basal evolutionary divergence, and the standardized effect size of mean nearest taxon distance (SES MNTD), reflecting terminal divergence.

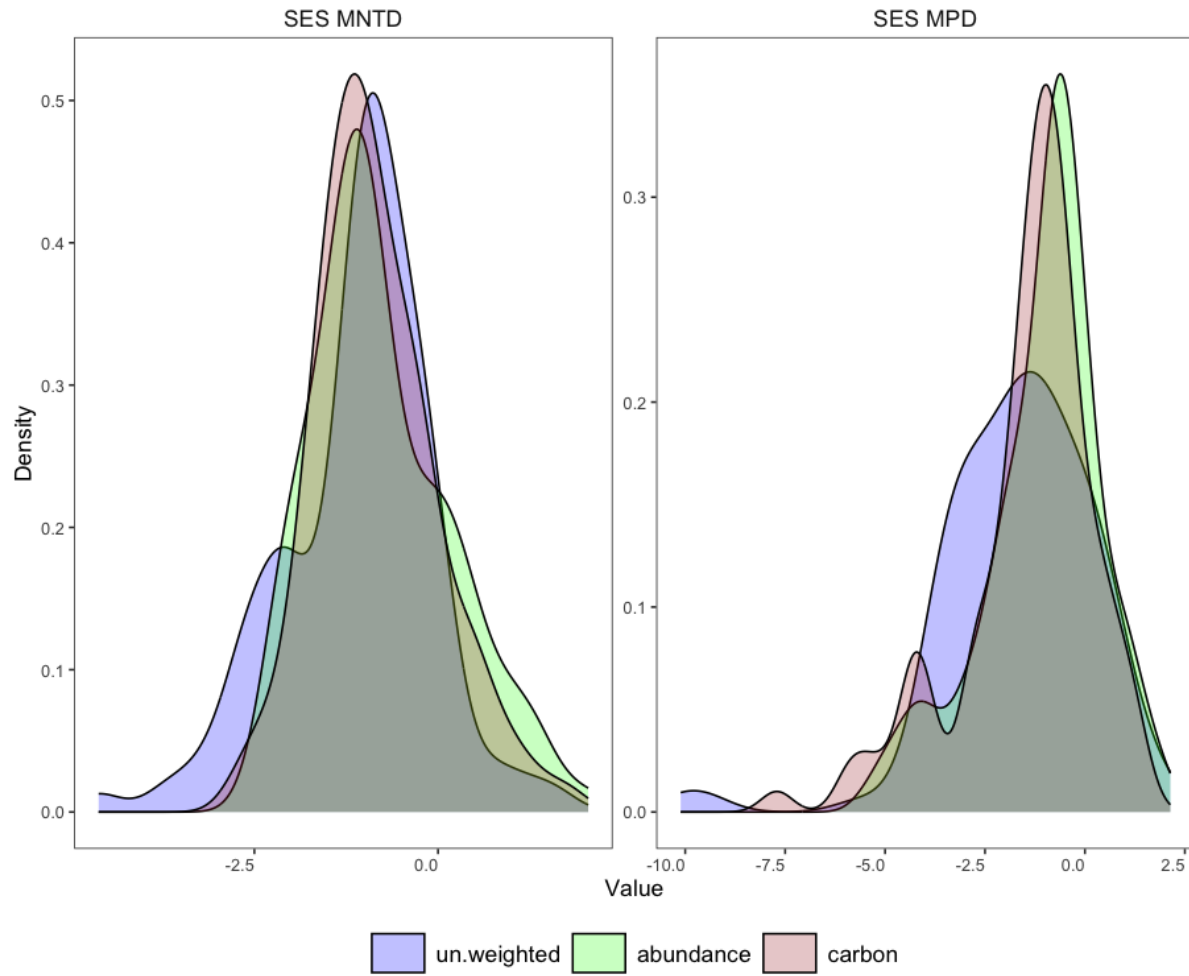


Figure 23: Density plots showing the distribution of phylogenetic diversity metrics under unweighted (presence–absence), abundance-weighted, and size-weighted frameworks. Metrics include the standardized effect size of mean pairwise distance (SES MPD), representing basal divergence, and the standardized effect size of mean nearest taxon distance (SES MNTD), representing terminal divergence.

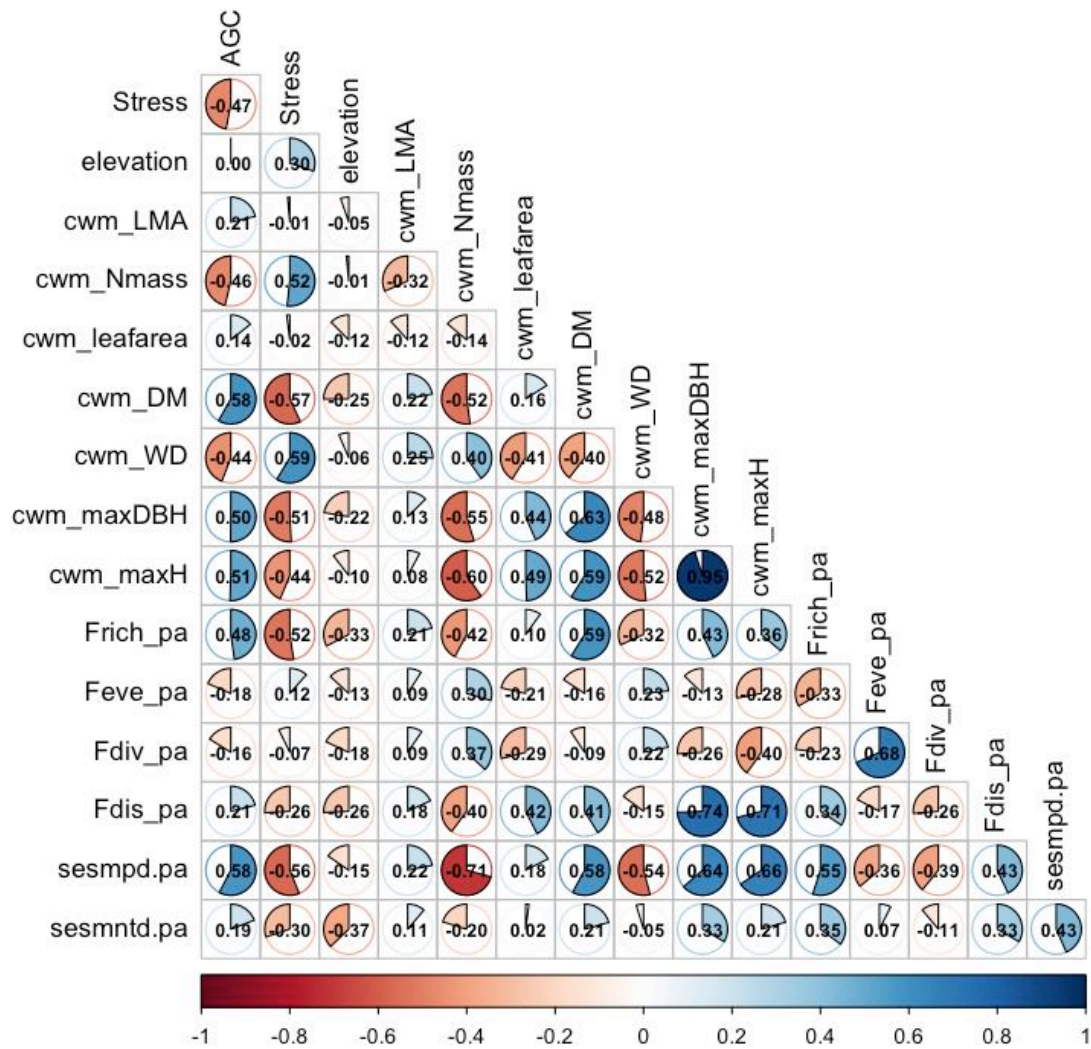


Figure 24: Correlation matrix showing relationships between abiotic variables (e.g., Chave's Environmental Stress index, elevation) and UNWEIGHTED biotic variables, including community-weighted means of functional traits, functional diversity metrics, and phylogenetic diversity (SES MPD and SES MNTD).

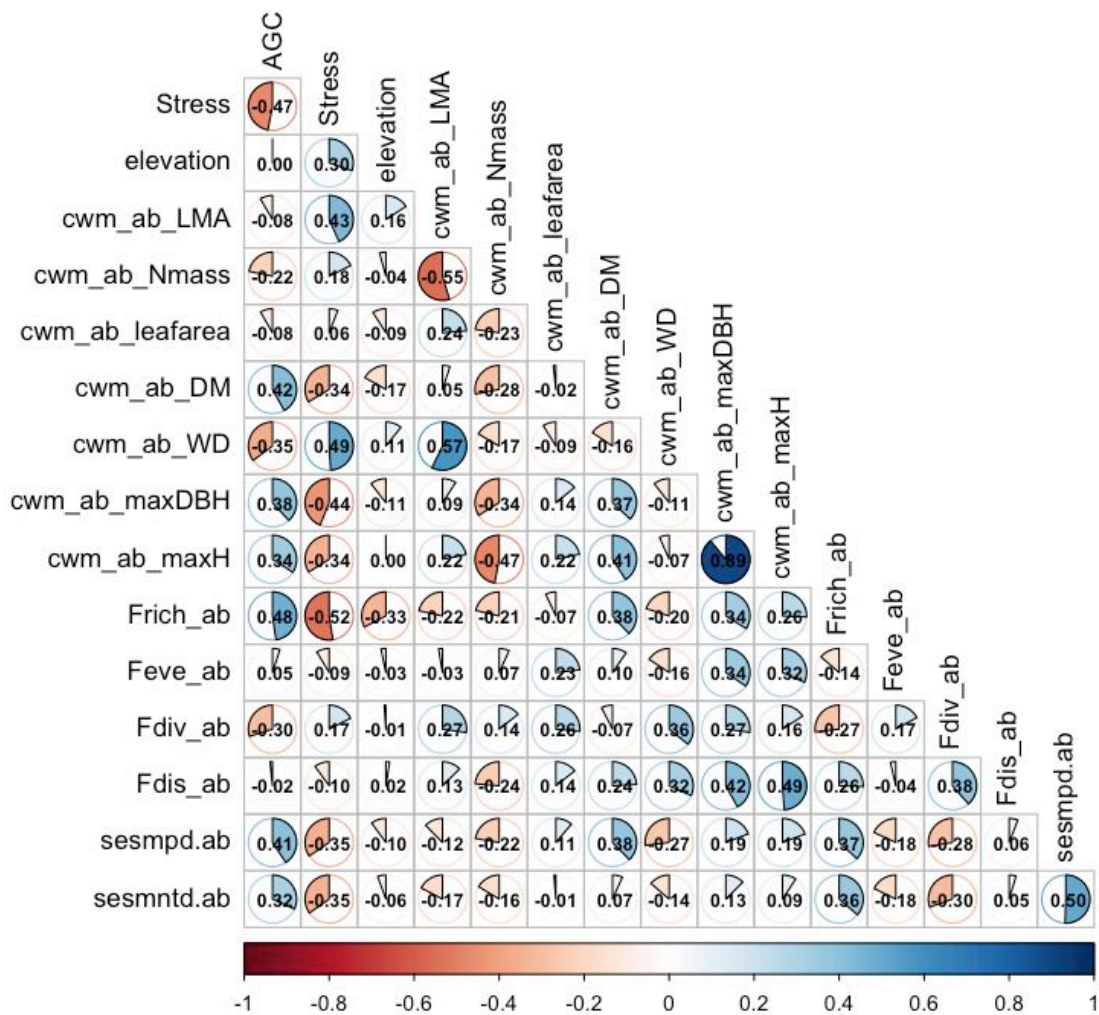


Figure 25: Correlation matrix showing relationships between abiotic variables (e.g., Chave's Environmental Stress index, elevation) and ABUNDANCE weighted biotic variables, including community-weighted means of functional traits, functional diversity metrics, and phylogenetic diversity (SES MPD and SES MNTD).

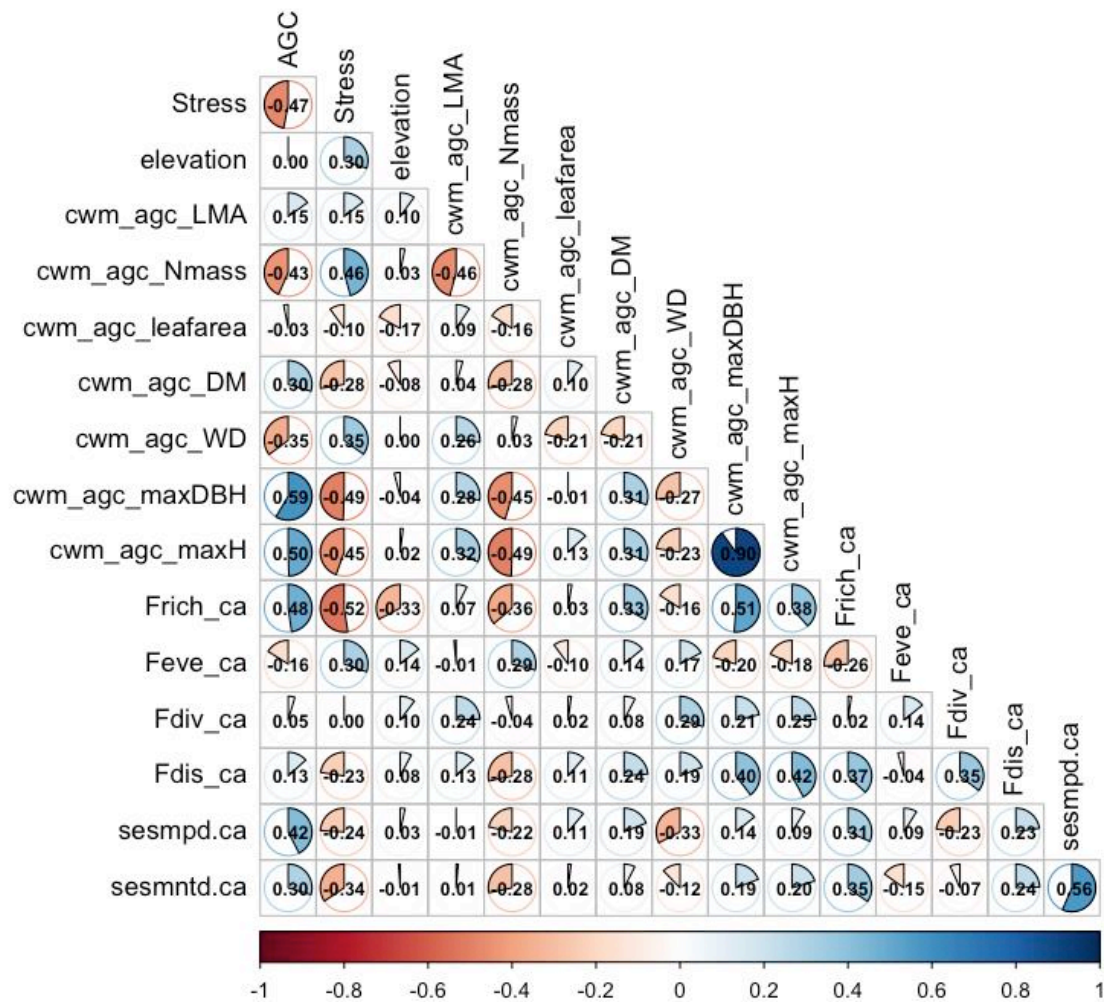


Figure 26: Correlation matrix showing relationships between abiotic variables (e.g., Chave's Environmental Stress index, elevation) and SIZE weighted biotic variables, including community-weighted means of functional traits, functional diversity metrics, and phylogenetic diversity (SES MPD and SES MNTD).

Table 13: Variation inflation factor (VIF)

Variables	Unweighted	Abundance	Size
Stress	3.95	2.84	2.50
Elevation	1.78	1.30	1.45
CWM Leaf Mass per Area	1.74	3.81	2.02
CWM Leaf Nitrate mass	3.06	3.06	2.37
CWM Leaf area	2.24	1.71	1.41
CWM seed diaspore mass	2.47	1.67	1.40
CWM Wood density	4.00	2.76	2.23
CWM max DBH	24.35	8.28	7.95
CWM max Height	25.58	8.43	7.25
Functional richness	2.39	2.18	2.20
Functional evenness	2.87	1.57	1.52
Functional divergence	3.26	2.94	1.51
Functional dispersion	3.00	2.48	1.97
SES MPD	4.54	1.85	2.26
SES MNTD	2.11	1.63	1.79

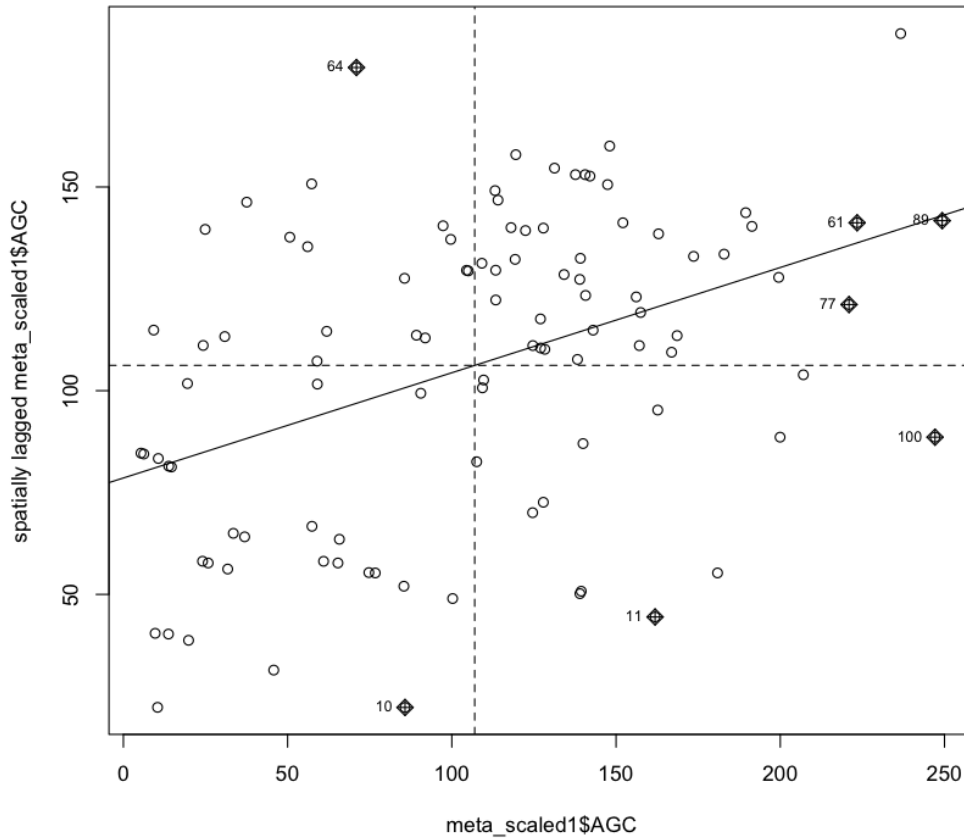


Figure 27: Moran's scatter plot illustrating spatial autocorrelation in above-ground carbon (AGC) across study plots in the Western Ghats. The plot shows a positive spatial autocorrelation pattern, with a Moran's I statistic of 0.258, indicating that sites with similar AGC values are spatially clustered rather than randomly distributed.

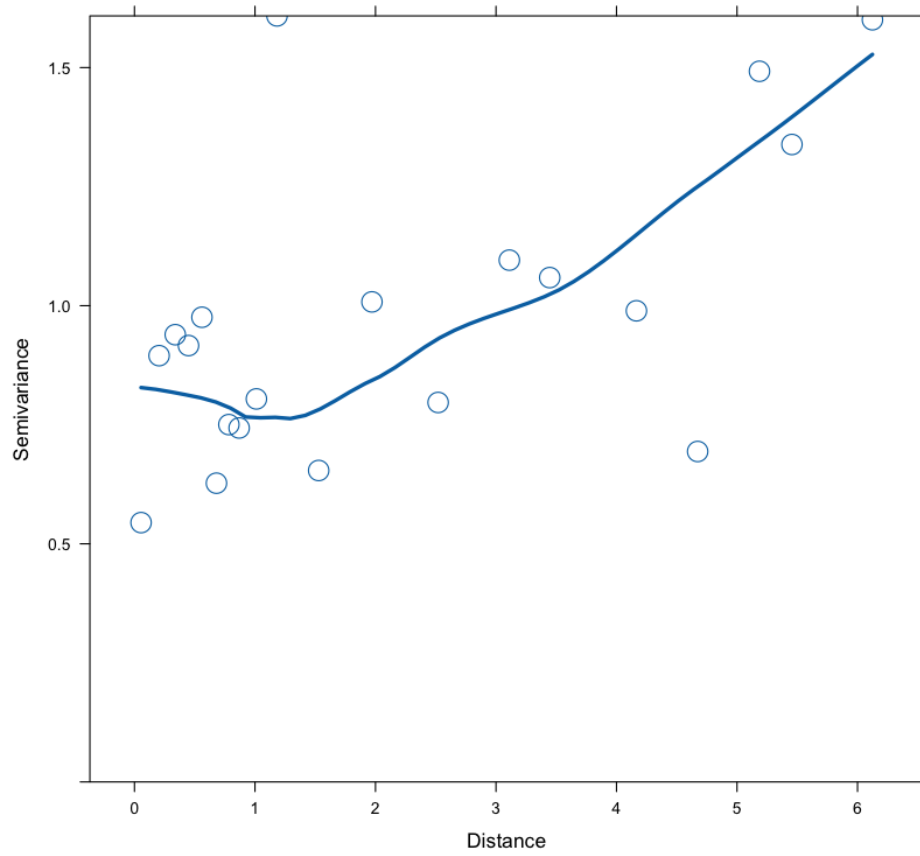


Figure 28: Empirical variogram showing spatial autocorrelation in above-ground carbon (AGC) across study plots in the Western Ghats. The variogram indicates positive spatial autocorrelation at shorter distances, with semivariance increasing as distance between plots increases, demonstrating that nearby sites are more similar in AGC than distant ones.

Table 14: Model selection results comparing four spatial correlation structures (exponential, Gaussian, spherical, and rational quadratic) for the generalized least squares (GLS) model of above-ground carbon (AGC) as a function of Chave's Environmental Stress index and elevation. Model fit was evaluated using Akaike's Information Criterion (AIC).

	Exponential	Gaussian	Spherical	Rational
AGC ~ Chave's E stress + Elevation	1067.42	1067.06	1073.67	1066.73

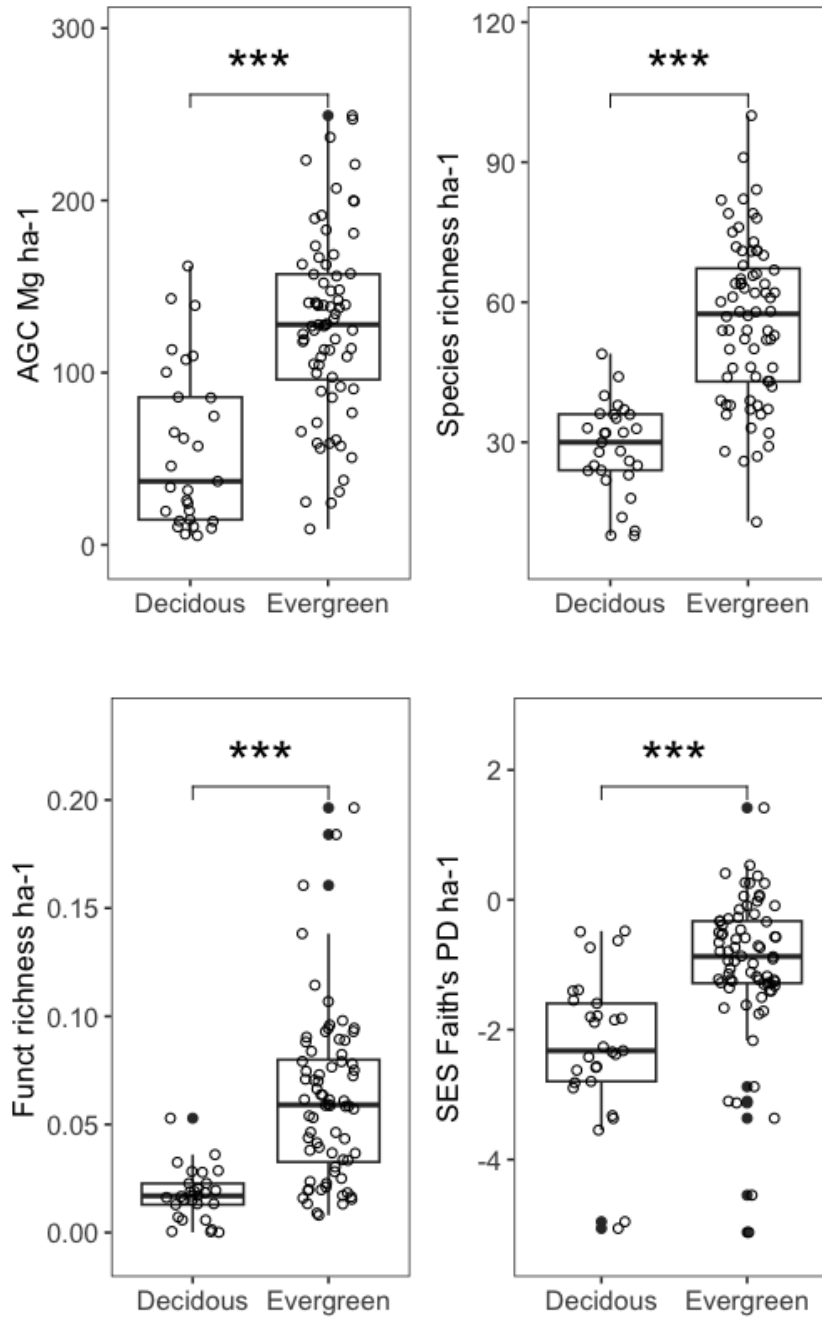


Figure 29: Comparison of above-ground carbon storage (AGC; Mg ha⁻¹), species richness (species ha⁻¹), functional richness (FRic; ha⁻¹), and standardized effect size of phylogenetic diversity (SES Faith's PD; ha⁻¹) between deciduous and evergreen forest plots in the Western Ghats

Table 15: Results of independent t-tests comparing above-ground carbon (AGC), species richness, functional richness, and standardized effect size of Faith's phylogenetic diversity between deciduous and evergreen forest types in the Western Ghats.

Variable	Forest type	mean	SE	t - value	DF	p-value
AGC	Deciduous	56.09	8.07	-6.25	99	<0.001
	Evergreen	127.44	6.33			
Species richness	Deciduous	28.65	1.82	-10.07	87.07	<0.001
	Evergreen	56.06	2.02			
Functional richness	Deciduous	0.017	0.002	-8.73	94.64	<0.001
	Evergreen	0.061	0.004			
SES faith's Phylogenetic diversity	Deciduous	-2.26	0.20	-5.45	99	<0.001
	Evergreen	-0.96	0.12			

Table 16: Blomberg's K statistics testing for phylogenetic signal (phylogenetic conservatism) in functional traits and above-ground carbon (AGC) of woody plant species in the Western Ghats. Values of K close to 0 indicate weak phylogenetic signal, whereas values closer to 1 indicate strong conservatism of traits along the phylogeny.

	K	PIC variance observed mean	PIC variance random mean	p-value
Maximum DBH	0.15	11.30	1160.06	0.001
Maximum Height	0.14	7.12	66.79	0.001
Wood density	0.16	0.001	0.01	0.001
Leaf area	0.30	1370367	28827290	0.001
Leaf nitrate mass	0.24	1.06	21.73	0.001
Leaf mass area	0.002	4744.86	908.13	0.979
Seed Diaspore mass	0.31	66488.17	1600763	0.001
AGC Mg ha-1	0.18	623.29	7599.04	0.025

Table 17: Independent effects of environmental variables on above-ground carbon (AGC) as estimated from generalized least squares (GLS) models.

	Value	SE	t-value	p-value	AIC	R2
(Intercept)	108.61	6.75	16.10	0.00	1083.65	35.44
Chave's E stress (CES)	-31.20	6.74	-4.63	0.00		
Elevation	13.19	6.68	1.97	0.05		

Table 18: Independent effects of community-weighted means (CWMs) of functional traits (WD - Wood density, SDM - Seed diaspore mass, LN - Leaf Nitrogen, LMA - Leaf mass per area, LA - Leaf area) on above-ground carbon (AGC) under three modeling frameworks: unweighted, abundance-weighted, and size-weighted generalized least squares (GLS) models.

	Unweighted				Abundance weighted				Size weighted			
	Value	SE	t	p	Value	SE	t	p	Value	SE	t	p
(Intercept)	108.54	6.12	17.72	0.00	108.99	6.72	16.22	0.00	108.22	6.01	18.00	0.00
CES	-11.13	9.03	-1.23	0.22	-27.24	8.40	-3.24	0.00	-22.54	7.45	-3.02	0.00
Elevation	10.76	6.91	1.56	0.12	12.85	6.67	1.93	0.06	8.26	6.23	1.33	0.19
CWM WD	-12.80	7.62	-1.68	0.10	-14.03	6.87	-2.04	0.04	-14.97	5.40	-2.77	0.01
CWM SDM	22.94	6.36	3.61	0.00	14.81	5.45	2.72	0.01	8.48	5.32	1.59	0.11
CWM LN	-0.87	7.20	-0.12	0.90	7.09	7.96	0.89	0.38	-6.93	7.85	-0.88	0.38
CWM LMA	7.14	4.31	1.66	0.10	15.51	8.21	1.89	0.06	10.90	6.22	1.75	0.08
CWM LA	-1.83	5.90	-0.31	0.76	-1.88	5.06	-0.37	0.71	-4.97	4.34	-1.15	0.25

Table 19: Independent effects of functional traits diversity on above-ground carbon (AGC) under three modeling frameworks: unweighted, abundance-weighted, and size-weighted generalized least squares (GLS) models.

	Unweighted				Abundance weighted				Size weighted			
	Value	SE	t	P	Value	SE	T	p	Value	SE	t	p
(Intercept)	108.38	6.38	17.00	0.00	107.76	6.22	17.33	0.00	108.86	6.53	16.67	0.00
CES	-20.82	6.98	-2.98	0.00	-16.99	6.81	-2.50	0.01	-20.19	7.01	-2.88	0.00
Elevation	16.04	6.94	2.31	0.02	18.57	6.45	2.88	0.00	20.02	6.63	3.02	0.00
F. Richness	25.65	6.29	4.08	0.00	30.96	6.47	4.78	0.00	32.38	6.08	5.32	0.00
F. Evenness	1.71	5.98	0.29	0.78	5.09	4.67	1.09	0.28	5.06	4.02	1.26	0.21
F. Divergence	-3.87	6.97	-0.55	0.58	-1.81	5.89	-0.31	0.76	8.45	5.08	1.66	0.10
F. Dispersion	-5.59	6.35	-0.88	0.38	-9.63	5.96	-1.61	0.11	-10.48	5.18	-2.02	0.04

Table 20: Independent effects of phylogenetic diversity (standardised effect size (SES) mean pairwise distance (SES MPD) and mean nearest taxon distance (MNTD) on above-ground carbon (AGC) under unweighted, abundance-weighted, and size-weighted generalized least squares (GLS) models.

	Unweighted				Abundance weighted				Size weighted			
	Value	SE	T	P	Value	SE	T	p	Value	SE	t	p
(Intercept)	107.49	5.86	18.33	0.00	107.73	6.30	17.10	0.00	109.09	6.49	16.82	0.00
CES	-18.92	6.55	-2.89	0.00	-23.80	6.58	-3.62	0.00	-27.32	6.67	-4.09	0.00
Elevation	11.55	6.30	1.83	0.07	12.72	6.32	2.01	0.05	11.15	6.38	1.75	0.08
SES MPD	26.48	6.70	3.95	0.00	16.82	5.39	3.12	0.00	21.44	5.23	4.10	0.00
SES MNTD	-1.61	5.73	-0.28	0.78	5.81	5.04	1.15	0.25	-1.36	5.66	-0.24	0.81

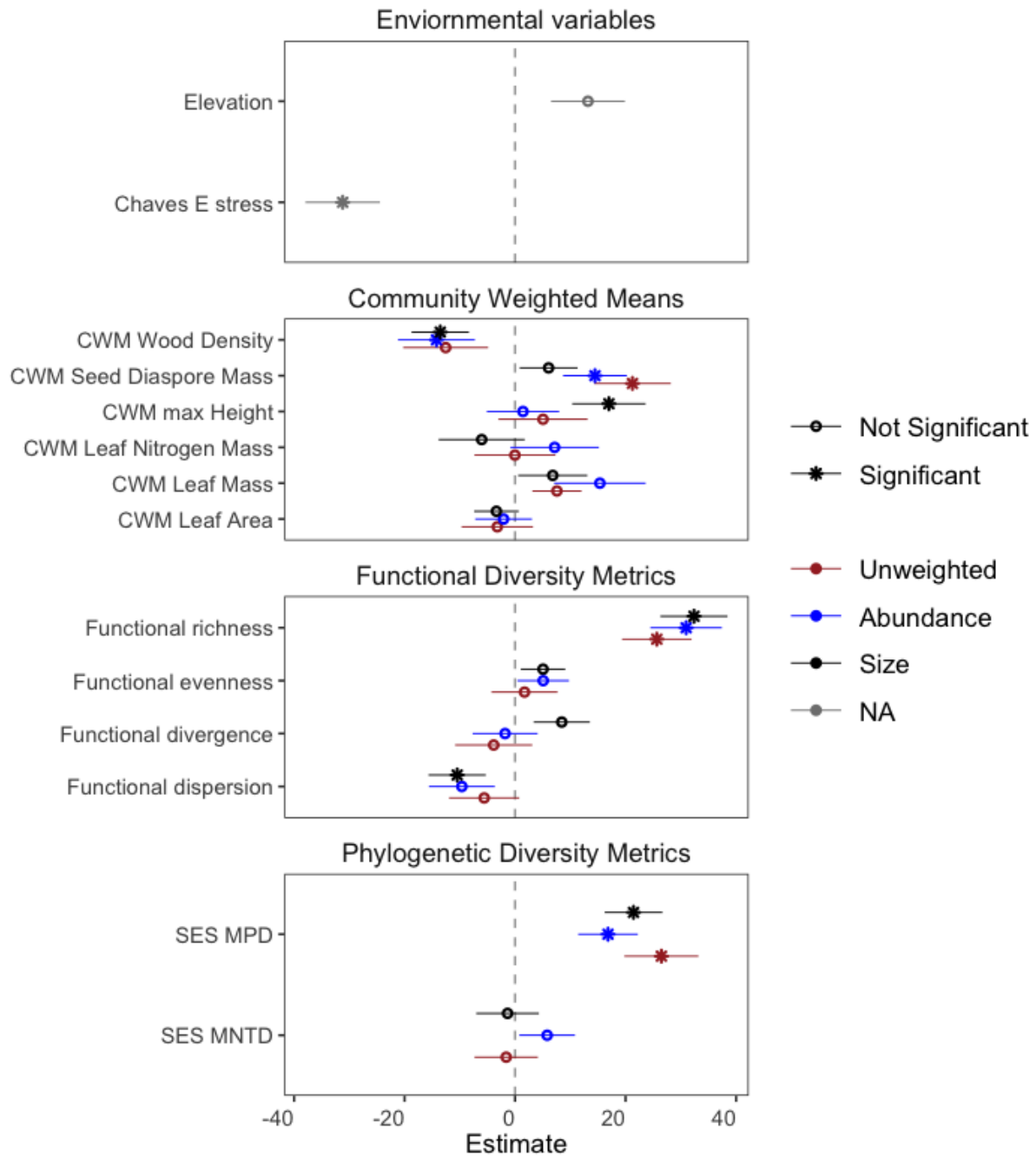


Figure 30: Independent effects of environmental gradients (Chave's Environmental Stress index and elevation), community-weighted means of functional traits (CWMs), functional diversity metrics (functional richness, evenness, divergence, and dispersion), and phylogenetic diversity metrics (SES MPD and SES MNTD) on above-ground carbon (AGC) under unweighted, abundance-weighted, and size-weighted generalized least squares (GLS) models.

Table 21: Model comparisons examining the independent and combined effects of Chave's environmental stress (CES), elevation, community-weighted means of functional traits (CWM), functional diversity, and phylogenetic diversity on above-ground carbon (AGC). Models were evaluated under unweighted, abundance-weighted, and size-weighted frameworks using Akaike's Information Criterion (AIC), ΔAIC , and explained variance (R^2).

Model	Weights	AIC	ΔAIC	R^2
Stress + Elevation		1083.65		35.44
Stress + Elevation + CWM	Unweighted	1071.34	12.31	48.0
	Abundance	1078.10	5.55	44.66
	Size	1077.89	5.76	44.77
Stress + Elevation + CWM + Functional diversity	Unweighted	1070.93	12.72	52.37
	Abundance	1066.57	17.08	54.38
	Size	1069.77	13.88	52.91
Stress + Elevation + CWM + Functional diversity + Phylogenetic diversity	Unweighted	1071.23	12.42	54.09
	Abundance	1063.02	20.63	57.67
	Size	1060.89	22.76	58.55

Table 22: Generalized least squares (GLS) model results testing the independent effects of environmental gradients (Chave's Environmental Stress index and elevation), community-weighted means (CWM) of functional traits, and multiple dimensions of functional diversity on above-ground carbon (AGC) under unweighted, abundance-weighted, and size-weighted frameworks.

	Unweighted				Abundance weighted				Size weighted			
	Value	SE	t	P	Value	SE	t	p	Value	SE	t	p
(Intercept)	108.88	6.21	17.52	0.00	108.82	6.14	17.73	0.00	108.65	6.22	17.47	0.00
CES	-10.85	9.57	-1.13	0.26	-18.83	8.26	-2.28	0.03	-13.57	7.96	-1.71	0.09
Elevation	11.41	7.27	1.57	0.12	18.24	6.49	2.81	0.01	13.32	6.66	2.00	0.05
CWM WD	-8.93	7.60	-1.17	0.24	-9.56	7.77	-1.23	0.22	-15.00	5.58	-2.69	0.01
CWM SDM	19.87	6.65	2.99	0.00	13.17	5.36	2.46	0.02	2.62	5.18	0.51	0.61
CWM LN	0.02	7.54	0.00	1.00	9.55	8.20	1.16	0.25	-7.87	7.61	-1.03	0.30
CWM LMA	6.52	4.31	1.51	0.13	15.88	8.20	1.94	0.06	6.53	5.99	1.09	0.28
CWM LA	0.03	6.18	0.01	1.00	2.92	5.14	0.57	0.57	-2.99	3.46	-0.86	0.39
F. Richness	13.34	6.73	1.98	0.05	25.91	6.44	4.03	0.00	24.76	6.42	3.85	0.00
F. Evenness	-1.34	6.37	-0.21	0.83	1.87	4.95	0.38	0.71	2.55	4.85	0.53	0.60
F. Divergence	-4.04	7.35	-0.55	0.58	-4.55	6.28	-0.72	0.47	8.79	5.31	1.66	0.10
F. Dispersion	-9.31	6.82	-1.37	0.18	-5.91	6.53	-0.91	0.37	-3.83	5.73	-0.67	0.51

Table 23: Generalized least squares (GLS) model results testing the combined effects of environmental gradients (Chave's Environmental Stress index [CES] and elevation), community-weighted means (CWMs) of functional traits (WD -Wood density, SDM - Seed diaspore mass, LN -Leaf Nitrogen, LMA -Leaf mass per area, LA - Leaf area), functional (functional richness, evenness, divergence, and dispersion), and phylogenetic diversity (SES MPD and SES MNTD) on above-ground carbon (AGC) under unweighted, abundance-weighted, and size-weighted frameworks.

	Unweighted				Abundance weighted				Size weighted			
	Value	SE	t	p	Value	SE	t	p	Value	SE	t	p
(Intercept)	108.29	6.15	17.60	0.00	108.25	6.23	17.39	0.00	108.93	5.96	18.28	0.00
CES	-11.05	9.68	-1.14	0.26	-16.01	8.26	-1.94	0.06	-14.47	7.62	-1.90	0.06
Elevation	13.92	7.40	1.88	0.06	17.91	6.52	2.75	0.01	13.34	6.38	2.09	0.04
CWM WD	-3.16	8.49	-0.37	0.71	-8.55	7.65	-1.12	0.27	-7.73	5.62	-1.37	0.17
CWM SDM	18.93	6.80	2.78	0.01	11.06	5.45	2.03	0.05	3.80	4.86	0.78	0.44
CWM LN	4.30	7.86	0.55	0.59	9.92	7.98	1.24	0.22	-4.54	7.17	-0.63	0.53
CWM LMA	4.29	4.70	0.91	0.36	15.09	7.99	1.89	0.06	4.08	5.69	0.72	0.48
CWM LA	2.89	6.43	0.45	0.65	1.83	4.97	0.37	0.71	-1.45	3.05	-0.48	0.63
F. Richness	11.53	6.80	1.69	0.09	23.62	6.44	3.67	0.00	21.92	6.26	3.50	0.00
F. Evenness	-0.59	6.67	-0.09	0.93	4.26	4.93	0.86	0.39	-3.05	4.70	-0.65	0.52
F. Divergence	-2.61	7.59	-0.34	0.73	-1.93	6.05	-0.32	0.75	14.04	5.16	2.72	0.01
F. Dispersion	-9.27	6.78	-1.37	0.18	-6.14	6.32	-0.97	0.33	-7.77	5.45	-1.43	0.16
SES MPD	14.44	8.45	1.71	0.09	9.42	5.40	1.75	0.08	18.13	5.51	3.29	0.00
SES MNTD	0.27	6.00	0.05	0.96	5.45	4.81	1.13	0.26	-2.89	5.39	-0.54	0.59

Chapter 3 - Above Ground Carbon Accumulation Rates across Forest Types in the Western Ghats Biodiversity Hotspot.

3.1 Introduction

Tropical forests are crucial for the global carbon cycle and thus for the global climate because they sequester large amounts of atmospheric carbon in above- and below-ground biomass. Therefore, it is important to understand the underlying ecological mechanisms that determine carbon accumulation rates in tropical forest ecosystems. By integrating insights from ecological theories and empirical studies, this manuscript examines the factors influencing AGC accumulation in tropical forests and highlights their implications for conservation and forest management strategies.

Diameter growth rates of surviving trees play a critical role in determining aboveground carbon accumulation (AGC) rates in forests. Functional traits, which include morphological and physiological characteristics of individual species, directly influence these growth rates and therefore AGC accumulation. For example, trees with denser wood, smaller leaf area, and larger seed size tend to have higher survival rates and slower growth rates. Despite their slower growth, these trees reach larger diameters and heights, resulting in significant AGC accumulation. In contrast, trees with softer wood, larger leaf area, and smaller seed sizes generally have lower survival rates and faster growth rates, and ultimately lower AGC accumulation.

Tree species in forests with different functional characteristics have different growth rates, reach different heights, consume resources differently and thereby occupy unique ecological niches. In species-rich and functionally diverse forests, these differences facilitate complementary resource use above and below ground, enabling greater AGC accumulation and storage. This phenomenon is expressed in the niche complementarity hypothesis (Loreau et al. 2001), which states that functional biodiversity improves ecosystem function through complementary resource use.

However, functional redundancy, the overlap in ecological roles between species within a community influences these dynamics. Increasing redundancy can lead to greater niche overlap, thereby reducing AGC accumulation. Conversely, reducing functional redundancy minimizes niche overlap and potentially improves AGC accumulation and storage. For example, increasing diversity of shade-tolerant tree species is resulting in a broader range of canopy architectures (e.g., variations in shape, size, and branching patterns) and stratification levels (emergent, canopy, subcanopy, and understory). This diversity leads to more efficient light capture and higher forest productivity.

Despite the great diversity of tropical forest ecosystems, only a few tree species are typically abundant and structurally dominant. The functional characteristics of these dominant species such as their growth rates, wood density, leaf size, seed size and canopy structure largely determine the AGC accumulation and storage potential of forest stands. This is consistent with the sampling effect or mass ratio hypothesis (Tilman 1999), which suggests that ecosystem functions such as carbon storage are primarily determined by the characteristics of the most dominant species. The

interplay between functional traits, species richness and dominance dynamics highlights the complex mechanism controlling AGC accumulation in forests. Understanding these mechanisms provides important insights into the carbon dynamics of forests and the role of biodiversity in mitigating climate change.

Measuring functional traits for all tree species is both time-consuming and expensive, and there is also the risk of selecting irrelevant or yet unidentified traits that may not accurately predict growth or AGC accumulation. However, ecological adaptations are shaped by environmental conditions and the biological interactions experienced by the ancestors of modern taxa. All organisms bear the imprint of these influences as products of their evolutionary history.

Because of similarities in resource use inherited from common ancestors, competition tends to be stronger between closely related species than distantly related species. This influences species coexistence, as closely related species often exhibit similar functional trait values and ecological niche preferences owing to their shared evolutionary history (Macarthur and Levins 1967). Phylogenetic conservatism illustrates how closely related taxa tend to preserve their ancestral ecological and functional traits (Wiens and Graham 2005).

Based on assumptions of phylogenetic conservatism, the phylogenetic relationships between species within a community can be used as a proxy for the relationship between functional traits. Then, phylogenetic niche conservatism assumes that the functional characteristics of species are conserved across evolutionary lineages, thus establishing a connection between phylogenetic and ecological function. On this basis, species can coexist within a community either as phylogenetically closely related and functionally similar taxa or as phylogenetically distant and functionally distinct taxa (Webb et al. 2002). Functional similarity between closely related species can lead to increased competition and potentially limit coexistence. Functional dissimilarity of distantly related species can reduce competition and facilitate coexistence through niche differentiation.

Phylogenetic relatedness is a useful tool for ecological studies that focus on functional trait relationships and community assembly processes. In contrast to direct trait measurement, this method provides a theoretically sound and economical way to view ecological interactions through the lens of evolutionary history. The relevant, missing, and unidentified functional traits are also accounted for by phylogenetic relatedness metrics. Understanding the dynamics of AGC accumulation and species coexistence in forest ecosystems requires knowledge of these factors.

Global studies show that biodiversity increases productivity in forest ecosystems (Zhang et al. 2012; Liang et al. 2016; Sullivan et al. 2017). Furthermore, a global study by (Hordijk et al. 2023) found that when species richness is low, unevenly distributed communities are more productive, while when species richness is high, evenly distributed communities are more productive, because in forests with high species diversity there are typically few dominant and many rare species.

In tropical forests in Bolivia, Brazil, and Costa Rica (Finegan et al. 2015) attribute positive effects on biomass productivity to community weighted means (CWM) highlighting the role of abundant

or dominant traits such as specific leaf area (SLA), force to tear the leaf, Leaf dry matter content (LDMC), leaf phosphorous content supporting the sampling effect or mass ratio hypothesis. In temperate secondary forests of northeast China, (Hao et al. 2020) find that functional diversity increases productivity, consistent with the niche complementarity hypothesis. Acquisitive traits (e.g., greater specific leaf area and leaf nitrogen concentration) enhance productivity, while conservative traits (e.g., greater wood density) enhance the long-term accumulation, demonstrating the mass-ratio hypothesis. Conversely, (Yuan et al. 2018) find that CWM of leaf phosphorous content predicted productivity in secondary forests but not in old growth forest of northeastern China.

Earlier phylogenetic diversity productivity relationships were focused on experimental grassland communities and demonstrated positive effects of phylogenetic diversity (Cadotte et al. 2012; Cadotte 2015b; 2015a; 2013). Recently many studies only including species and phylogenetic diversity effects on productivity show positive effects of phylogenetic diversity. Like, (Souza et al. 2019) emphasize niche complementarity by demonstrating positive effects of phylogenetic neighbour lineage diversity on biomass productivity in tropical Amazon forests. Similarly, (Satdichanh et al. 2019) highlights that phylogenetic diversity has exhibited positive relationship with young secondary forest but not older in southeast Asian tropical forests. In temperate and boreal forests of eastern Canada, (Paquette and Messier 2011) also highlight niche complementarity, showing that functional and phylogenetic diversity positively affect tree biomass productivity. However, they note that these effects are more pronounced in climatically stressful boreal forests than in stable temperate forests. Similarly, (Jia and Wang 2024) demonstrates positive effects of total lineage Faiths phylogenetic diversity on productivity within mixed forests in northeastern China.

In contrast, (Sande et al. 2017) found limited importance of mass ratio hypothesis based on functional traits richness and community weighted means for the productivity in Bolivian tropical moist forest, instead they find soil texture, soil water availability and forest structure determine above ground biomass productivity. On the contrary, (Castaño et al. 2024; Yuan et al. 2021a) do not find significant effects of phylogenetic diversity on productivity. Instead, they highlight that few large trees primarily determine productivity patterns in terra firme tropical forests of Amazon and temperate forests of northeastern China. Climatic variation across united states of America influenced the biodiversity productivity relationships across forest types, where biodiversity productivity relationships was positive in dry climates and hump shaped in wet climates (Fei et al. 2018).

The relationship between biodiversity and productivity are context dependent, varying across, local, regional and global scales and differing by forest type and diversity metrics (taxonomic, functional and phylogenetic) (Liang et al. 2016; Dormann et al. 2019). This complexity underscores the need for further studies and comparative analyses to refine our understanding of these relationships and inform management practices at local and regional scales.

Many studies have incorporated abundance in community weighted means, functional (Hao et al. 2018) and phylogenetic diversity metrics (Cadotte et al. 2012; Castaño et al. 2024; Souza et al. 2019). Many studies have applied structural dominance (e.g., basal area or biomass) in community weighted mean and functional diversity metrics (Finegan et al. 2015; Sande et al. 2017; Yuan et al. 2018; Hao et al. 2020; Prado-Junior et al. 2016). However, abundant species not necessarily has to be structurally dominant in terms larger diameter and height. For instance, *Terminalia anogeissina* in dry forest and *Agrostistachys boornensis* in evergreen forest are highly abundant but structurally smaller trees but accumulate and stock AGC with their higher abundance. However, species like *Cullenia exarillata* and *Vateria indica* are as large statured trees accumulating and stock large proportions of AGC. And some structurally dominant taller tree species are rare. Therefore, I preferred on using both unweighted, abundance and carbon weighted functional and phylogenetic metrics. Similarly, as CWM and functional traits abundance or basal area weights depicts plants reproductive and growth performance, why phylogenetic diversity metrics are restricted to abundance in many studies and not basal area or carbon. However, so far no studies have incorporated structural dominance (e.g., biomass or basal area) in phylogenetic diversity metrics. Integrating such metrics aligns with the mass-ratio hypotheses, which suggest that dominant species with beneficial traits drive key ecosystem processes like carbon storage and accumulation (Tucker et al., 2017).

The selection or mass ratio hypothesis proposes that species-rich communities are likely to include species whose traits enhance ecosystem function. Abundance-weighted measurements also illustrate how common species with traits that favour carbon sequestration influence ecosystem function. Metrics that emphasize structural dominance, such as tree size (including height and diameter), basal area, and biomass, complement this perspective by illustrating how large tree characteristics influence carbon storage capacity. These findings are relevant in primary, climax, old growth and undisturbed forests, where large and tall trees play a crucial role in ecosystem functioning (Lutz et al., 2018). By combining abundance-, carbon weighted functional and phylogenetic relatedness indices, I aim to provide a more comprehensive view of the role of biodiversity in ecosystem productivity.

Therefore, I hypothesize that forests with functionally distinct and phylogenetically distant with favourable environmental conditions are more resilient and efficient at accumulating and storing carbon, whereas water stress reduces this ability.

Second, unweighted and abundance- and size-weighted community functional traits, functional and phylogenetic diversity affect AGC accumulation differently depending on species traits, dominance, and environmental conditions (Figure 31). I answer the following questions in this chapter. What specific functional traits promote AGC accumulation when weighted by abundance and carbon metrics? How does variability in functional traits between dominant carbon-rich species influence AGC storage efficiency? How does phylogenetic diversity, weighted by abundance and carbon, affect AGC accumulation rates in different forest types in the Western Ghats? Are communities resilient to climate variability in terms of AGC accumulation rates?

3.2 Methods

3.2.1 Data description

The central western ghats low elevation evergreen forest (CWG-L-EV) represents a wet lowland tropical evergreen forest located in the foothills of the Western Ghats within the Pushpagiri Wildlife Sanctuary in Karnataka, India (Figure 32 & 34). This site, part of the west coast tropical evergreen forest type (Champion & Seth, 1968; Pascal, 1988), experiences heavy monsoonal rainfall, with an annual average precipitation of around 5100 mm, most of which falls between June and October during the southwest monsoon. Peak rainfall occurs between June and August (>1000 mm), and rainfall is minimal from December to March (<100 mm). The dominant tree species here include *Dipterocarpus indicus* (Dipterocarpaceae), *Kingiodendron pinnatum* (Fabaceae) and *Humboldtia brunonis* (Fabaceae). In 1990, four 1 ha linear plots (~350 x 20 m) were laid out at an elevation of 450 m in the mid-elevation wet evergreen forest. As with other long-term monitoring plots, all woody stems ≥ 10 cm DBH were tagged, mapped, and identified following Condit's (1999) standardized protocol. The trees in these plots were monitored in 1990, 1994, 1998, 2002, 2007, and 2010 by Dr. BR Ramesh from French Institute Pondicherry and published the data (Pélissier et al. 2011) (Table 24).

The Southern Western Ghats Medium Evergreen Forest (SWG-M-EV) sites are located within the topographically heterogeneous Southern Western Ghats in the Kalakad Mundanthurai Tiger Reserve (KMTR) (Figure 33). The region experiences both southwest and northeast monsoons with an average annual rainfall of over 3500 mm, with most rainfall concentrated in the northeast monsoon season. The average maximum temperature is around 24°C, while the minimum temperature is around 16°C. The site locations in KMTR are located at an altitude of 1200 m, amidst moist, evergreen, medium-altitude tropical forests. The predominant tree species here include *Cullenia exarillata* (Bombacaceae), *Palaquium ellipticum* (Sapotaceae) and *Aglaia bourdillonii* (Meliaceae). Three 1 ha linear plots (250 x 40 m) were established at this elevation in which all stems ≥ 10 cm DBH were marked, mapped and identified according to the methods described by Condit (1999). These plots were monitored over several time periods: 1999, 2004, 2011, 2016, and 2021 by Dr R Ganesan from Ashoka Trust for Research in Ecology and Environment (ATREE) (Ganesh et al. 1996) (Figure 33, Table 24). In March 2021, I also conducted wood core collection using an incremental core drill to estimate wood density by water displacement (Pérez-Harguindeguy et al. 2013).

The Biligiri Rangaswamy Temple Tiger Reserve (BRT) in Karnataka, India represents a dry tropical forest system (Figure 35). This location is characterized by an elevation range of 600 m to 1500 m above sea level and an annual precipitation gradient of 600 mm in the lower elevations to 3000 mm in the higher elevations. BRT is subject to strong seasonal fluctuations with temperatures between 9°C (minimum) and 40 °C (maximum). The landscape is mainly composed of dry deciduous and scrub forests, which cover almost 90% of the protected area. The predominant species in these forests include *Acacia chundra*, *Diospyros melanoxylon* and *Chloroxylon swietenia* in the scrub forests and *Terminalia anogeissiana*, *Terminalia crenulata* and *Terminalia bellirica*

(all belonging to the *Combretaceae* family) in the dry deciduous forests. Ten 1 ha square plots (100 x 100 m) were established in this region, with five plots in scrub forest and five in dry deciduous forest (DDF). All logs ≥ 1 cm DBH were marked, mapped and identified using the protocol of (Condit 1998), making this site notable for the inclusion of smaller logs. Monitoring took place at regular intervals in 2002, 2007, 2011 and 2017 by Dr R Ganesan from Ashoka Trust for Research in Ecology and Environment (ATREE) (Table 24).

The long-term ecological monitoring plots at KMTR, BRT, and Uppangala offer crucial data on forest dynamics across a wide range of tropical forest types (Table 24). The standardized monitoring protocols, as established by Condit (1999), allow for consistent tracking of species composition, growth patterns, and forest structure over time. These plots represent diverse ecosystems -from the wet evergreen forests of KMTR and Uppangala to the dry deciduous and scrub forests of BRT -and provide insights into how tropical forests respond to varying environmental pressures, including rainfall variability, topographical challenges, and seasonal temperature fluctuations. The comprehensive data from these sites contribute significantly to our understanding of tropical forest resilience and their ability to adapt to changing environmental conditions.

3.2.2 Estimation of Above Ground Biomass Carbon and accumulation

Similar to section 2.2.2. In addition to that I have considered AGC gains based on individual growth of surviving trees and recruitment into the 10 cm DBH category, I divided AGC gains by the number of years between census intervals for analysis:

$$\text{AGC gains} = \frac{\text{AGC growth} + \text{AGC recruitment}}{\text{Number of years}}$$

3.2.3 Environmental variables

I have used functions from “*sp*” and “*raster*” packages in R to obtain daily temperature, precipitation and elevation data for each plot and monitoring year from the WorldClim data set (<https://www.worldclim.org>). Information on El Nino Southern Oscillation (ENSO) was collected from the Australian Bureau of Meteorology <http://www.bom.gov.au/climate/history/enso/> . The Oceanic Nino Index is an accepted criteria used by the National Oceanic and Atmospheric Administration (NOAA) for identifying El Nino (warm) and La Nina (cool) events in the tropical Pacific (3.4 region i.e., 5 N-5 S, 120 E-170 W).

For each census interval I extracted monthly precipitation values and assumed 100 mm evapotranspiration to calculate a maximum climatological water deficit (CWD) a commonly used metric of dry season intensity for tropical forests (Hubau, Lewis, Phillips, Affum-Baffoe, Beeckman, et al. 2020; Sullivan et al. 2020). Monthly CWD values were calculated for each subsequent series of 12 months (complete years). The monthly CWD estimation begins with the wettest month of the first year in the interval and is calculated as monthly evapotranspiration (ET) minus monthly precipitation (P). Then, CWD values for the subsequent 11 months (i) were calculated recursively as: $\text{CWD}_i = \text{ET} - \text{P}_i + \text{CWD}_{i-1}$, where negative CWD_i values were set to

zero (no drought conditions; adapted from Hubau et al., 2020). I then calculated the annual maximum climatic water deficit (MCWD) as the largest monthly CWD value for every complete year within the census interval. Larger MCWD values indicate more severe water deficits.

3.2.4 Functional traits diversity

I have collected functional trait values for maximum attainable diameter and height, wood density, leaf area, leaf nitrate mass, leaf mass area and diaspore mass. I have estimated the maximum attainable diameter and height from the dataset. Wood density, leaf area, leaf nitrate mass, leaf mass area and diaspore mass were determined from (Díaz et al. 2022). For traits like Leaf Area, Leaf Nitrogen Mass, and Leaf Mass per Area, a substantial portion of the data is available at the species level, covering 82%, 78%, and 79% of species respectively (Table 25).

I have estimated community weighted mean of functional traits including the weights of presence (unweighted), abundance and carbon (instead of basal area) using “*weighted.mean*” function from “*dplyr*” R package. I have used abundance and carbon weights as an indicator of plants performance. Because I find species like *Terminalia anogeiessiana* in dry forests and *Agrostistachys boornensis* are highly abundant but structurally smaller in size but accumulate and stock AGC with their higher abundance. However, species like *Cullenia exarillata* and *Vateria indica* are as large statured trees accumulating and stock large proportions of AGC. I find variations among unweighted, abundance and carbon weighted community means (CWM) (Figures 36 & 37).

I have also estimated presence, abundance and carbon weighted functional richness, divergence, evenness and dispersion metrics using “*dbFD*” function from “*FD*” R package. I find variations among unweighted, abundance and carbon weighted functional diversity indices (Figures 38-39). However, the density for functional evenness appears highly skewed, with a sharp peak at one end. This suggests a lack of variability in this metric across the weighting schemes. And also functional richness did not vary among weighted schemes.

3.2.5 Phylogeny reconstruction

Same as section 1.2.3. (Figures 40-42)

3.2.6 Phylogenetic diversity metrics

Similar to section 1.2.4. However, I have included abundance and above-ground carbon (AGC) weights in estimations of functional traits community weighted mean (CWM), and phylogenetic (mean pairwise distance (MPD) and phylogenetic mean nearest taxon distance (MNTD)) diversity metrics. The difference between abundance and dominance and presence weighted mean pairwise distance (MPD) and mean nearest taxon distance (MNTD), and standardized effect size (SES) metrics, lies in how they account for species abundance and dominance in their calculations (Figure 43 & 44). Presence weighted MPD and MNTD based on presence based distance matrix reflects the overall phylogenetic structure of a community. In contrast, abundance-weighted MPD and MNTD modify these calculations by weighting the distances by the relative abundance of each species, meaning that more abundant species have a greater influence on the overall metric. When

incorporating above-ground carbon (AGC) weights into these metrics, the focus shifts to the stand structural dominance of species. AGC-weighted MPD and MNTD account for the carbon stored in the above-ground parts of each woody plant or tree species, thereby adjusting the metric to reflect the influence of species with greater structural dominance on the phylogenetic structure (Figure 43 & 44). This approach highlights how dominant species in terms of both abundance and carbon shape the community's phylogenetic diversity. Essentially, presence weighted metrics provide a comprehensive overview of phylogenetic diversity, while abundance-weighted and AGC-weighted metrics offer deeper insights into how species abundance and biomass influence phylogenetic composition of a community.

3.2.7 Statistical analysis

To explore the relationships between Above-Ground Carbon (AGC) accumulation rates and explanatory variables representing environmental, functional, and phylogenetic diversity, I developed multiple linear mixed-effects models. Separate models were created for community-weighted means (CWM), functional diversity, and phylogenetic diversity metrics. Each metric was calculated under three distinct weighting schemes: presence, abundance, and carbon weights. Random effects for site and census terms were included to account for spatial and temporal autocorrelation, ensuring robust parameter estimates.

To facilitate meaningful comparison of predictors, all explanatory variables were standardized using the "scale" function in R. The response variable, AGC accumulation, was square root transformed to meet the assumptions of normality, as determined by residual diagnostic plots (Figure 45). This transformation minimized skewness and ensured that model residuals followed a normal distribution.

To mitigate potential multicollinearity, I conducted Pearson correlation analysis among explanatory variables and excluded predictors with correlation coefficients exceeding ± 0.7 (Figure 46). Additionally, Variance Inflation Factor (VIF) analysis was performed on retained variables to ensure that VIF values were below 5 (table 26). This step minimized collinearity while retaining key predictors necessary for explaining AGC accumulation patterns.

The significance of predictor slopes was assessed by calculating 95% confidence intervals (CIs) for each parameter. Confidence intervals were determined as the parameter estimate $\pm (1.96 \times \text{standard error})$. Predictors with CIs overlapping zero were considered nonsignificant at the 0.05 level, ensuring a robust interpretation of the effects.

I evaluated model performance using the Akaike Information Criterion (AIC), where lower values indicated better model fit. Additionally, marginal R^2 (variance explained by fixed effects) and conditional R^2 (variance explained by both fixed and random effects) metrics were calculated to assess the explanatory power of the models.

To ensure the robustness of the model, several diagnostic tests were carried out to satisfy the normality, homoscedasticity and linearity assumptions. Model residuals were visually inspected

using Q-Q plots and histograms to confirm their adherence to a normal distribution. Homoscedasticity assumptions of the model was confirmed by plotting residuals against fitted values. Patterns or trends in these plots would indicate heteroscedasticity and prompt possible model adjustments. The independence of the residuals was checked by plotting the residuals based on census term and forest types. No significant autocorrelation was observed, confirming the adequacy of the random effects structure.

To disentangle the independent and joint contributions of abiotic and biotic factors, I performed variation partitioning analysis of response (AGC gain) and predictors utilising the “*varpart*” function from the “*vegan*” R package. This analysis decomposed the variance in AGC accumulation into pure abiotic contributions (MCWD and elevation), pure biotic contributions (CWM, functional, and phylogenetic diversity), and shared contributions of abiotic and biotic factors. The unweighted or presence, abundance, and size-weighted metrics were analysed independently.

The main objective of this methodological framework was to determine the relative contributions of environmental, functional and phylogenetic diversity metrics and their interactions in shaping AGC accumulation rates in the species-rich tropical forests of the Western Ghats. By integrating robust statistical techniques, comprehensive diagnostics and variation partitioning, this study provides a detailed understanding of the ecological processes underlying carbon dynamics in this critical hotspot.

3.3 Results

3.3.1 Disproportionate AGC storage and temporal patterns in accumulation rates between forest types

I have found significant differences in AGC stocks and accumulation rates between forest types (Table 27). The mid-elevation evergreen forests of the Southwestern Ghats (SWG-M-EV) consistently exhibited the highest AGC stocks, ranging between 274 and 290 Mg ha⁻¹, during the observation period (Table 27). Primarily due to higher annual rainfall and lower seasonality. On the other hand, the low-elevation evergreen forests of the Central Western Ghats (CWG-L-EV) had AGC stocks much lower than SWG-M-EV between 112 and 121 Mg ha⁻¹. However, although, CWG-L-EV forests receive more rainfall than SWG-M-EV forests, their longer dry season compared to SWG-M-EV restrict their carbon storage capacity. Furthermore, large trees in SWG-M-EV are not only abundant but also stored significantly more AGC than those in CWG-L-EV forests.

The DDF forests had much lower AGC stocks, ranging between 38 and 42 Mg ha⁻¹, despite the presence of large trees (Table 27). Conversely, scrub forests with only 11 to 14 Mg ha⁻¹ AGC stocks are also characterized by the absence of large trees, but are characterized by a high stem density per hectare of species with resprouting abilities. This pattern is primarily due to the dry season lasting more than six months, which primarily limits carbon accumulation.

Only SWG-M-EV forests displayed more variation in AGC accumulation from 3.57 to 1.86 Mg ha⁻¹ year⁻¹ when compared to other forest types (Figure 47, Table 27). AGC accumulation was higher in 2000 and 2012 due to the favorable climate, but El Nino-caused droughts caused decline in AGC accumulation. On the other hand, AGC accumulation in CWG-L-EV forests decreased slightly but steadily from 1.93 to 1.48 Mg ha⁻¹ year⁻¹, indicating the impact of longer dry seasons. AGC accumulation rates were considerably lower in scrub forests and dry deciduous forests (DDF), ranging from 0.41 to 0.82 Mg ha⁻¹ year and 0.55 to 0.88 Mg ha⁻¹ year, respectively (Figure 47, Table 27). These trends most likely represent potential limits on physiological stress due to maximum climatic water deficit.

I have observed that some dominant species contribute disproportionately to stand-level above ground carbon stock (AGC) and accumulation in all four forest types in this study (Table 28). In the mid elevation evergreen forests of the Southwestern Ghats (SWG-M-EV), the dominant species *Cullenia exarillata*, *Palaquium ellipticum*, and *Myristica beddomei* together stored 53.9% (151.8 Mg ha⁻¹), 16% (45.1 Mg ha⁻¹), and (15.84 Mg ha⁻¹) of the total AGC (Table 23). In the low-elevation evergreen forests of the Central Western Ghats (CWG-L-EV), *Vateria indica*, *Dipterocarpus indicus* and *Myristica dactyloides* contributed 21.1% (24.92 Mg ha⁻¹), 14.9% (17.63 Mg ha⁻¹), and 12% (14.21 Mg ha⁻¹) of the total AGC stocks. In the dry deciduous forests (DDF), species from the genus *Terminalia*, including *T. anogeissiana*, *T. elliptica*, and *T. bellirica*, dominated AGC storage, contributing 36.8% (14.8 Mg ha⁻¹), 13.1% (5.3 Mg ha⁻¹), and 12.6% (5.1 Mg ha⁻¹), respectively. In the scrub forests, the predominant species *Chloroxylon swietenia*, *Hardwickia binata* and *Dalbergia lanceolaria* stored 31.1% (4.06 Mg ha⁻¹), 15.5% (2.0 Mg ha⁻¹) and 14.5% (1.89 Mg ha⁻¹) AGC stocks. Among these, *Cullenia exarillata*, *Palaquium ellipticum* and *Vateria indica* were also the largest AGC accumulators in the Western Ghats, with accumulation rates of 1.44, 0.51 and 0.44 Mg ha⁻¹ year⁻¹, respectively (Table 28).

3.3.2 Effects of abiotic variables on AGC accumulation rates

The maximum climatic water deficit (MCWD) has a significant negative effect on AGC accumulation rates (Figure 48, Table 30). This finding highlights the critical role of water deficits induced by latitudinal gradient in regulating carbon accumulation in tropical forest ecosystems of Western Ghats. In contrast, elevation does not appear to have a significant influence on AGC accumulation, suggesting that the effects of altitude-related climatic and environmental gradients may be less pronounced than water deficit in the region studied. These results highlight MCWD as an important abiotic driver of AGC dynamics and highlight the need for targeted management strategies in areas with high climatic water deficit.

3.3.3 Effects of Community Weighted Means (CWM) on AGC accumulation rates

The community unweighted mean of wood density exhibited significant negative effects, suggesting that communities dominated by species with denser wood may have slower carbon accumulation, potentially owing to trade-off between growth rate and structural investment (Figure 48, Table 31). In contrast, the community abundance and carbon weighted means of seed diaspore mass had significant positive effects, indicating that traits favouring dispersal or reproduction

investment may enhance AGC accumulation. Additionally, the unweighted mean of leaf area showed significant negative effects on AGC accumulation which may reflect trade-offs between larger leaf sizes and growth or carbon storage efficiency.

3.3.4 Effects of functional diversity on AGC accumulation rates

Abundance weight-based functional richness has significant positive effects on AGC accumulation rates, highlighting the role of various functional traits in improving carbon accumulation in tropical forests (Figure 48, Table 32). However, depending on the weighting method, opposite effects were observed for functional evenness and dispersion. In particular, the unweighted community mean of functional evenness showed significant positive effects on AGC accumulation rates, suggesting that communities with more evenly distributed functional traits may achieve higher AGC accumulation. Conversely, abundance-weighted functional evenness had significant negative effects, perhaps suggesting that trait dominance of a few common species may limit AGC accumulation. However, I encounter limitations in estimates of feature richness and evenness. I find that functional richness shows no differences across all weights. The density for functional evenness appears to be highly skewed, with a sharp peak at one end. This suggests a lack of variability in this metric between weighting schemes.

I found significant positive effects of abundance-weighted functional dispersion on AGC accumulation rates, suggesting that trait variability in dominant species increases AGC. In contrast, size-weighted functional dispersion showed significant negative effects, suggesting that trait variability between species that contribute most to carbon stock may not always result in higher AGC accumulation. These contrasting trends highlight the complexity of the interactions between trait diversity, species dominance, and ecosystem function.

3.3.5 Effects Phylogenetic diversity on AGC accumulation rates

The analysis shows that metrics of phylogenetic diversity significantly influence AGC accumulation rates (Figure 48, Table 33). In particular, the abundance-weighted SES MPD (standardised effect size of mean pairwise distance) and size-weighted SES MNTD (standardised effect size of mean nearest taxon distance) show significant positive effects on AGC accumulation rates. The positive effects suggest, that cooccurrence of abundant or structurally dominant and phylogenetic distantly related species with distinct functional traits, increases AGC accumulation, due to complementary resource use. These results highlight the importance of phylogenetic diversity in shaping ecosystem processes.

3.3.6 Shifting contributions of environment, functional and phylogenetic diversity across unweighted, abundance and size-weighted models

I have assessed the independent and joint contributions of environmental factors, community-weighted means (CWM), functional diversity, and phylogenetic diversity in unweighted, abundance-weighted, and size-weighted models (Figures 49-51). I find that contributions shift under different weighting schemes, providing insights into independent and joint contributions of

abiotic and biotic variables in explaining AGC accumulation rates in western ghats biodiversity hotspot.

The independent contribution of the environment decreased significantly in all models, from 6.6% in the unweighted model to 2.5% in the abundance-weighted model and further to 1.1% in the size-weighted model. The role of the environment decreases when abundance and carbon are considered as weighting factors in estimating functional and phylogenetic diversity.

The community weighted means independent contribution increased from 0.5% in the unweighted model to 0.7% in the abundance-weighted model and increased significantly to 4.1% in the size-weighted model. This pattern highlights the growing influence of species traits (weighted by carbon metrics) on AGC accumulation in the carbon weighted model.

The independent contribution of functional diversity, on the other hand, steadily declined from 2.7% in the unweighted model to 1.5% in the abundance-weighted model and, finally, to 0% in the size-weighted model. According to this, other factors might amplify the impact of functional diversity, especially in size-weighted models. .

Phylogenetic diversity showed a consistent independent contribution, with higher values in the weighted models. compared to its value in the unweighted model, 2.1% in the abundance-weighted model and 1.6% in the size-weighted model. This indicates that phylogenetic relatedness among abundance and carbon weights better explains the variance for AGC accumulation.

The combined effects of CWM and the environment decreased from 7.6% in the unweighted model to 4.3% in the abundance-weighted model but increased to 5.5% in the size-weighted model. This recovery in the carbon model suggests a stronger interaction between traits and environmental variables within the carbon weighting model in explaining AGC accumulation.

The joint contributions of functional diversity and environment followed a decreasing trend, from 6.2% in the unweighted model to 5.2% in the abundance-weighted model and further decreased to 1.8% in the size-weighted model. This reduction is consistent with the decreasing independent role of functional diversity in the carbon model.

The absence of combined effects between phylogenetic diversity and environment suggests that phylogenetic diversity drives AGC accumulation patterns independently of environmental factors. There was a clear shift in the combined contributions of CWM, functional diversity, and environment. These increased dramatically, from 0.9% in the unweighted model to 19.4% in the abundance-weighted model and further to 37.7% in the size-weighted model. This significant increase highlights the complex interaction of traits, diversity and environment in the size-weighted model in explaining AGC accumulation patterns.

The joint contribution of CWM, phylogenetic diversity, and the environment exhibited mixed trends: it was 5.4% in the unweighted model, dropped to 1.1% in the abundance-weighted model, and then rose to 2.8% in the size-weighted model. This fluctuation suggests that the inclusion of carbon weighting alters the relative importance of phylogenetic diversity in joint effects.

According to my findings, size-weighted models are able to capture more intricate and cooperative relationships than either abundance-weighted or unweighted models. In the carbon model, CWM becomes the dominant factor, and functional diversity becomes less important. In elucidating AGC accumulation patterns, the combined effects of traits, diversity, and environment are especially noticeable in carbon weighting, which reflects the intricate ecological dynamics connected to structural dominance.

Overall, the results highlight the importance of considering different weighting schemes when identifying the complex contributions of functional and phylogenetic diversity variables. The size-weighted diversity model provides a more comprehensive view of the relationships between environment, functional traits and phylogenetic diversity.

3.4 Discussion

The trade-off between carbon uptake through tree growth and release through tree mortality is essential to the carbon balance of tropical ecosystems, which has a significant impact on climate change. These processes are driven by environmental factors such as rainfall and temperature, yet the responses of tropical forests to changing climatic conditions remain unclear. This is particularly relevant for the Western Ghats, India, one of the 36 global biodiversity hotspots, which harbours extensive and diverse tropical forests, comprising rare and endemic species.

The Western Ghats experience a tropical monsoon climate characterized by distinct wet and dry seasons. Most rainfall occurs during the southwest monsoon (June to September) and the northeast monsoon (October to December), with a summer dry season lasting from December to March. During the dry season, low rainfall, high temperatures and low humidity enforce a physiological stress on forest ecosystems, influencing their carbon dynamics.

I observe significant differences in AGC stocks among forest types. Southwestern Ghats mid-elevation evergreen forests (SWG-M-EV) exhibited the highest AGC stocks, ranging from 274 to 290 Mg ha⁻¹ over the observation period (Table 27). This is likely driven by higher annual precipitation and reduced seasonality compared to other forest types. In contrast, Central Western Ghats low-elevation evergreen forests (CWG-L-EV) had moderate AGC stocks (112 to 121 Mg ha⁻¹), constrained by a longer dry season and higher climatic water deficits. Notably, large trees in SWG-M-EV forests stored significantly more AGC than those in CWG-L-EV forests.

Dry deciduous forests (DDF) exhibited much lower AGC stocks, ranging from 38 to 42 Mg ha⁻¹, despite the presence of large trees (Table 27). Scrub forests, with AGC stocks of only 11 to 14 Mg ha⁻¹, had high stem density per hectare but lacked large trees. The lower precipitation and prolonged dry season (exceeding six months) in these forest types likely limit their carbon accumulation potential.

Temporal patterns revealed variability in AGC accumulation rates across forest types. SWG-M-EV forests showed the highest accumulation rates, ranging from 3.57 to 1.86 Mg ha⁻¹ year⁻¹ (figure 47 & Table 27). Peaks around 2000 and 2012 correspond to favorable environmental conditions, while

declines in recent years align with El Nino-induced droughts. In contrast, CWG-L-EV forests exhibited moderate but consistent reductions in AGC accumulation rates, from 1.93 to 1.48 Mg ha⁻¹ year⁻¹, driven by prolonged dry spells and higher climatic water deficits.

DDF and scrub forests displayed significantly lower AGC accumulation rates, ranging from 0.55 to 0.88 Mg ha⁻¹ year⁻¹ and 0.41 to 0.82 Mg ha⁻¹ year⁻¹, respectively (Figure 47 & Table 27). These patterns likely reflect physiological stress caused by extreme climatic water deficits, which limit growth potential in these forest types.

These results indicate a significant reduction in AGC stocks and accumulation rates with increasing maximum climatic water deficits (MCWD). The impacts of El Nino Southern Oscillation (ENSO) phases are particularly evident, with El Nino-induced prolonged dry spells during 2002–2003, 2004–2005, and 2006–2007 reducing AGC gains across forest types (Table 29). These patterns mirror findings in other tropical regions, including Amazonian, African, and Southeast Asian forests, where El Nino events reduce AGC accumulation through stem growth suppression and recruitment failure (Bennett et al. 2023; Hubau, Lewis, Phillips, Affum-Baffoe, Beeckman, et al. 2020; Qie et al. 2017).

Globally, AGC in tropical forests is concentrated in a remarkably small number of highly abundant species (Bastin et al. 2015b; Fauset, Michelle O. Johnson, et al. 2015; Lee et al. 2002). Similarly, my findings indicate that a few dominant species disproportionately contribute to AGC stocks across all forest types in the study.

In the southwestern Ghats mid elevation evergreen forest (SWG-M-EV), *Cullenia exarillata*, *Palaquium ellipticum*, and *Myristica beddomei* collectively stored 53.9% (151.8 Mg ha⁻¹), 16% (45.1 Mg ha⁻¹), and 10% (15.84 Mg ha⁻¹), respectively, of total AGC (Table 28). In the Central Western Ghats low-elevation evergreen forests (CWG-L-EV), dominant species like *Vateria indica* contributed 21.1% (24.92 Mg ha⁻¹), followed by *Dipterocarpus indicus*, 14.9% (17.63 Mg ha⁻¹), and *Myristica dactyloides* 12% (14.21 Mg ha⁻¹) of total AGC stocks. In the dry deciduous forests (DDF), species from the genus *Terminalia*, including *T. anogeissiana*, *T. elliptica*, and *T. bellirica*, dominated AGC storage, contributing 36.8% (14.8 Mg ha⁻¹), 13.1% (5.3 Mg ha⁻¹), and 12.6% (5.1 Mg ha⁻¹), respectively. Among these, *Cullenia exarillata*, *Palaquium ellipticum* and *Vateria indica* were also the largest AGC accumulators in the Western Ghats, with accumulation rates of 1.44, 0.51 and 0.44 Mg ha⁻¹ year⁻¹ respectively (Table 28).

These findings align with global trends, where large, abundant species play a disproportionate role in carbon storage (Ali et al. 2019; Bastin et al. 2015b; Pioniot et al. 2022; Slik et al. 2013). Large trees store significant quantities of carbon and contribute significantly to accumulation under changing climatic conditions. Recent studies have highlighted that large size class trees drive AGC stock and dynamics in tropical (Ali et al. 2019; Bastin et al. 2015b; Pioniot et al. 2022; Slik et al. 2013) and temperate forests (Yuan et al. 2021b).

The unweighted community mean of wood density demonstrates significant negative effects on carbon accumulation, highlighting a critical trade-off in forest ecology (Figure 48 & Table 31).

Communities dominated by species with denser wood exhibit slower carbon accumulation compared to those with softer wood. This dynamic is particularly evident across forest types, where denser wood is more prevalent in dry forests and softer wood in evergreen forests.

This pattern can be explained with three ecological mechanisms. First, in dry forests, climatic water deficit imposes significant hydraulic constraints on trees. To enhance survival under these conditions, species prioritize structural investment by producing denser wood, which confers greater mechanical strength and drought resilience (Prado-Junior et al. 2016). However, this prioritization comes at a cost of reduced growth rates, slowing biomass accumulation and consequently carbon storage rates (Becknell et al. 2021; de Meira Junior et al. 2020). Second, high fire frequency in dry forests further amplifies the selection of denser wood. Denser wood is less flammable and contributes to post fire survival, yet this adaptation reduces the community's ability to sequester carbon rapidly, as slow growing, fire resistant species dominate (Kodandapani et al. 2008; Otterstrom et al. 2006; Pulla et al. 2015). Third, the intrinsic trade-off between structural investment and growth rate underscores the observed pattern. While denser wood enhances longevity and persistence, it limits the capacity for rapid biomass turnover and carbon uptake, contrasting sharply with the faster dynamics of softer wood species in evergreen forests.

Thus, have following implications for forest carbon storage. In evergreen forests, with lower water deficit and fire frequency, species in evergreen forests invest less in structural density, resulting in softer wood. This allows for faster growth and higher biomass turnover, leading to more rapid carbon accumulation. In contrast the dominance of dense wood species in dry forests contributes to slower carbon accumulation despite potentially longer-term carbon storage. This pattern reflects the ecological trade off imposed by environmental stressors such as water deficit and fire.

This hypothesis integrates the complex interplay of biotic traits and abiotic pressures in shaping forest carbon dynamics. It suggests that dense wood species while critical for ecosystem stability in stressful environments, constrain the pace of carbon sequestration, these findings underscore the need to consider trait environment interaction when evaluating forest carbon dynamics across biomes.

The community abundance and size weighted means of seed diaspore mass exhibited significant positive effects on AGC accumulation, aligning with the mass ratio hypothesis (Figure 48 & Table 31). This hypothesis suggests that dominant species with traits maximizing ecosystem functions disproportionately drive carbon storage and accumulation. Large seed diaspore mass is strongly linked with large stature trees, which are characterised by slow growth, long life spans, and substantial carbon accumulation capabilities (Lohbeck et al. 2015).

In this study, larger seed diaspore mass is predominantly found in evergreen forests, while smaller seed diaspore mass more common in dry forests (Figure 36). This pattern reflects environmental filtering, where water availability and resource competition favour large seeds in evergreen forests, enabling species to establish and dominate under shaded, nutrient demanding conditions (Shivaprakash et al. 2018).

Large seed diaspores are linked with large stature, longevity and resilience and enhanced reproductive success (Nerlekar et al. 2019). Species with large seeds, like *Cullenia exarillata* and *Palaquium ellipticum*, grow into slow-growing long-living trees with substantial structural biomass (Ganesh et al. 1996). These species exhibit low mortality rates and contribute to carbon storage over extended periods. Larger seeds provide nutrient reserves for seedling establishment, ensuring higher survival rates in competitive understory environments (Ganesan 2001; Selwyn and Ganesan 2009).

Larger seed diaspores are often dispersed by large mammals and birds, such as the endemic and endangered lion tailed macaques (Ganesh 1995; Ganesh and Davidar 2001; 1999). These dispersal agents facilitate long distance seed transport, reducing negative neighbourhood density effects of conspecifics on seedling survival and growth (Seidler and Plotkin 2006). This process helps maintain genetic diversity and forest composition, further supporting AGC accumulation.

Dominant tree species like *Cullenia exarillata* and *Palaquium ellipticum* play a pivotal role in AGC accumulation, storing significantly higher quantities of carbon per hectare per year compared to other tree species in the study. These trees, dispersed by lion tailed macaques, form a critical component of the forest carbon storage potential. Their contribution emphasizes the interconnectedness of biodiversity, species traits and ecosystem processes (Ganesh and Davidar 1999).

The reliance of large seed species on faunal dispersers underscores the importance of maintaining animal populations in tropical forests. Defaunation caused by habitat destruction, hunting and climate change can disrupt seed dispersal networks (Bello et al. 2015; Harrison et al. 2013). This in turn limits the recruitment of large seed species, reducing the forest's capacity for carbon storage and accumulation. Studies have shown that forests with reduced densities of large seed dispersers exhibit shifts toward species with smaller seeds, which may store less carbon over time (Osuri et al. 2016). Protecting large arboreal mammals and birds is therefore essential for maintaining tropical forest carbon dynamics (Chanthorn et al. 2019).

The positive effects of seed diaspore mass on AGC accumulation underscore the critical role of large seed species in tropical forest carbon dynamics. Species like *Cullenia exarillata* and *Palaquium ellipticum* exemplify how ecological traits and faunal interactions drive carbon storage processes. However, the disruption of these interactions through defaunation threatens to undermine forest resilience and carbon sequestration (Chanthorn et al. 2019). Conservation strategies must prioritise protecting key dispersers, like lion tailed macaques, and their habitats to sustain the ecological and carbon storage functions of tropical forests (Devy and Ganesh 2021).

For functional dispersion, I found significant positive effects of abundance weighted functional dispersion on AGC accumulation rates (Figure 48 & Table 32). This finding suggests that trait variability among dominant species enhances AGC accumulation. In contrast, carbon weighted functional dispersion exhibited significant negative effects, indicating that variability among species contributing most to carbon stocks may not always translate into higher AGC accumulation.

These opposing trends underscore the complexity of interactions between trait diversity, species dominance and ecosystem functioning.

Abundance weighted functional dispersion reflects the variability in functional traits among the dominant species within a community (Figure 48 & Table 32). This variability enhances AGC accumulation for following reasons. First, higher trait variability among dominant species allows ecosystems to exploit diverse resource pools more efficiently, reducing overlap in resource use and enhancing overall productivity. Second, the diversity of functional traits enables niche differentiation, where species perform distinct ecological roles. This reduces competition and increases the efficiency of resource capture, contributing to biomass accumulation and AGC storage. Studies have shown that ecosystems with higher functional diversity tend to be more productive and resilient (Hao et al. 2020). For example, tropical forest with diverse functional traits among dominant species exhibit higher AGC accumulation due to complimentary interactions (Finegan et al. 2015; Prado-Junior et al. 2016).

Size weighted functional dispersion emphasizes the traits of species that contribute most to carbon stocks (Figure 48 & Table 32). Unlike abundance weighted dispersion, higher variability in these traits may lead to inefficiencies, reducing AGC accumulation. Trait variability among high carbon contributors can indicate a lack of complementarity, where species with divergent traits fail to optimize resource use. This redundancy may lead to competition or inefficiencies in carbon sequestration processes. Dominance by species with diverse traits might destabilize carbon storage due to slower growth rates or reduced compatibility in ecological functions. Species contributing most to carbon stocks often exhibit slower growth rates. High variability in these traits could limit AGC accumulation by reducing uniformity in carbon storage efficiency.

The opposing effects of abundance weighted, and carbon weighted functional dispersion highlight the interplay between diversity, dominance and function. Abundance weighted dispersion prioritizes widespread trait variability, fostering resource capture and carbon assimilation. This mechanism aligns with the niche complementarity hypothesis, which suggests that functional diversity enhances ecosystem productivity. Size weighted dispersion focuses on dominant contributors, where extreme trait variability may hinder uniformity and efficiency in carbon storage. This effect aligns with the functional redundancy hypothesis, emphasising that variability among high carbon contributors might reduce ecosystem performance.

Understanding the contrasting effects of functional dispersion can guide conservation and restoration efforts. Focus on maintaining trait variability among dominant species to optimize resource use and AGC storage. While functional diversity is beneficial, excessive variability among high carbon contributors should be managed to avoid inefficiencies in carbon storage. Select species with complementary traits for planting efforts to maximize AGC accumulation while ensuring long term carbon storage stability.

The contrasting effects of abundance weighted, and size weighted functional dispersion illustrate the intricate relationships between trait diversity, species dominance, and ecosystem function.

While abundance weighted dispersion enhances AGC accumulation through optimized resource use, size weighted dispersion inefficiencies reflect the challenges of managing trait variability in high carbon contributors. These insights emphasise the need for targeted conservation strategies that balance functional diversity with ecosystem stability for maximizing carbon sequestration in forests.

Phylogenetic diversity metrics significantly influence AGC accumulation rates. Specifically, abundance weighted SES MPD (standardised effect size of mean pairwise distance) and size weighted SES MNTD (mean nearest taxon distance) exhibit significant positive effects on AGC accumulation (Figure 48 & Table 33). These findings highlight the critical role of phylogenetic relatedness among species in shaping ecosystem processes.

The following are the mechanisms underpinning the positive effects. First, greater phylogenetic diversity, especially when weighted by abundance or size, reflect functional trait divergence. Phylogenetic distant species are more likely to possess distinct traits that reduce niche overlap, enabling complementary resource use and higher overall productivity (Souza et al. 2019; Satdichanh et al. 2019). Second, phylogenetic distance correlates with unique evolutionary traits, such as nitrogen fixation, high wood density or specialised adaptations to resource use (Mensah et al. 2024; Chave et al. 2007). These traits can disproportionately enhance AGC accumulation by improving resource use efficiency and ecosystem stability. Third, abundance weighted SES MPD emphasizes the role of dominant species in driving ecosystem processes. Greater phylogenetic diversity among abundant species likely reflects functional complementarity, boosting biomass production (Jia and Wang 2024; Hao et al. 2018; Cadotte et al. 2009). Size weighted SES MNTD highlights the traits of species contributing most to carbon stocks. Positive effects suggest that phylogenetically distant dominant species possess traits enhancing carbon sequestration and storage (Souza et al. 2019).

Selecting species combinations that maximize phylogenetic diversity could enhance AGC accumulation in reforestation efforts. Including phylogenetically distant species ensures functional complementarity and improves ecosystem productivity. Preserving phylogenetic diversity is crucial for maintaining the ecosystem processes that support carbon storage. Conservation efforts should prioritize habitats with high phylogenetic diversity to safeguard their carbon sequestration potential. Abundance weighted and carbon weighted phylogenetic metrics provide complementary perspectives. Management strategies should consider both to optimize AGC accumulation and ecosystem stability.

The significant positive effects of abundance weighted SES MPD and size weighted SES MNTD on AGC accumulation rates highlight the importance of phylogenetic diversity in driving ecosystem processes (Figure 48 & Table 33). By promoting complementary resource use and incorporating unique traits from distant lineages, phylogenetic diversity enhances carbon storage efficiency. These findings emphasize the need to prioritize evolutionary relationships in biodiversity conservation and forest management to optimize carbon sequestration and support ecosystem resilience.

This study elucidates the shifting roles of environmental factors, functional diversity, and phylogenetic diversity in explaining AGC (above-ground carbon) accumulation across unweighted, abundance-weighted, and size-weighted models (Figures 49-51). The results reveal that the independent and joint contributions of these variables vary significantly under different weighting schemes, highlighting the complex interactions between abiotic and biotic factors in shaping carbon storage dynamics.

The independent contribution of environmental variables decreased markedly across the models, from 6.6% in the unweighted model to 2.5% in the abundance-weighted model and further to 1.1% in the size-weighted model (Figures 49-51). This trend suggests that while environmental factors set the foundational conditions for ecosystem processes, their relative importance diminishes as biotic factors like species abundance and size metrics become more prominent. Weighted models, particularly those emphasizing carbon stocks, appear to prioritize species-level traits and interactions over abiotic drivers, reflecting the increasing dominance of intrinsic ecological processes in explaining AGC accumulation.

CWM exhibited an opposite trend, with its independent contribution increasing progressively across the models, from 0.5% in the unweighted model to 0.7% in the abundance-weighted model and 4.1% in the size-weighted model (Figures 49-51). This pattern underscores the growing influence of species traits, particularly those linked to carbon storage such as wood density and growth rates, in determining AGC under size-weighted models. These findings emphasize that size-weighted models amplify the role of functional traits in structural dominance, aligning with ecological theories that traits directly related to biomass storage have the strongest impact on carbon dynamics.

The independent contribution of functional diversity declined progressively, from 2.7% in the unweighted model to 1.5% in the abundance-weighted model and eventually to 0% in the size-weighted model (Figures 49-51). This suggests that functional diversity's explanatory power diminishes when dominant species traits are accounted for, particularly in size-weighted models where structural traits of dominant species overshadow collective functional variability. This decline may reflect redundancy in functional traits, where the traits of carbon-dominant species alone suffice to explain AGC accumulation.

Phylogenetic diversity demonstrated a stable independent contribution across the models, with slightly higher values in weighted models, 2.1% in the abundance-weighted model and 1.6% in the size-weighted model compared to its contribution in the unweighted model. This consistency suggests that phylogenetic relatedness operates independently of environmental factors and functional diversity, offering evolutionary insights into AGC dynamics. Weighted models may better capture the unique contributions of phylogenetically distant species, which often possess distinct traits critical for carbon storage.

The joint contributions of traits, diversity, and the environment reveal intricate ecological interactions. For instance, the combined effects of CWM and environmental factors declined in the

abundance-weighted model (7.6% to 4.3%) but increased in the size-weighted model (5.5%), suggesting a stronger synergy between traits and environmental conditions under carbon-dominant scenarios. Similarly, the joint contributions of functional diversity and the environment decreased progressively, aligning with the diminished independent role of functional diversity in weighted models.

Interestingly, there were no joint effects observed between phylogenetic diversity and environmental factors across any model, reinforcing the idea that phylogenetic diversity operates independently of abiotic gradients. However, the joint contributions of CWM, functional diversity, and the environment increased significantly from 0.9% in the unweighted model to 19.4% in the abundance-weighted model and further to 37.7% in the size-weighted model (Figures 49-51). This dramatic rise reflects the intricate interplay of traits, diversity, and environmental variables in size-weighted models, where structural dominance magnifies the combined effects of these factors.

These findings underscore the importance of considering different weighting schemes to uncover the nuanced contributions of ecological variables to AGC accumulation. Size-weighted models capture more complex and synergistic interactions, offering a more integrative perspective on carbon dynamics. The prominence of CWM in size-weighted models highlights the need to prioritize traits directly linked to carbon storage in forest conservation and management strategies. Furthermore, the stable contribution of phylogenetic diversity suggests that preserving evolutionary lineages is essential for maintaining ecosystem stability and maximizing carbon sequestration. In contrast, the diminishing role of functional diversity in weighted models calls for its strategic use, especially in early successional stages or under less structured systems.

By disentangling the independent and joint contributions of environmental, functional, and phylogenetic diversity metrics, this study demonstrates the dynamic interactions driving AGC accumulation in the Western Ghats biodiversity hotspot. Size-weighted models emerge as particularly powerful in elucidating these interactions, emphasizing the importance of species traits and phylogenetic diversity over environmental gradients. These insights provide a robust framework for informing conservation strategies, reforestation efforts, and ecosystem management to optimize carbon storage in diverse forest systems.

This study highlights the complex interplay between environmental conditions, species traits, functional diversity and phylogenetic diversity in shaping aboveground carbon accumulation (AGC) in the Western Ghats, a global biodiversity hotspot. The results show significant differences in AGC stocks and accumulation rates between different forest types, with the highest carbon accumulation observed in the evergreen forests of the Southwest Ghats. These variations are mainly caused by differences in water availability, climatic factors and the dominance of certain tree species with characteristics suitable for their environment.

Examining the role of functional traits such as wood density and seed diaspore mass reveals critical trade-offs in carbon storage dynamics. Communities dominated by species with denser wood exhibit slower AGC accumulation, reflecting a trade-off between structural investment and growth

rate, particularly under conditions of high water stress and high fire frequency. In contrast, forests containing species with larger seed diaspores exhibit increased carbon accumulation, highlighting the importance of ecological traits such as tall stature, longevity, and resilience in promoting AGC storage. The role of faunal dispersers, such as lion-tailed macaques, further highlights the connection between biodiversity and carbon dynamics and highlights the cascading effects of defaunation on carbon sequestration potential.

Phylogenetic diversity was found to be a key factor in AGC accumulation, especially when weighted by abundance and size. Greater phylogenetic diversity among dominant species was associated with increased trait complementarity, reduced competition, and improved resource use efficiency, leading to enhanced carbon storage. This supports the idea that maintaining evolutionary relationships is critical to maintaining carbon dynamics and ecosystem resilience.

The results also show contrasting effects of functional dispersion on AGC accumulation. Abundance-weighted functional dispersion, reflecting greater trait variability between dominant species, was associated with increased AGC accumulation through niche differentiation and reduced competition. In contrast, size-weighted functional dispersion showed negative effects, suggesting that variability between carbon-dominant species can lead to inefficiencies in carbon sequestration, highlighting the challenges of managing trait diversity for carbon optimization.

Finally, I showed that the contributions of environmental, functional and phylogenetic diversity to AGC accumulation are highly dynamic and vary between unweighted, abundance-weighted and size-weighted models. The decreasing role of environmental factors in weighted models highlights the growing influence of intrinsic ecological processes, while the increasing importance of community weighted means (CWM) in size-weighted models highlights the importance of species-level traits related to carbon storage. The robust contribution of phylogenetic diversity across all models highlights its importance for ecosystem stability and carbon accumulation.

These findings have profound implications for conservation and reforestation strategies aimed at optimizing carbon sequestration in tropical forests. The significant role of large, phylogenetically divergent species in carbon accumulation emphasizes the need to prioritize these species in forest management and reforestation efforts. Conservation strategies must focus on maintaining functional and phylogenetic diversity, particularly in the face of changing climatic conditions and increasing defaunation pressures. Protecting key faunal dispersers and promoting species combinations that maximize phylogenetic and functional diversity will be crucial to sustaining the resilience and productivity of tropical forest ecosystems.

By incorporating different weighting schemes, this study provides a nuanced understanding of how species traits, ecological processes, and evolutionary history interact to drive carbon dynamics. In particular, size-weighted models capture the complex and synergistic relationships that contribute to AGC accumulation and provide a powerful tool for targeted conservation and management actions. Ultimately, effective management of functional and phylogenetic diversity is key to

maximizing carbon storage and ensuring the long-term stability of tropical forest ecosystems in the face of ongoing environmental change.

3.5 Conclusion

This study provides an integrative assessment of how environmental conditions, functional traits, and phylogenetic diversity interact to shape aboveground carbon (AGC) storage and accumulation in the tropical forests of the Western Ghats, a global biodiversity hotspot. By applying unweighted, abundance-weighted, and size-weighted models, I reveal how the relative importance of abiotic versus biotic drivers shifts with species dominance and carbon contribution.

These findings indicate that environmental stress, particularly climatic water deficit and extended dry seasons, significantly constrains AGC accumulation, whereas elevation and stable climatic conditions promote higher carbon storage. However, as models increasingly weight species by abundance or carbon contribution, the role of environmental variables diminishes, highlighting the growing influence of intrinsic ecological and evolutionary processes in regulating carbon dynamics.

Functional trait analyses underscore critical trade-offs that determine carbon storage potential. Communities dominated by dense-wood species, common in dry forests, exhibit enhanced resilience to drought and fire but lower AGC accumulation due to slow growth. In contrast, large-seeded species in evergreen forests contribute disproportionately to long-term AGC storage, supported by faunal dispersal networks that maintain recruitment and genetic diversity. These findings emphasize the ecological interconnectedness of plant traits and animal dispersers, and the cascading consequences of defaunation for forest carbon dynamics.

Phylogenetic diversity emerged as a consistent and independent predictor of AGC across all models. Greater phylogenetic divergence among abundant and carbon-dominant species was associated with enhanced niche complementarity, reduced competition, and improved resource use efficiency, thereby increasing carbon storage. This result highlights the dual importance of evolutionary history and structural dominance in driving ecosystem productivity, providing strong support for both the niche complementarity and mass ratio hypotheses.

Notably, functional dispersion exerted contrasting effects depending on the weighting scheme. Abundance-weighted functional dispersion enhanced AGC accumulation by increasing trait variability among dominant species, thereby promoting resource complementarity. In contrast, size-weighted dispersion negatively affected AGC, reflecting inefficiencies introduced by excessive trait divergence among high-carbon contributors. These patterns underscore the complexity of managing trait diversity for carbon optimization.

Taken together, the results demonstrate that conserving and enhancing AGC in tropical forests requires explicit consideration of both functional and phylogenetic diversity in tandem with environmental conditions. Size-weighted models in particular provide a powerful framework for

disentangling the joint contributions of traits, dominance, and evolutionary history, revealing the synergistic mechanisms underpinning carbon dynamics.

From a conservation and management perspective, these findings underscore the urgency of protecting phylogenetically diverse lineages, functionally important species, and key faunal dispersers that sustain recruitment and long-term carbon storage. Reforestation and restoration initiatives should prioritize species combinations that maximize both functional complementarity and evolutionary diversity to enhance resilience and optimize carbon sequestration under changing climatic conditions.

Ultimately, this study highlights the need for integrative biodiversity–carbon strategies that couple ecological, evolutionary, and environmental perspectives. Such an approach will be central to safeguarding the carbon balance and resilience of tropical forests in the Western Ghats and beyond, thereby contributing meaningfully to global climate mitigation efforts.

3.6 Figures and Tables

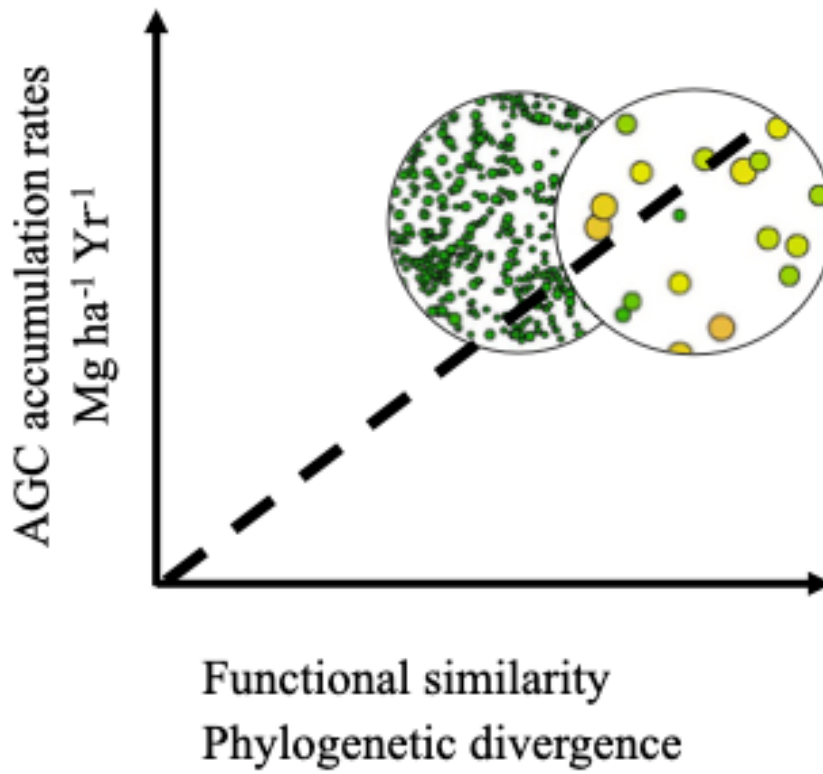


Figure 31: Conceptual framework linking phylogenetic community structure, environmental stress, and above ground carbon dynamics. Forest sites experiencing lower environmental stress and greater co-occurrence of evolutionarily distant woody plant species are hypothesised to exhibit higher above ground carbon (AGC) accumulation rates. In contrast, plots under higher environmental stress with greater co-occurrence of closely related species are predicted to have lower AGC accumulation rates.

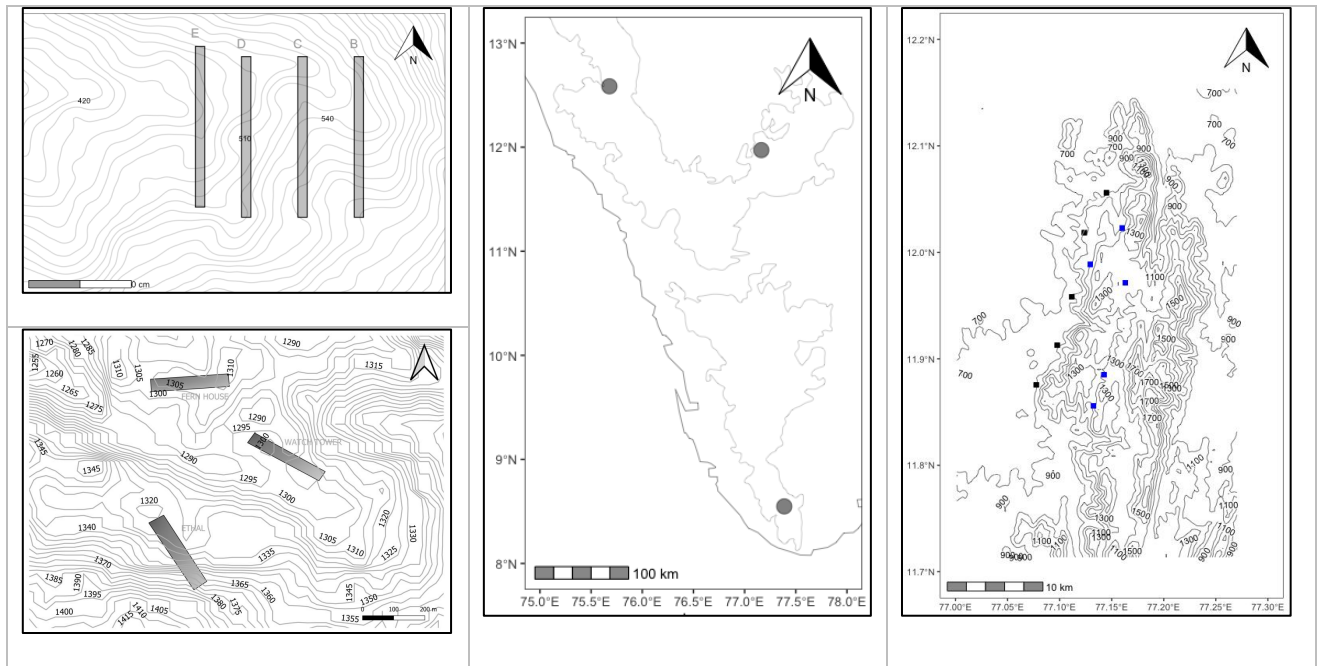


Figure 32: Location and elevation (m) of 1-ha long-term vegetation monitoring plots in the Western Ghats. The central panel shows peninsular India with the Western Ghats biodiversity hotspot boundary and locations of forest dynamics sites. The upper left inset depicts low-elevation tropical evergreen plots in the central Western Ghats with rectangular linear dimensions of 20×350 m. The lower left inset shows mid-elevation wet evergreen plots in the southern Western Ghats with rectangular dimensions of 40×250 m. The right inset illustrates the distribution of square 100×100 m tropical dry forest plots in the Western Ghats, where blue plots represent dry deciduous forests (DDF) and black plots represent scrub jungles.

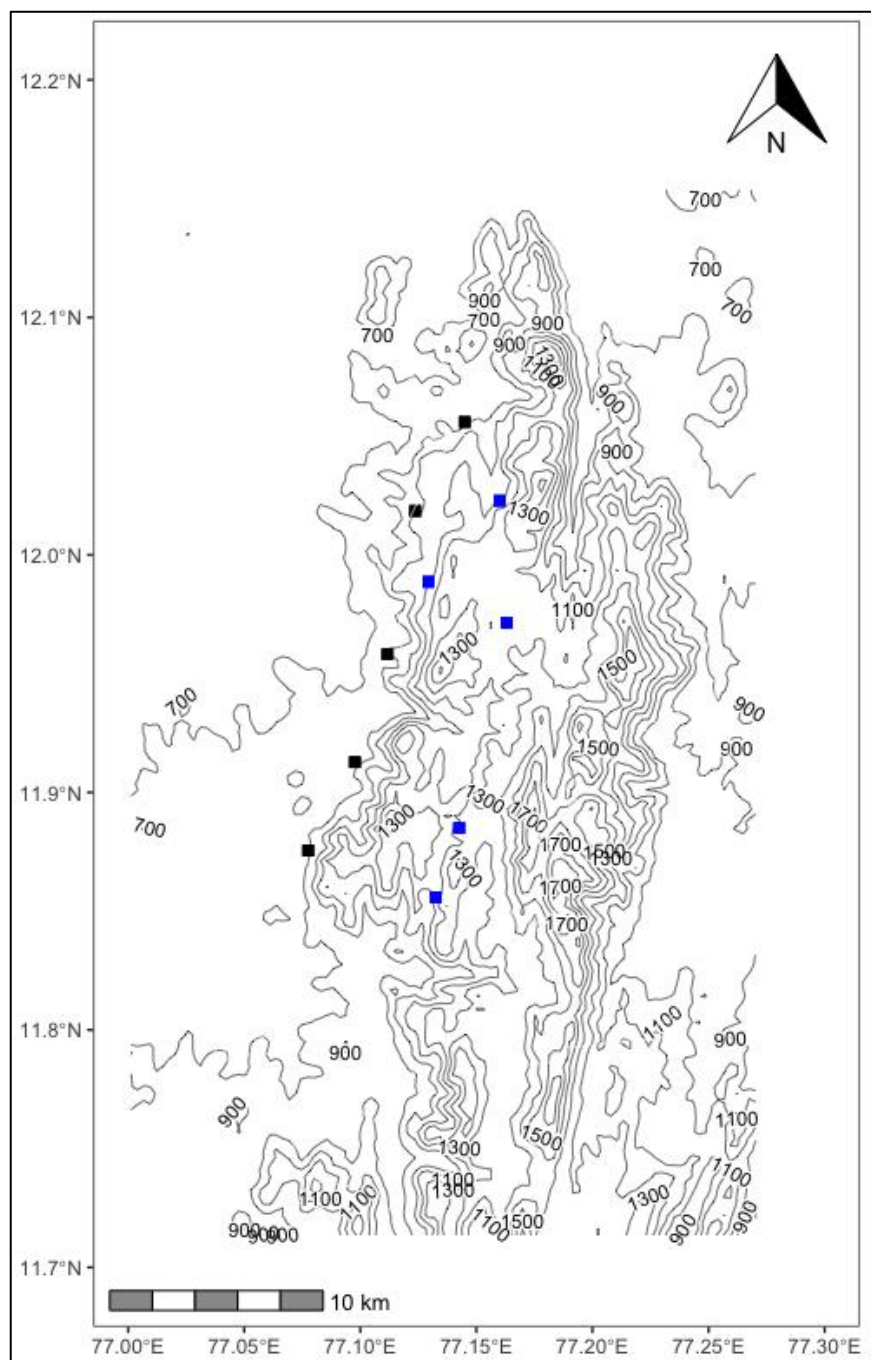


Figure 33: Distribution of square 100 × 100 m tropical dry forest plots in the Western Ghats, where blue plots represent dry deciduous forests (DDF) and black plots represent scrub jungles.

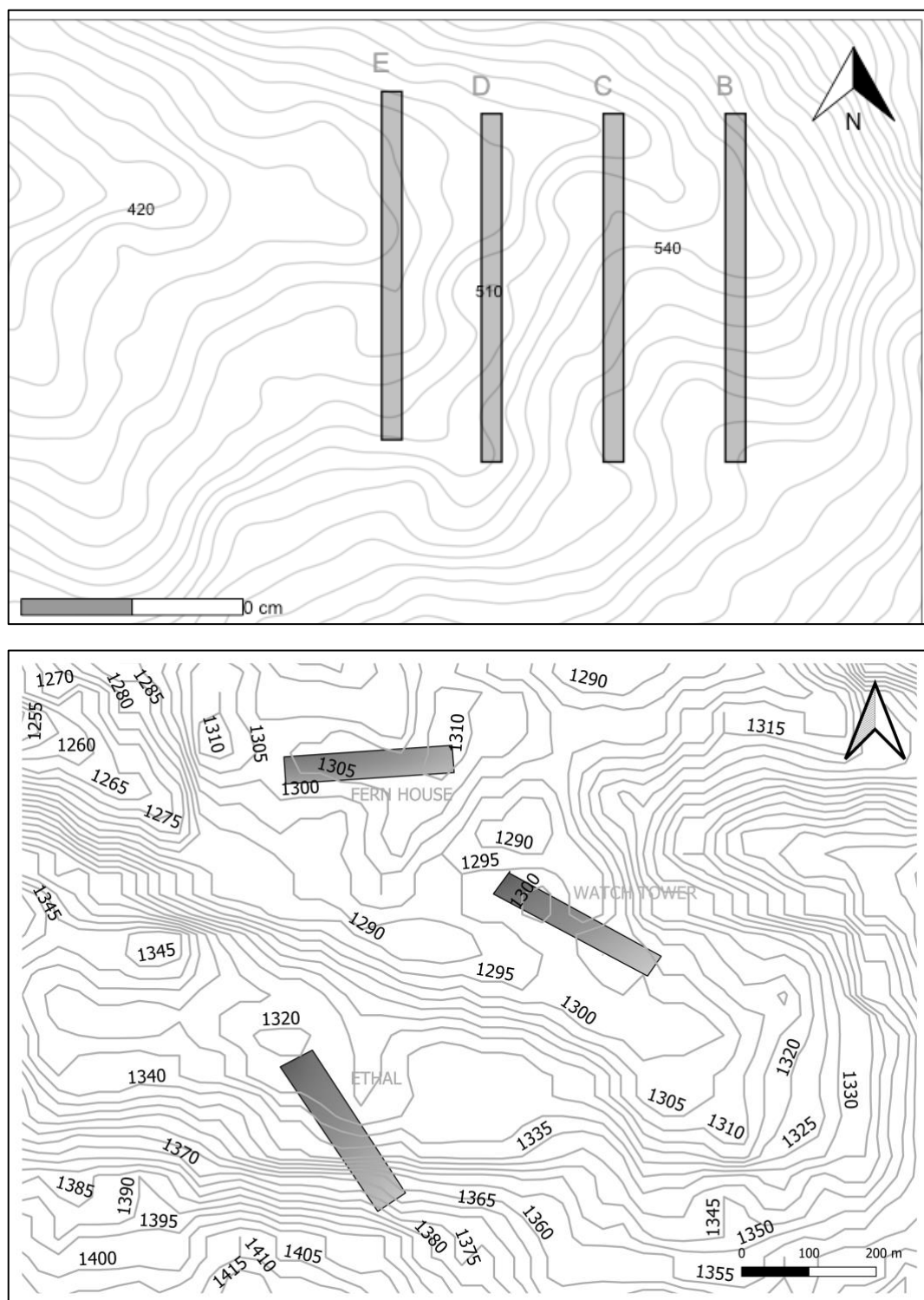


Figure 34: The upper inset depicts low-elevation tropical evergreen plots in the central Western Ghats with rectangular linear dimensions of 20×350 m. The lower inset shows mid-elevation wet evergreen plots in the southern Western Ghats with rectangular dimensions of 40×250 m.

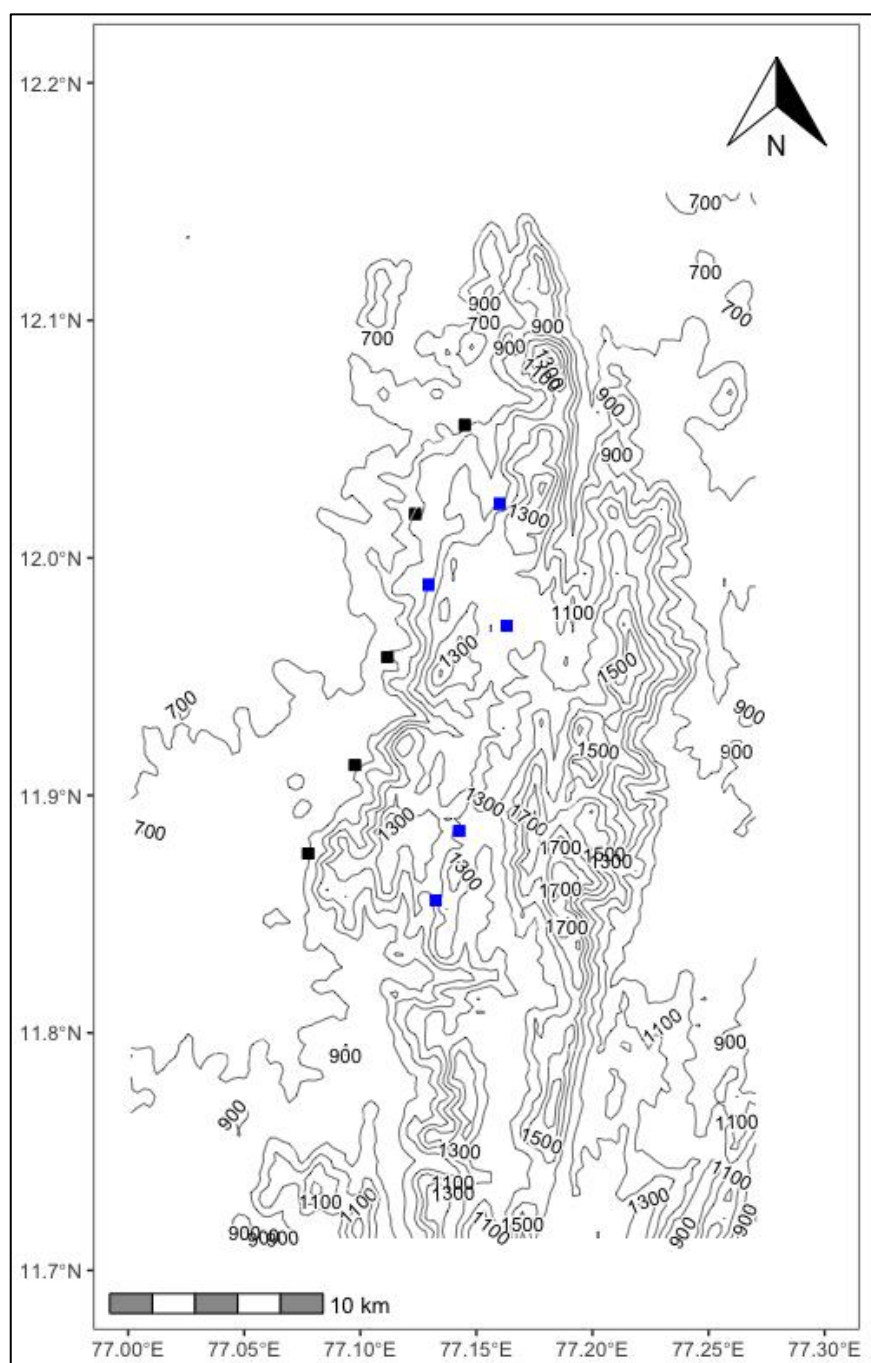


Figure 35: Distribution of square 100×100 m tropical dry forest plots in the Western Ghats, where blue plots represent dry deciduous forests (DDF) and black plots represent scrub jungles.

Table 24: Characteristics of long-term Forest Dynamics Plots (FDPs) established across the Western Ghats biodiversity hotspot. The table summarizes site names, elevation, plot dimensions, number of plots, total area, and years of repeated censuses for tropical evergreen, dry deciduous, and scrub forest sites.

Site names	Elevation	Dimension	plots	Size	Census years
Southern Western ghats Mid elevation ever green forest (SWG-M-EV)	1300 m	250 x 40 m	3	1 ha	1999, 2004, 2011, 2016, and 2021
Central western ghats low elevation evergreen forest (CWG-L-EV)	540 m	350 x 20 m	4	1 ha	1990, 1994, 1998, 2002, 2007, and 2010
Dry deciduous forest (DDF)	1100 m	100 x 100 m	5	1 ha	2002, 2007, 2011, and 2017
SCRUB forest	600 m	100 x 100 m	5	1 ha	2002, 2007, 2011, and 2017

Table 25: Proportion of functional trait data available at the species levels. Values indicate the number and percentage of species with trait data directly measured at the species level.

Functional traits	Data available for species	
		%
Leaf area	169	82
Leaf nitrogen mass	161	78
Leaf mass per area	163	79
Seed Diaspore Mass	170	83
Wood density	206	100
Maximum DBH	206	100
Maximum Height	206	100

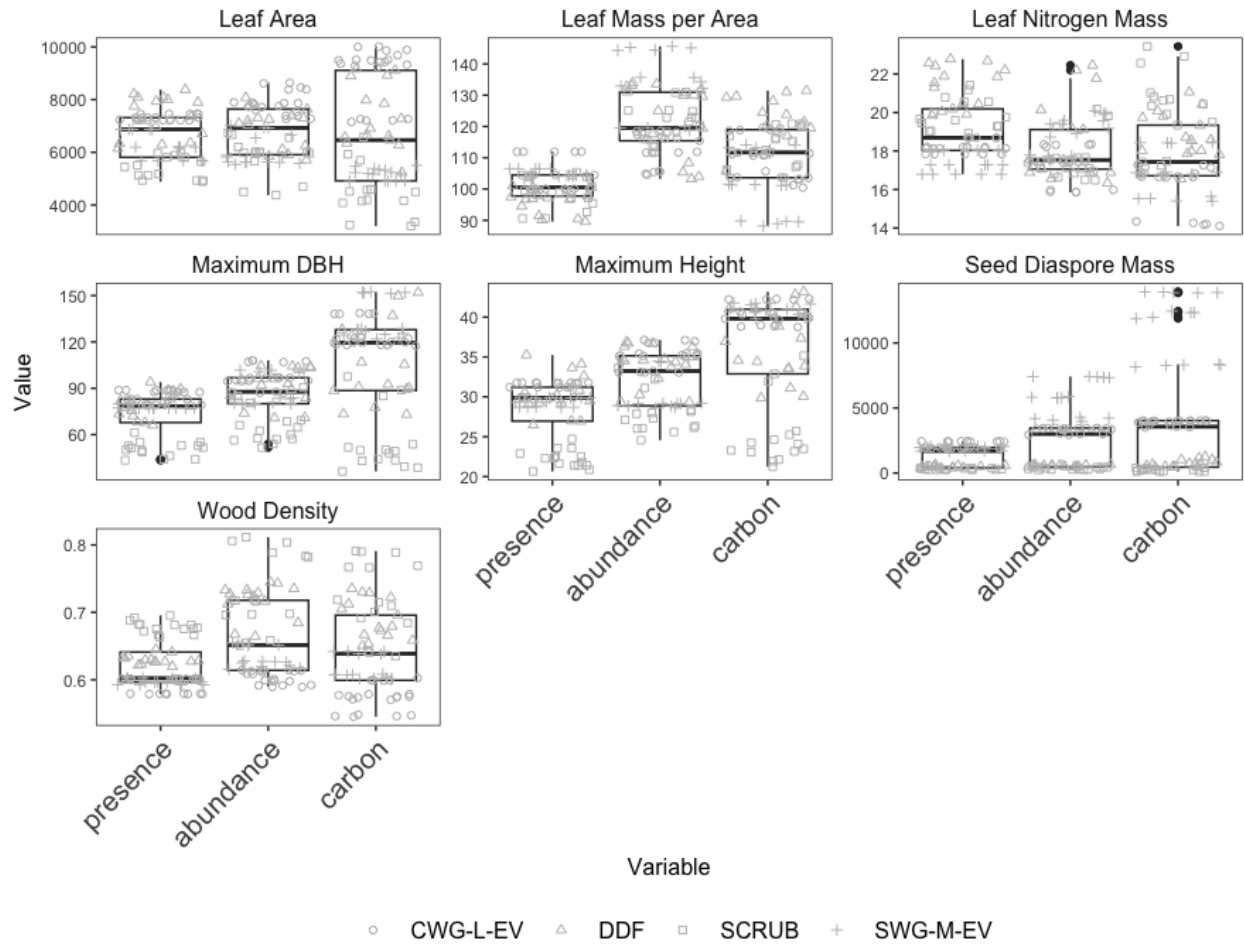


Figure 36: Variations in community-weighted means (CWM) of functional traits calculated using presence-based, abundance-weighted, and size-weighted approaches across forest types. Symbols denote forest types: plus, sign (+) for SWG-M-EV, open circles for CWG-L-EV, triangles for DDF, and squares for SCRUB.

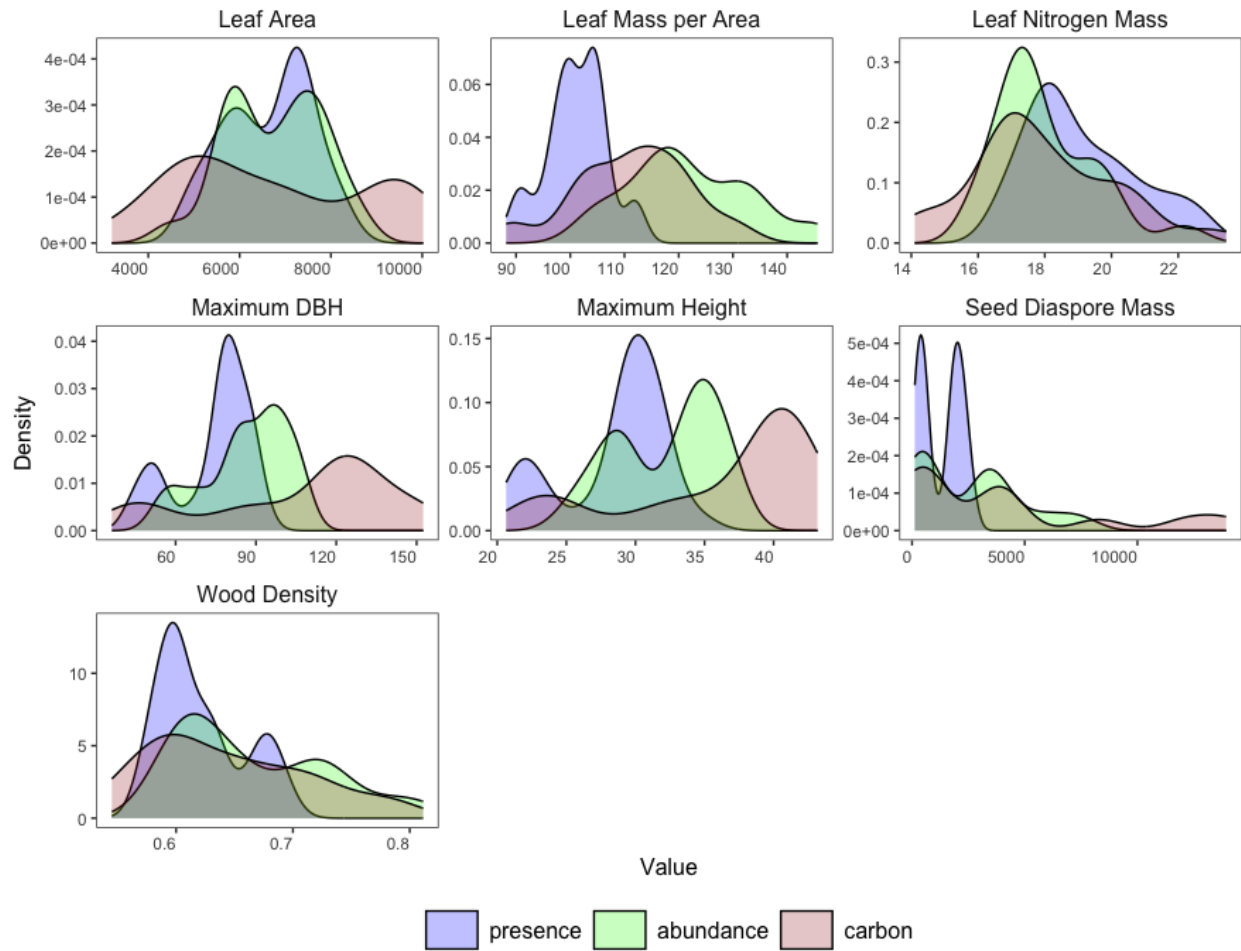


Figure 37: Density plots showing variation in community-weighted means (CWM) of functional traits under presence-based, abundance-weighted, and size-weighted frameworks. Colors distinguish the distributions for each weighting scheme, highlighting differences in trait values.

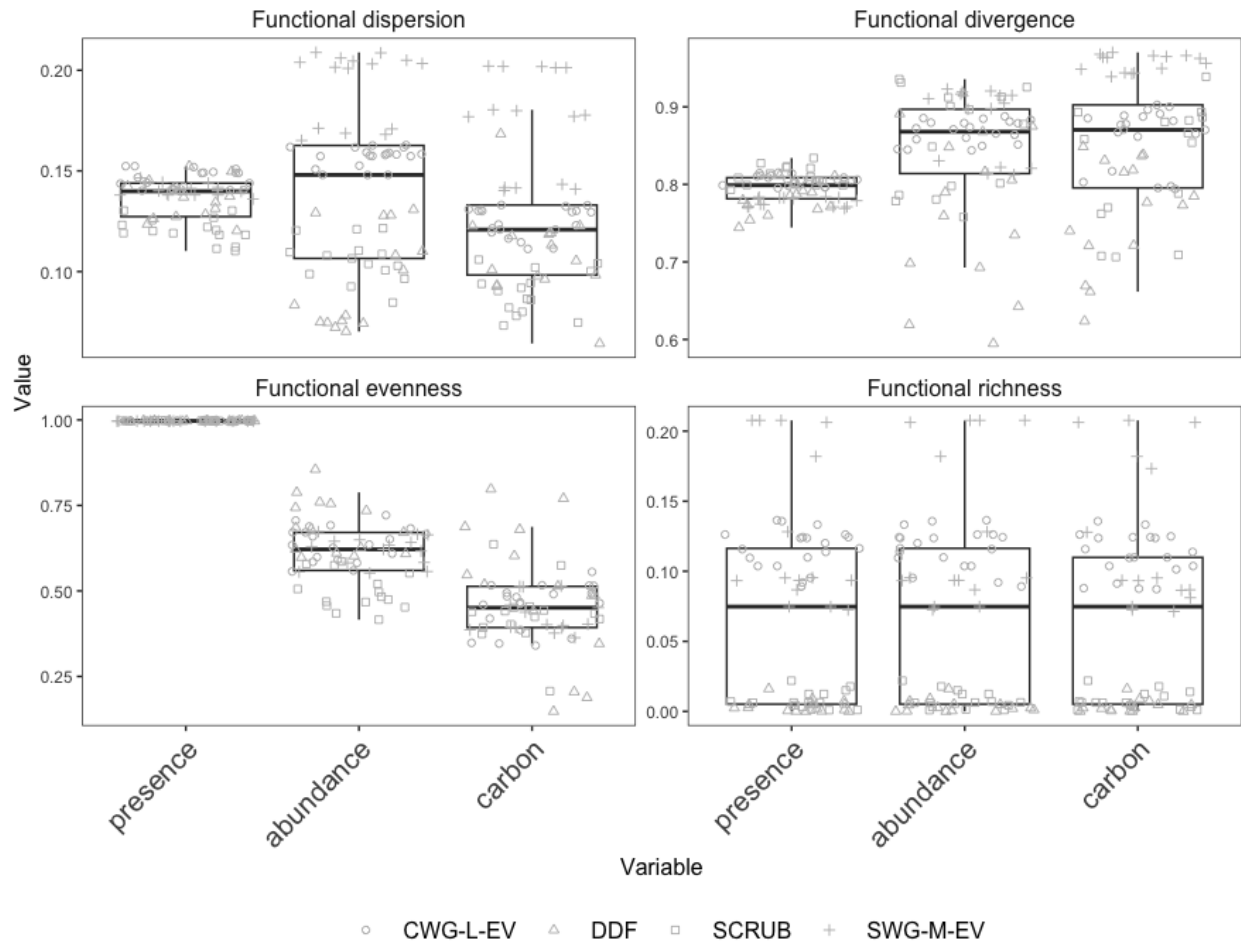


Figure 38: Variations in functional trait diversity metrics calculated using presence-based, abundance-weighted, and size-weighted approaches across forest types. Symbols denote forest types: plus, sign (+) for SWG-M-EV, open circles for CWG-L-EV, triangles for DDF, and squares for SCRUB.

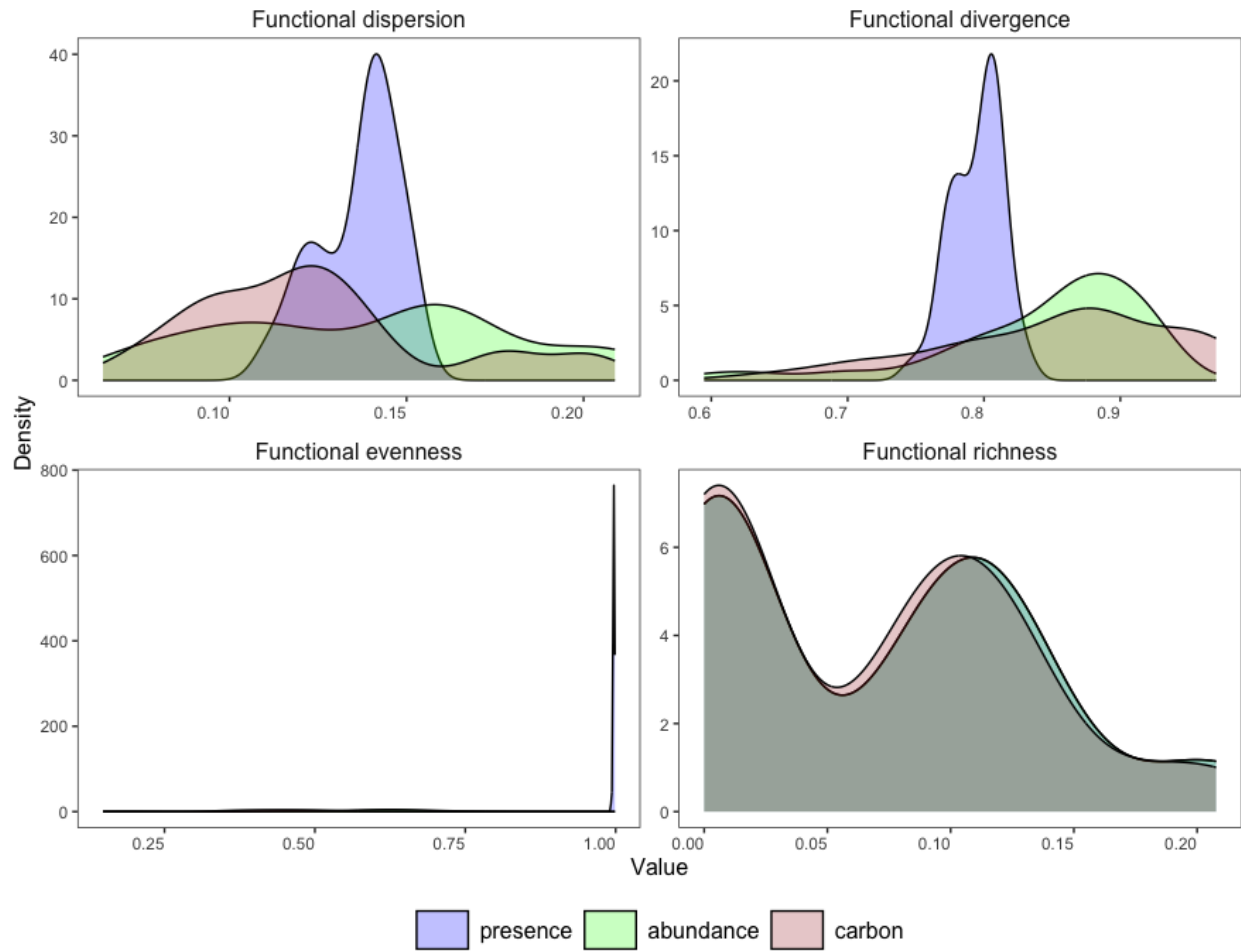


Figure 39: Density plots showing variation in functional traits diversity metrics under presence-based, abundance-weighted, and size-weighted frameworks. Colors distinguish the distributions for each weighting scheme, highlighting differences in functional diversity. The density for functional evenness appears highly skewed, with a sharp peak at one end. This suggests a lack of variability in this metric across the weighting schemes.

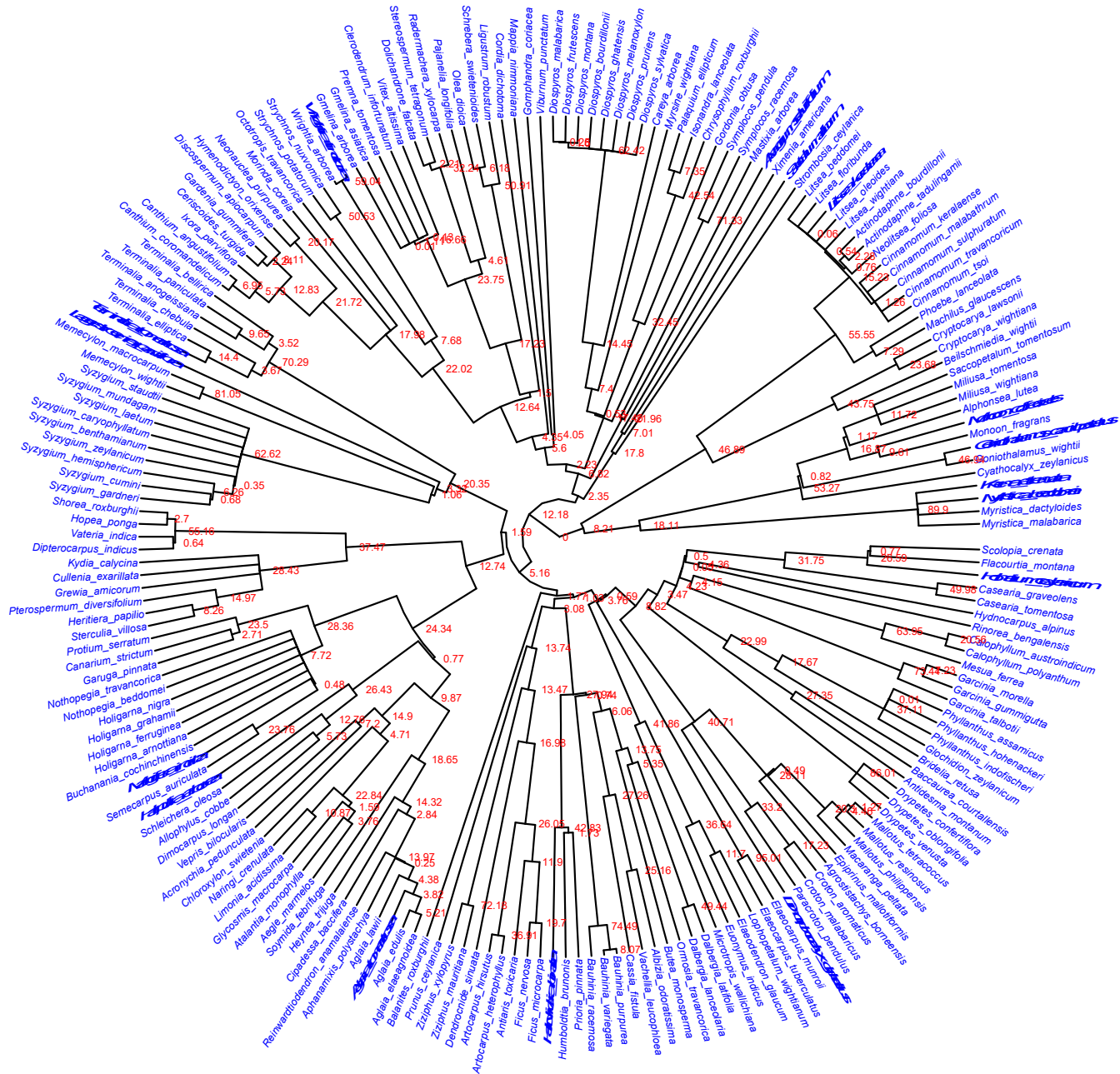


Figure 40: Phylogenetic tree of the 212 species recorded in the study, representing 144 genera and 50 families.

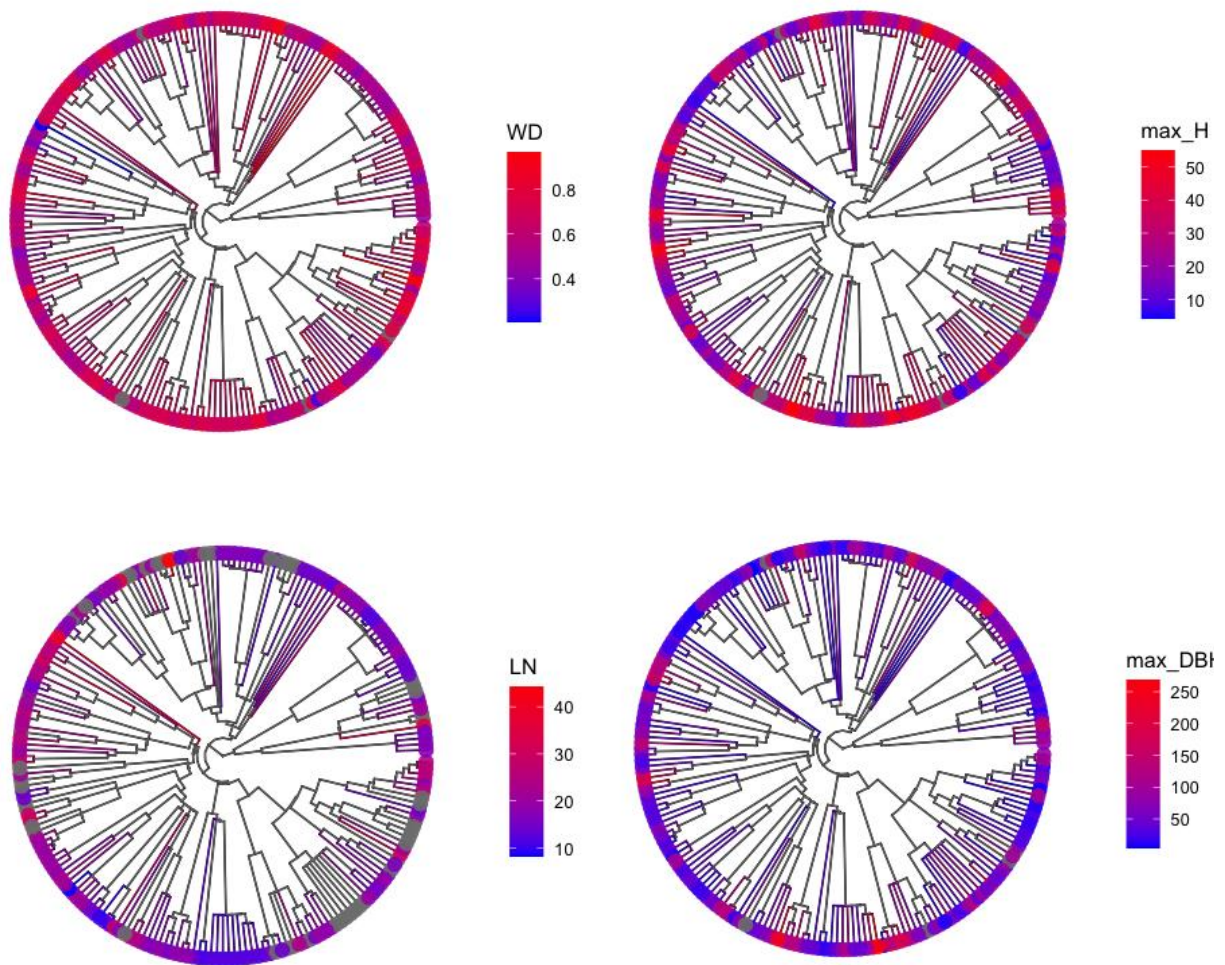


Figure 41: Phylogenetic tree of 212 woody plant species recorded across forest dynamics plots in the western ghats. Functional trait values are mapped onto the phylogenetic tree with gradients ranging from high (in red) to low (in blue).

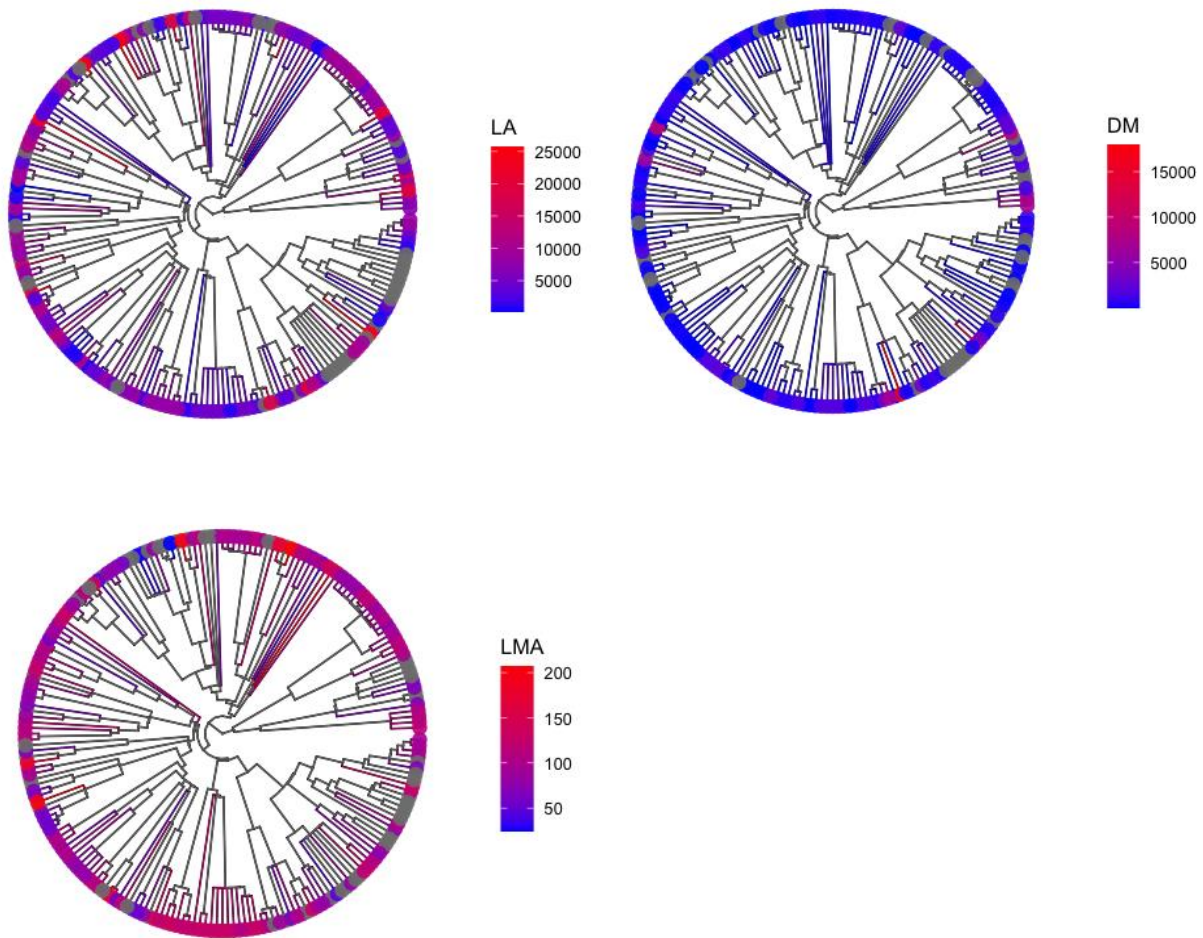


Figure 42 : Phylogenetic tree of 212 woody plant species recorded across forest dynamics plots in the western ghats. Functional trait values are mapped onto the phylogenetic tree with gradients ranging from high (in red) to low (in blue).

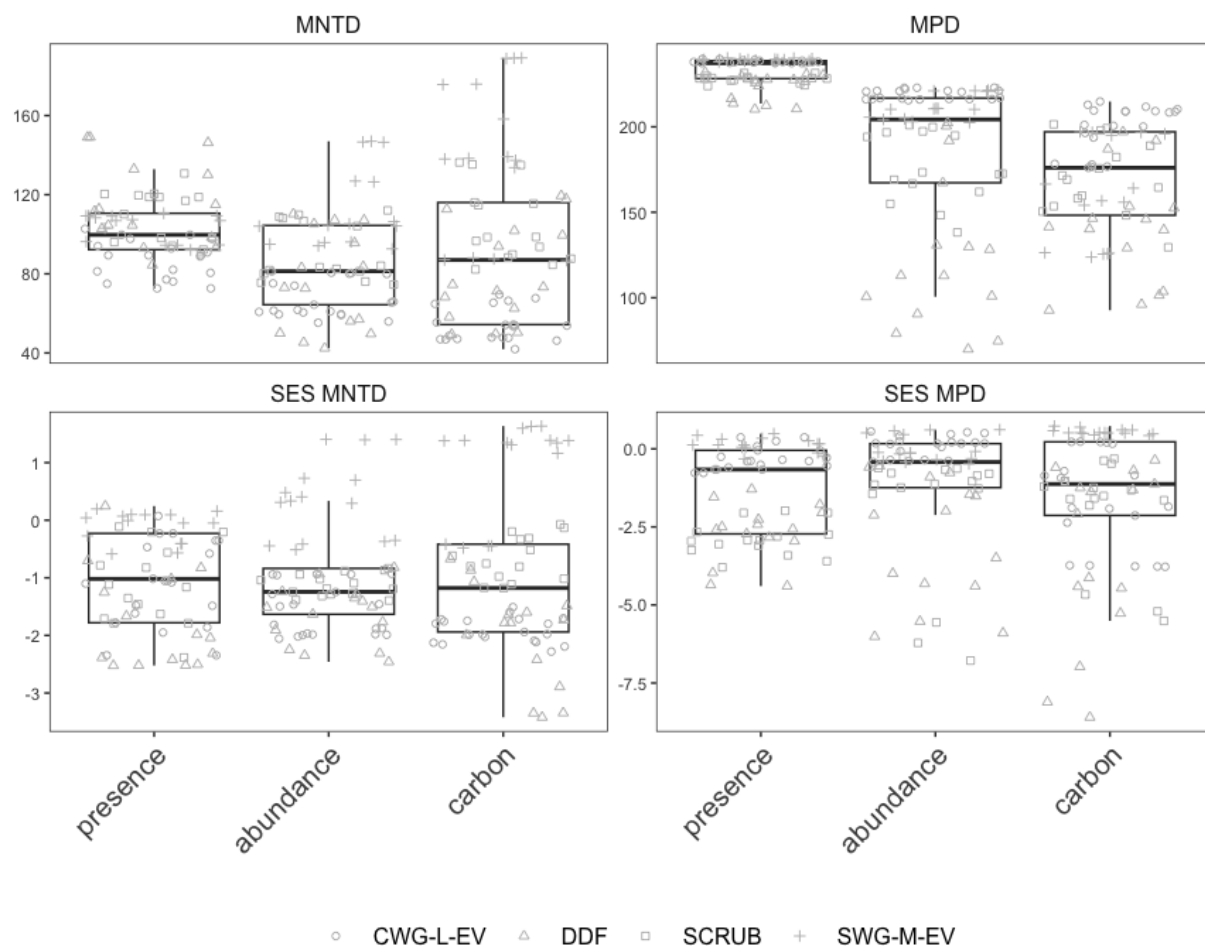


Figure 43: Variations in phylogenetic divergence metrics calculated using presence-based, abundance-weighted, and size-weighted approaches across forest types. Symbols denote forest types: plus, sign (+) for SWG-M-EV, open circles for CWG-L-EV, triangles for DDF, and squares for SCRUB.

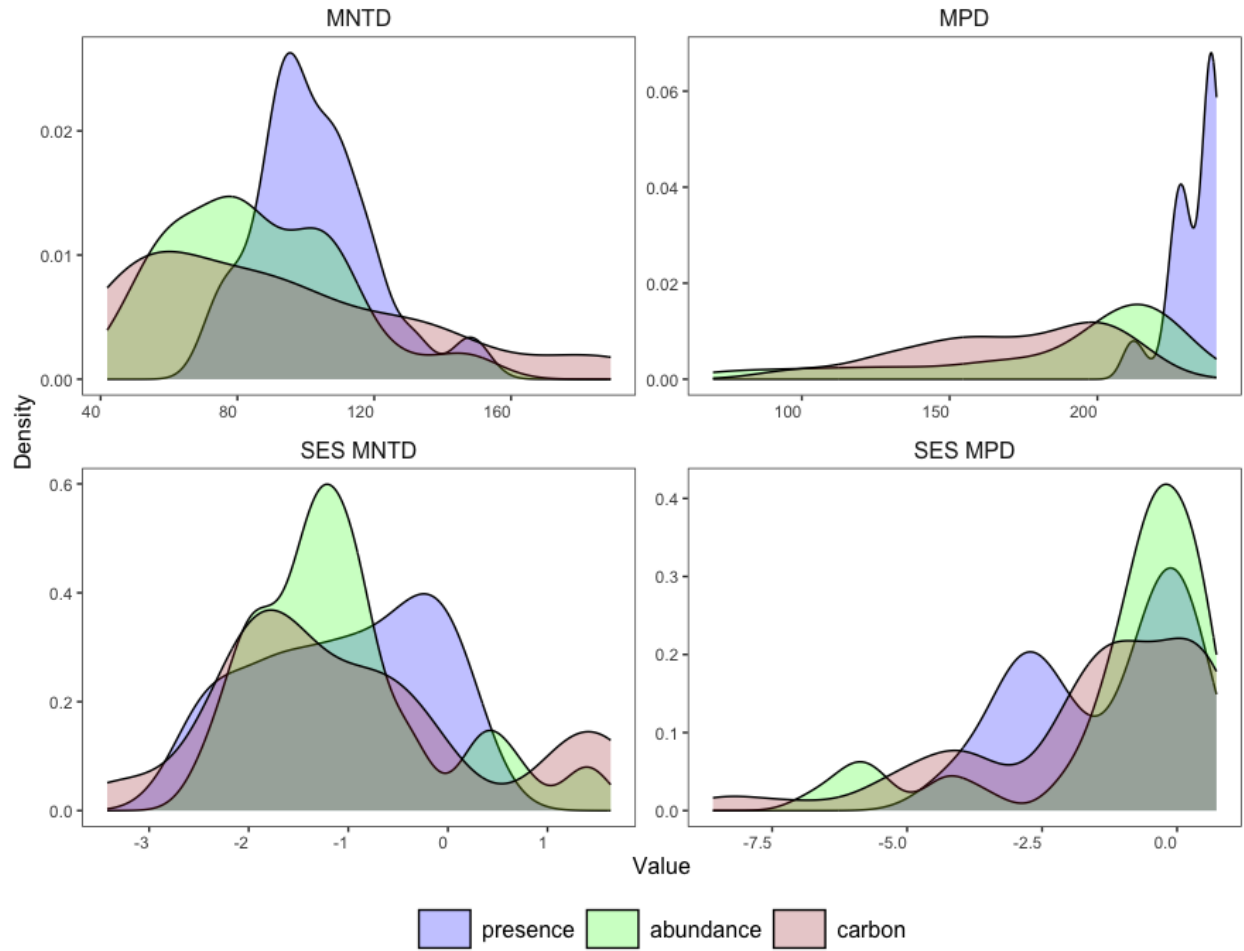


Figure 44: Density plots showing variation in phylogenetic diversity metrics under presence-based, abundance-weighted, and size-weighted frameworks. Colors distinguish the distributions for each weighting scheme, highlighting differences in phylogenetic diversity.

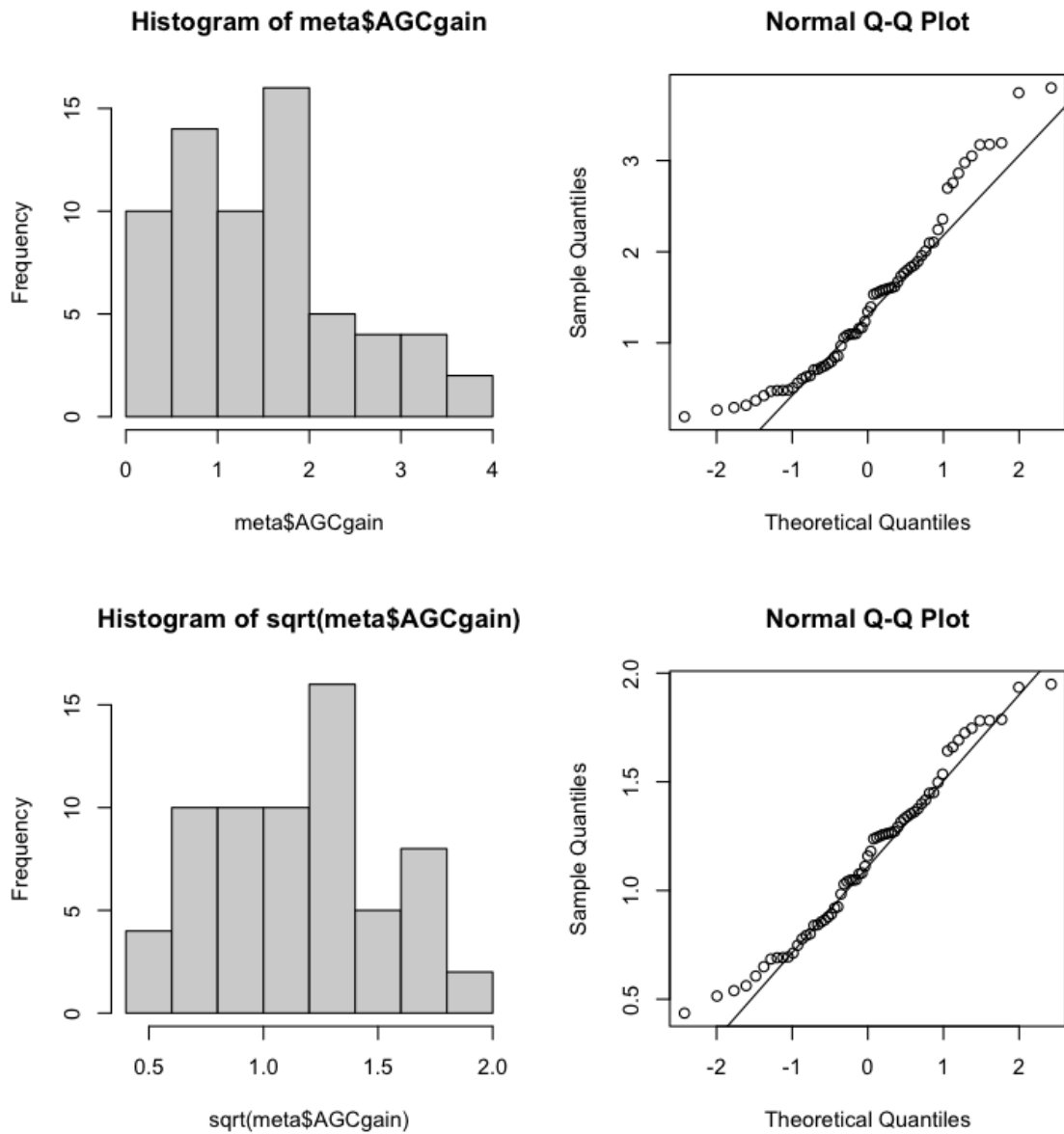


Figure 45: Histograms and Q–Q plots showing the distribution of above-ground carbon (AGC) gain data before (top) and after square root transformation (bottom). The transformation improved normality, as indicated by closer alignment of sample quantiles with the theoretical quantiles in the Q–Q plot.

Shapiro wilk test	<i>W</i>	<i>p</i> value
Not transformed	0.929	0.0011
Square root	0.974	0.203

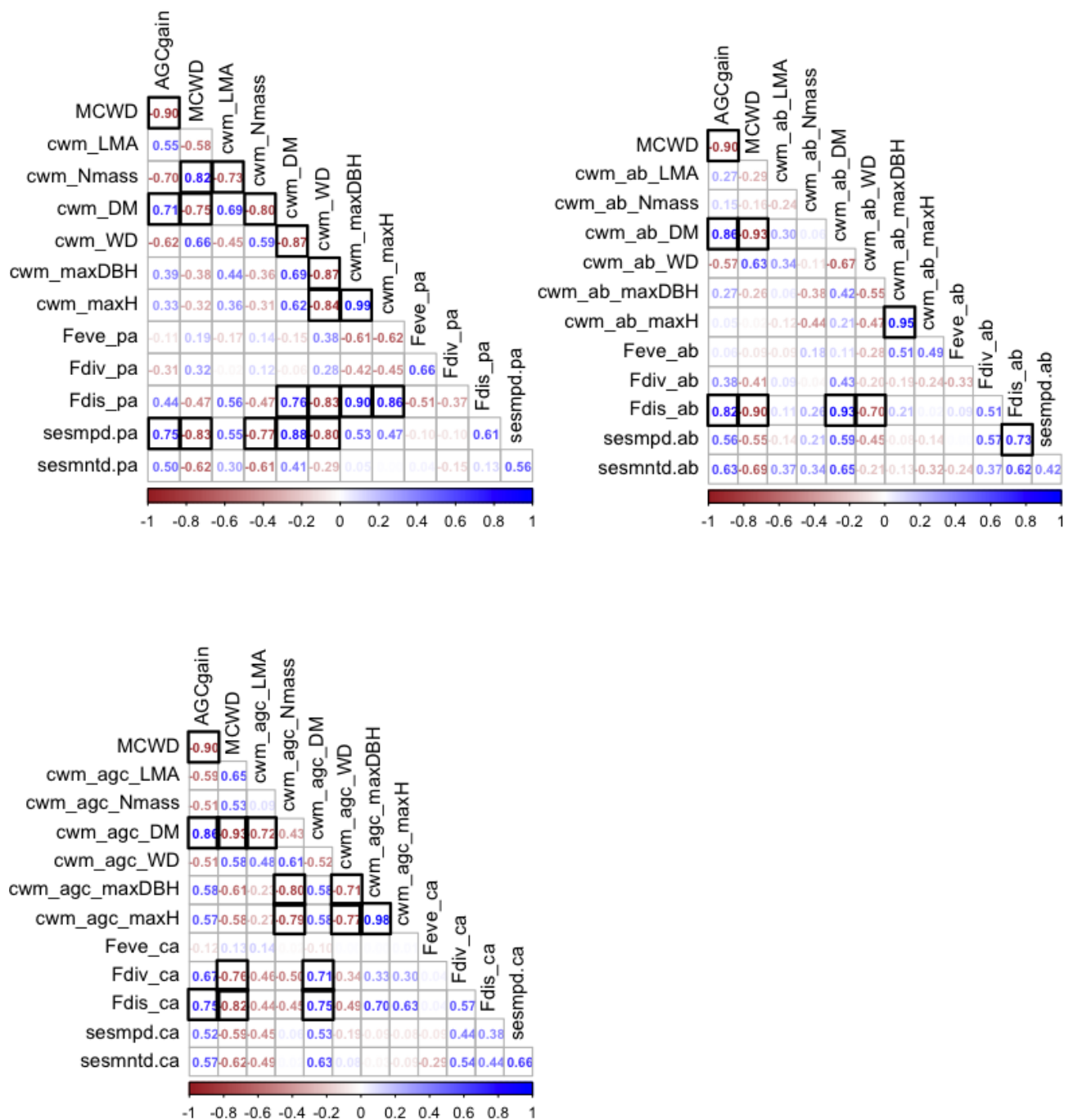


Figure 46: Pearson correlation matrices showing relationships between response and predictor variables. Panels represent (top left) unweighted, (top right) abundance-weighted, and (bottom) size-weighted functional and phylogenetic metrics. Strong positive and negative correlations are indicated by color gradients, with significant associations highlighted.

Table 26: Variation inflation factor (VIF)

	Unweighted	Abundance	Size
CWM leaf area	2.50	1.99	3.34
CWM leaf mass area	2.29	3.07	3.00
CWM leaf nitrate mass	3.98	1.75	3.61
CWM seed diaspore mass	-	4.82	4.84
CWM wood density	3.64	4.89	2.88
CWM max DBH	-	-	-
CWM max Height	-	-	-
Functional richness	1.99	2.26	2.71
Functional evenness	2.31	1.28	1.05
Functional divergence	1.76	1.68	1.58
Functional dispersion	2.69	2.81	2.62
SES MPD	1.46	1.21	1.78
SES MNTD	1.46	1.21	1.78

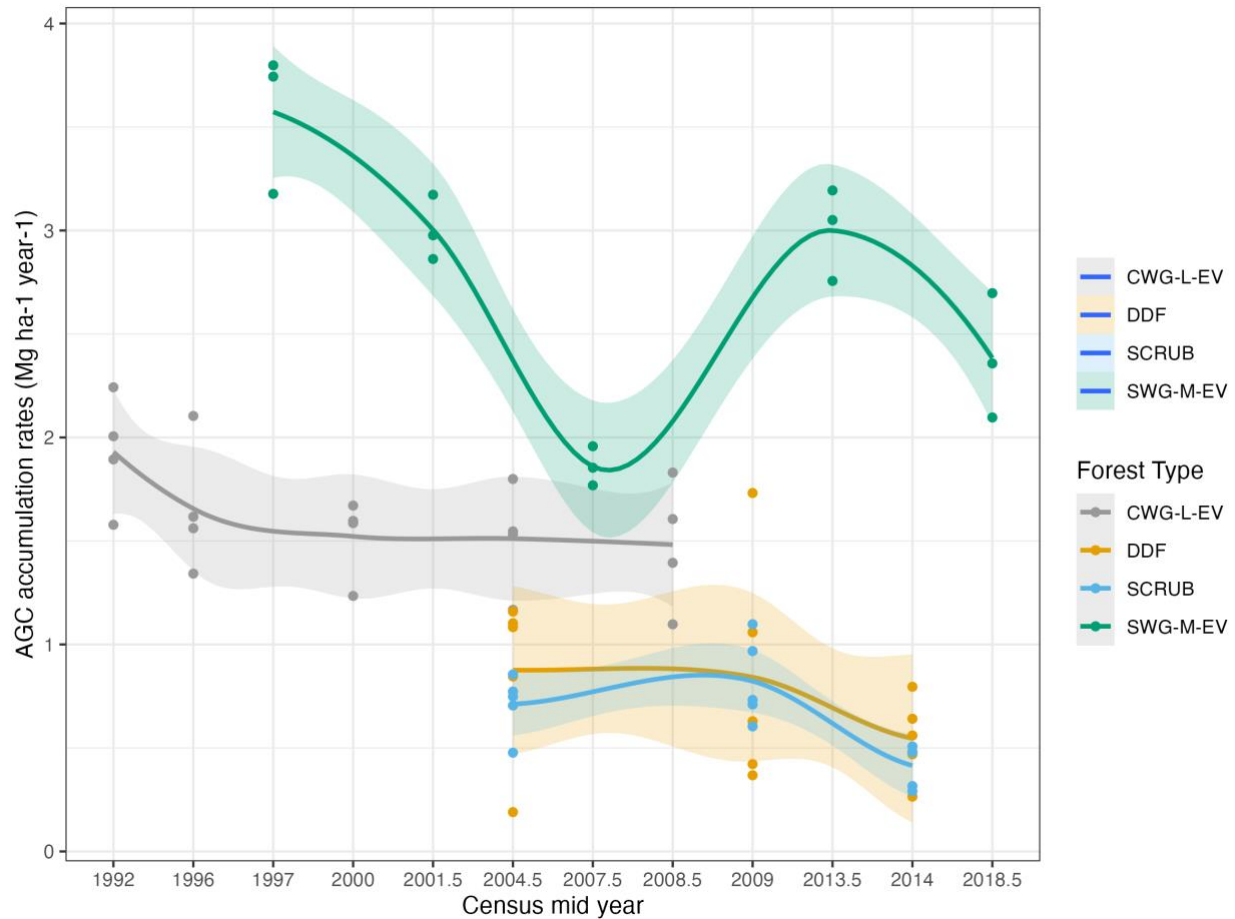


Figure 47: Temporal variation in above-ground carbon (AGC; Mg ha⁻¹ yr⁻¹) accumulation across 17 one-hectare long-term monitoring sites representing four forest types in the Western Ghats. The x-axis denotes the midpoint year of each census interval. Forest types include Southern Western Ghats mid-elevation evergreen (SWG-M-EV), Central Western Ghats low-elevation evergreen (CWG-L-EV), Dry Deciduous Forest (DDF), and Scrub Forest (SCRUB).

Table 27: Variations in above-ground carbon (AGC; $\text{Mg ha}^{-1} \text{yr}^{-1}$) and AGC gains across census intervals at 17 one-hectare sites spanning four forest types in the Western Ghats. Values represent mean AGC and mean annual AGC gains ($\pm$ SD) for Southern Western Ghats mid-elevation evergreen (SWG-M-EV), Central Western Ghats low-elevation evergreen (CWG-L-EV), Dry Deciduous Forest (DDF), and Scrub Forest (SCRUB).

Type	Term	Mean AGC ($\text{Mg ha}^{-1} \text{year}^{-1}$)	SD	Mean AGC gain ($\text{Mg ha}^{-1} \text{year}^{-1}$)	SD
SWG-M-EV	1995-1999	274.27	27.58	3.57	0.34
	1999-2004	280.00	29.07	3.00	0.16
	2004-2011	275.97	28.46	1.86	0.09
	2011-2016	286.14	28.64	3.00	0.22
	2016-2021	290.11	30.14	2.38	0.30
CWG-L-EV	1990-1994	112.96	16.27	1.93	0.28
	1994-1998	116.42	16.44	1.66	0.32
	1998-2002	118.59	16.83	1.52	0.20
	2002-2007	121.15	20.03	1.51	0.26
	2007-2010	119.97	20.92	1.48	0.31
DDF	2002-2007	39.41	28.45	0.88	0.40
	2007-2011	38.73	12.81	0.84	0.57
	2011-2017	42.99	23.93	0.55	0.20
SCRUB	2002-2007	11.05	1.59	0.71	0.14
	2007-2011	13.23	2.13	0.82	0.20
	2011-2017	14.81	2.27	0.41	0.10

Table 28: Above-Ground Carbon (AGC) storage (Mg ha^{-1}) and accumulation rates (Mg ha^{-1}) of dominant tree species across forest types in the Western Ghats.

Forest type	Species	Family	AGC Mg ha^{-1}	AGC gain Mg ha^{-1}
SWG-M-EV	<i>Cullenia exarillata</i>	<i>Malvaceae</i>	151.88	1.44
SWG-M-EV	<i>Palaquium ellipticum</i>	<i>Sapotaceae</i>	45.10	0.51
SWG-M-EV	<i>Syzygium gardneri</i>	<i>Myrtaceae</i>	16.52	0.03
SWG-M-EV	<i>Myristica beddomei</i>	<i>Myristicaceae</i>	15.84	0.10
SWG-M-EV	<i>Agrostistachys borneensis</i>	<i>Euphorbiaceae</i>	9.94	0.13
SWG-M-EV	<i>Ormosia travancorica</i>	<i>Fabaceae</i>	4.54	0.01
CWG-L-EV	<i>Vateria indica</i>	<i>Dipterocarpaceae</i>	24.92	0.44
CWG-L-EV	<i>Dipterocarpus indicus</i>	<i>Dipterocarpaceae</i>	17.63	0.16
CWG-L-EV	<i>Myristica dactyloides</i>	<i>Myristicaceae</i>	14.21	0.16
CWG-L-EV	<i>Prioria pinnata</i>	<i>Fabaceae</i>	8.03	0.06
CWG-L-EV	<i>Mesua ferrea</i>	<i>Calophyllaceae</i>	7.61	0.14
CWG-L-EV	<i>Knema attenuata</i>	<i>Myristicaceae</i>	6.27	0.06
CWG-L-EV	<i>Drypetes venusta</i>	<i>Putranjivaceae</i>	6.18	0.08
DDF	<i>Terminalia anogeissiana</i>	<i>Combretaceae</i>	14.88	0.37
DDF	<i>Terminalia elliptica</i>	<i>Combretaceae</i>	5.30	0.06
DDF	<i>Terminalia bellirica</i>	<i>Combretaceae</i>	5.10	0.03
DDF	<i>Grewia amicornum</i>	<i>Malvaceae</i>	3.72	0.04
DDF	<i>Miliusa tomentosa</i>	<i>Annonaceae</i>	3.25	0.11
DDF	<i>Dalbergia latifolia</i>	<i>Fabaceae</i>	2.24	0.06
SCRUB	<i>Chloroxylon swietenia</i>	<i>Rutaceae</i>	4.06	0.23
SCRUB	<i>Hardwickia binata</i>	<i>Fabaceae</i>	2.03	0.09
SCRUB	<i>Dalbergia lanceolaria</i>	<i>Fabaceae</i>	1.89	0.10
SCRUB	<i>Terminalia anogeissiana</i>	<i>Combretaceae</i>	1.06	0.05
SCRUB	<i>Terminalia elliptica</i>	<i>Combretaceae</i>	1.03	0.03

Table 29: Occurrence and intensity of El Niño and La Niña events between 1990 and 2021, classified as weak, moderate, strong, or very strong based on the Oceanic Niño Index (ONI). The table summarizes the frequency and duration of each category, highlighting interannual variability in the strength of ENSO phases across three decades.

El Nino				La Nina		
Weak	Moderate	Strong	Very Strong	Weak	Moderate	Strong
2004-05	1994-95	1991-92	1997-98	2000-01	1995-96	1998-99
2006-07	2002-03		2015-16	2005-06	2011-12	1999-00
2014-15	2009-10			2008-09	2020-21	2007-08
2018-19				2016-17		2010-11
				2017-18		

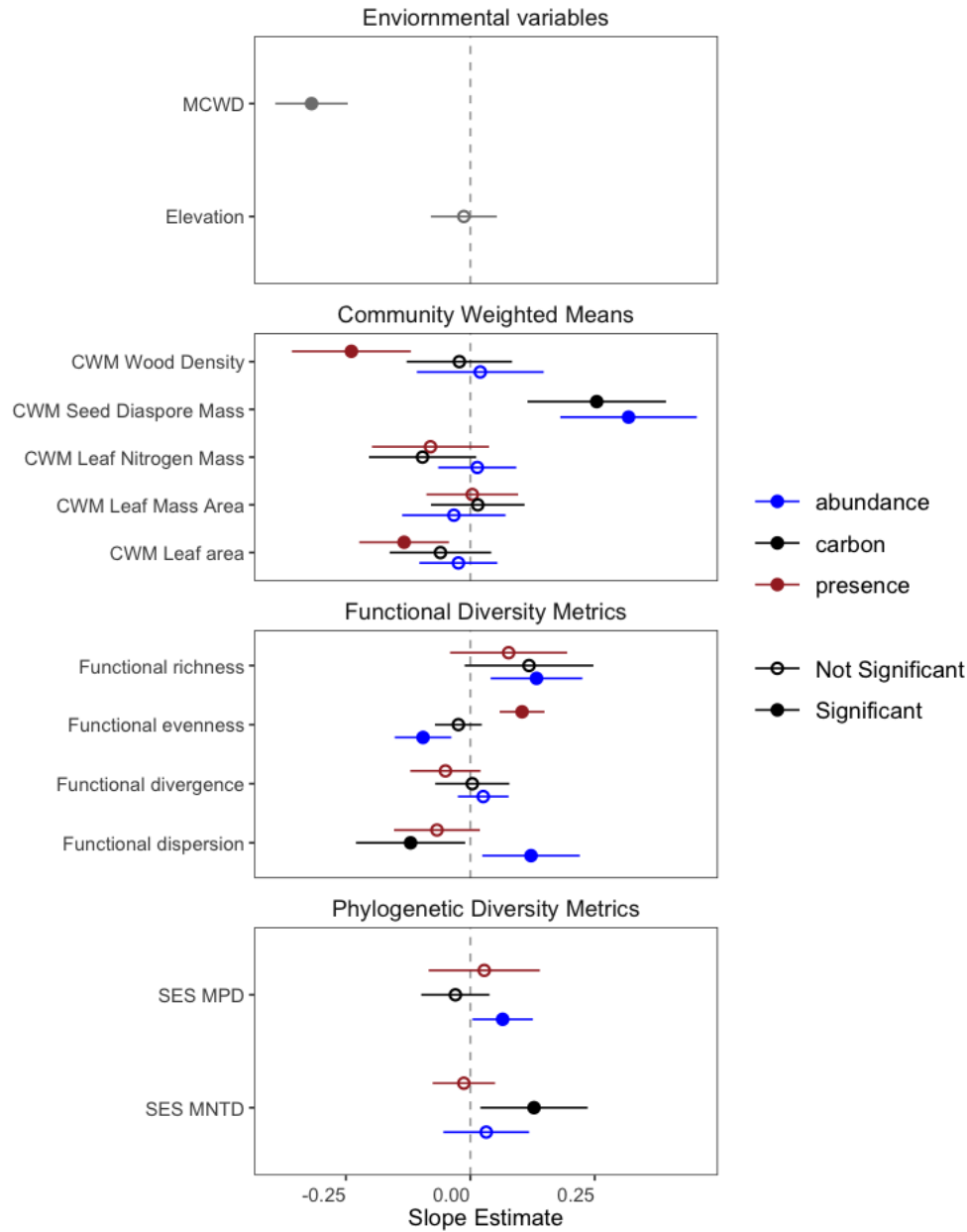


Figure 48: Results of linear mixed-effects models testing the influence of community-weighted means, functional diversity, and phylogenetic diversity metrics on above-ground carbon (AGC) accumulation. Models were analyzed under presence-based (brown), abundance-weighted (blue), and size or size-weighted (black) frameworks. Site and census interval were included as random effects to account for spatial and temporal autocorrelation. Filled circles indicate significant effects, and horizontal lines represent 95 % confidence intervals. To assess whether a slope differs significantly from zero, the 95% confidence interval (CI) for the slope parameter was calculated as the estimate $\pm (1.96 \times \text{standard error})$. If the CI includes zero, the slope is not significantly different from zero at the 0.05 level; if it excludes zero, the effect is considered statistically significant.

Table 30: Results of linear mixed-effects models testing the effects of elevation and maximum climatic water deficit (MCWD) on above-ground carbon (AGC) accumulation. Forest type and census interval were included as random effects to account for spatial and temporal variability.

Predictor	Estimate	CI lower	CI upper	t value	S/NS	AICc	R ² M	R ² C
intercept	1.156	1.073	1.238	27.516		-40.04	0.75	0.89
Elevation	-0.013	-0.077	0.051	-0.394	NS			
MCWD	-0.321	-0.393	-0.248	-8.698	S			

Table 31: Results of linear mixed-effects models testing the relationships between community-weighted mean (CWM) functional traits-calculated using presence-based, abundance-weighted, and size-weighted approaches-and above-ground carbon (AGC) accumulation. Forest type and census interval were included as random effects to account for spatial and temporal variability.

Weights	Predictor	Estimate	CI lower	CI upper	t value	S/NS	AICc	R ² M	R ² C
Presence	intercept	1.174	1.060	1.287	20.162		-25.42	0.56	0.89
	CWM LA	-0.133	-0.223	-0.043	-2.890	S			
	CWM LMA	0.004	-0.087	0.096	0.092	NS			
	CWM LN	-0.080	-0.198	0.038	-1.322	NS			
	CWM WD	-0.239	-0.359	-0.120	-3.925	S			
Abundance	Intercept	1.164	1.064	1.263	22.502		-26.90	0.67	0.89
	CWM LA	-0.024	-0.102	0.053	-0.612	NS			
	CWM LMA	-0.033	-0.137	0.071	-0.626	NS			
	CWM LN	0.014	-0.065	0.092	0.345	NS			
	CWM WD	0.020	-0.108	0.149	0.312	NS			
	CWM SDM	0.318	0.181	0.454	4.557	S			
Size	Intercept	1.157	1.053	1.260	21.702		-27.33	0.68	0.91
	CWM LA	-0.060	-0.163	0.043	-1.146	NS			
	CWM LMA	0.015	-0.079	0.109	0.312	NS			
	CWM LN	-0.096	-0.204	0.012	-1.736	NS			
	CWM WD	-0.022	-0.128	0.084	-0.411	NS			
	CWM SDM	0.254	0.114	0.395	3.560	S			

Table 32: Results of linear mixed-effects models testing the relationships between functional trait diversity - calculated using presence-based, abundance-weighted, and size-weighted frameworks - and above-ground carbon (AGC) accumulation. Forest type and census interval were included as random effects to account for spatial and temporal variability.

Weights	Predictor	Estimate	CI lower	CI upper	t value	S/ NS	AIC	R ² M	R ² C
Presence	intercept	1.156	0.844	1.467	7.245		-42.66	0.10	0.94
	F Dispersion	-0.067	-0.153	0.019	-1.522	NS			
	F Divergence	-0.050	-0.121	0.021	-1.382	NS			
	F Evenness	0.104	0.058	0.149	4.472	S			
	F Richness	0.077	-0.040	0.194	1.292	NS			
Abundance	intercept	1.166	1.009	1.322	13.216		-39.11	0.54	0.90
	F Dispersion	0.122	0.023	0.220	2.425	S			
	F Divergence	0.026	-0.024	0.076	1.018	NS			
	F Evenness	-0.095	-0.152	-0.039	-3.287	S			
	F Richness	0.133	0.041	0.224	2.838	S			
Size	intercept	1.161	0.831	1.490	6.888		-26.34	0.05	0.93
	F Dispersion	-0.120	-0.230	-0.010	-2.129	S			
	F Divergence	0.004	-0.071	0.078	0.093	NS			
	F Evenness	-0.024	-0.071	0.024	-0.971	NS			
	F Richness	0.118	-0.011	0.247	1.799	NS			

Table 33: Results of linear mixed-effects models testing the relationships between phylogenetic diversity - calculated using presence-based, abundance-weighted, and size-weighted frameworks - and above-ground carbon (AGC) accumulation. Forest type and census interval were included as random effects to account for spatial and temporal variability. Phylogenetic diversity was assessed using SES MPD (standardized effect size of mean pairwise distance) and SES MNTD (standardized effect size of mean nearest taxon distance).

Weights	Predictor	Estimate	CI lower	CI upper	t value	S/NS	AIC	R ² M	R ² C
Presence	intercept	1.159	0.853	1.164	7.391		-24.64	0.00	0.88
	SES MPD	0.028	-0.085	0.141	0.485	NS			
	SES MNTD	-0.013	0.032	-0.076	-0.391	NS			
Abundance	intercept	1.160	0.891	1.428	8.465		-31.13	0.06	0.87
	SES MPD	0.065	0.031	0.004	2.095	S			
	SES MNTD	0.032	0.044	-0.055	0.714	NS			
Size	intercept	1.149	0.868	1.429	-0.850		-29.64	0.09	0.89
	SES MPD	-0.030	0.035	-0.098	-0.850	NS			
	SES MNTD	0.128	0.055	0.021	2.337	S			

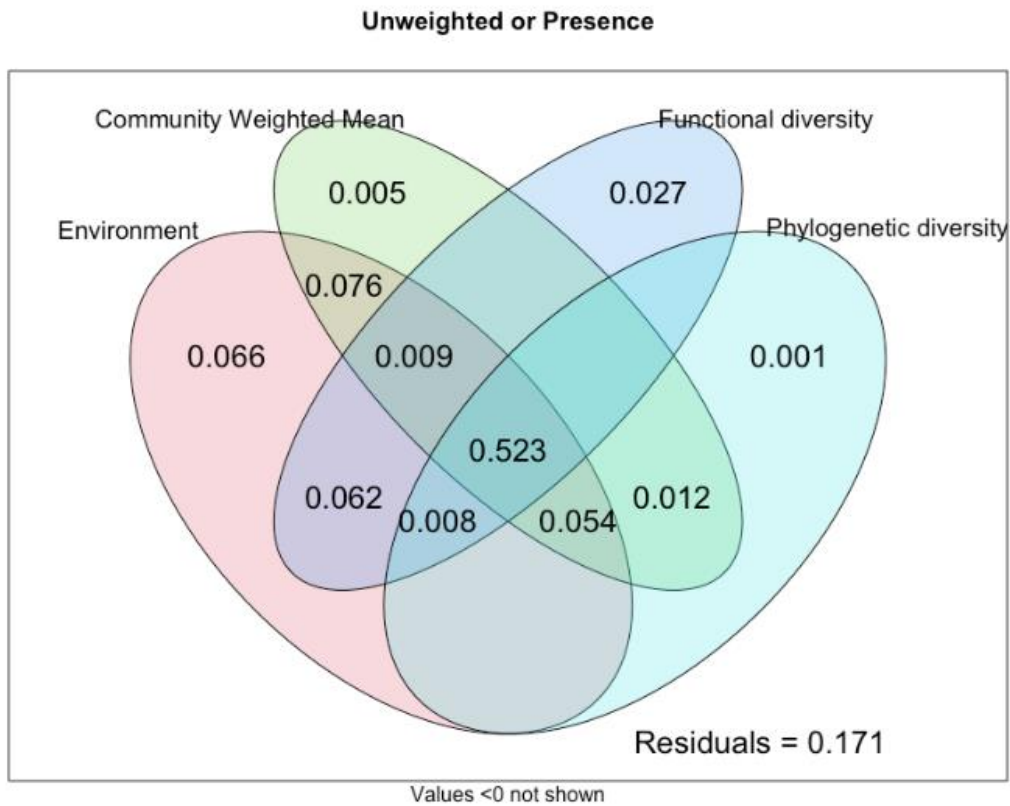


Figure 49: Venn diagram showing the variance partitioning of above-ground carbon (AGC) accumulation among four predictor groups: Environmental Variables, Community-Weighted Means (CWM), Functional Diversity, and Phylogenetic Diversity. Values in overlapping regions represent shared contributions of predictors, whereas non-overlapping sections indicate the unique variance explained by each predictor.

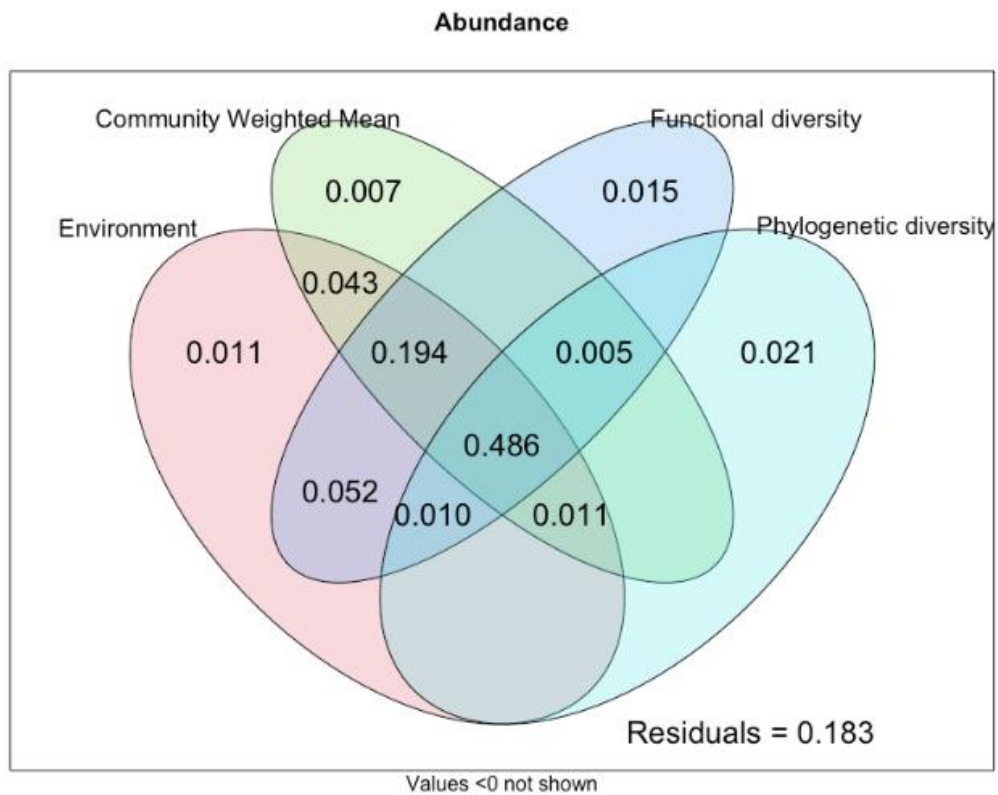


Figure 50: Venn diagram showing the variance partitioning of above-ground carbon (AGC) accumulation among four predictor groups: Environmental Variables, abundance weighted Community-Weighted Means (CWM), Functional Diversity, and Phylogenetic Diversity.

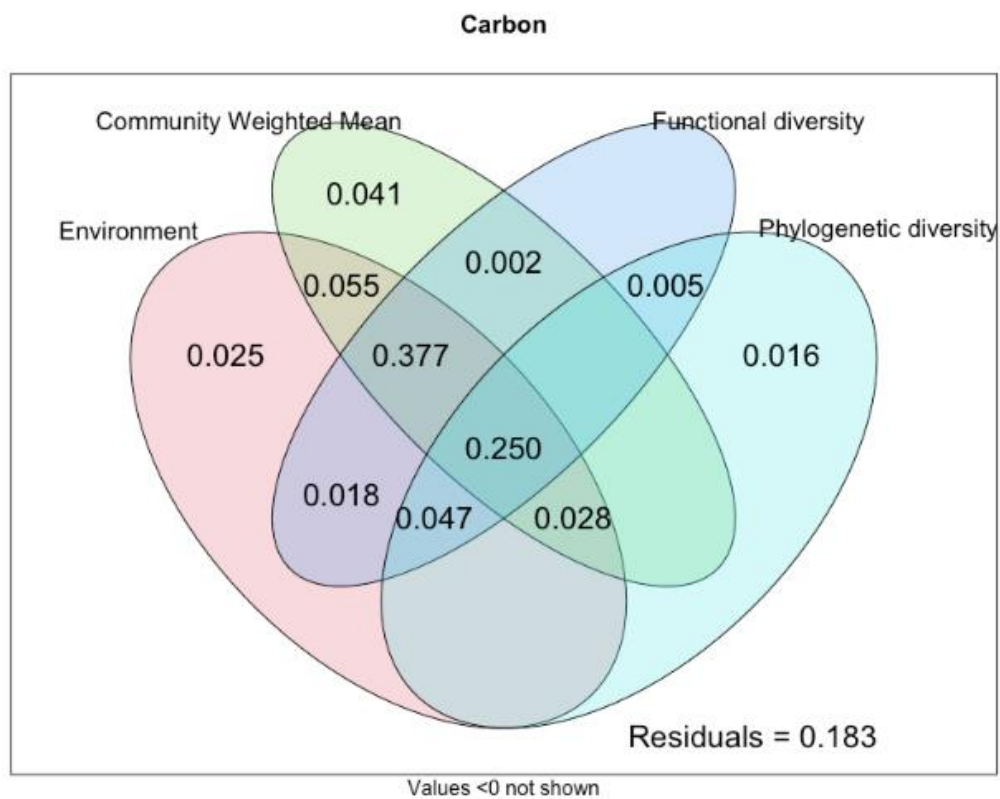


Figure 51: Venn diagram showing the variance partitioning of above-ground carbon (AGC) accumulation among four predictor groups: Environmental Variables, size weighted Community-Weighted Means (CWM), Functional Diversity, and Phylogenetic Diversity.

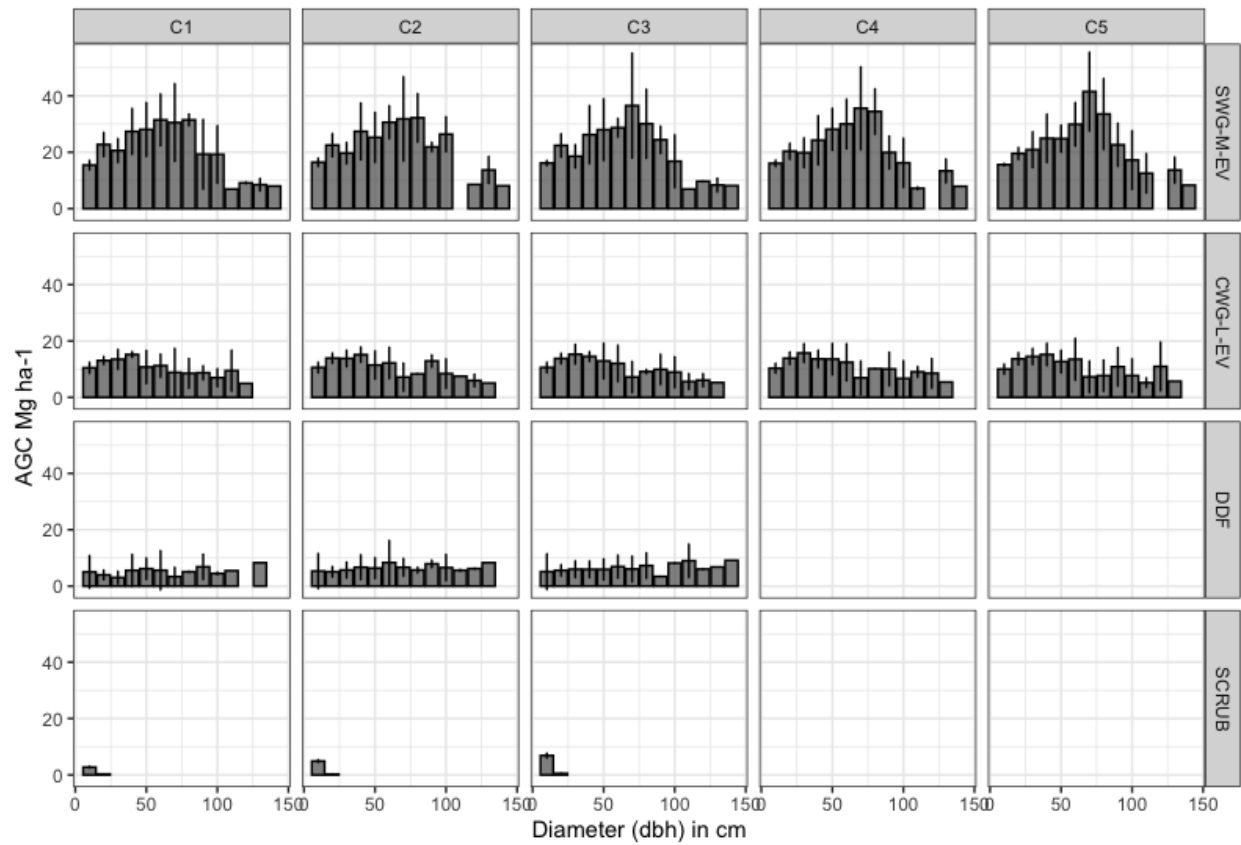


Figure 52: Annual variation in above-ground carbon (AGC; Mg ha⁻¹) across diameter at breast height (DBH) classes, shown by forest type. The figure highlights temporal dynamics (C1–C5 census intervals) and structural contributions of different size classes to overall carbon storage.

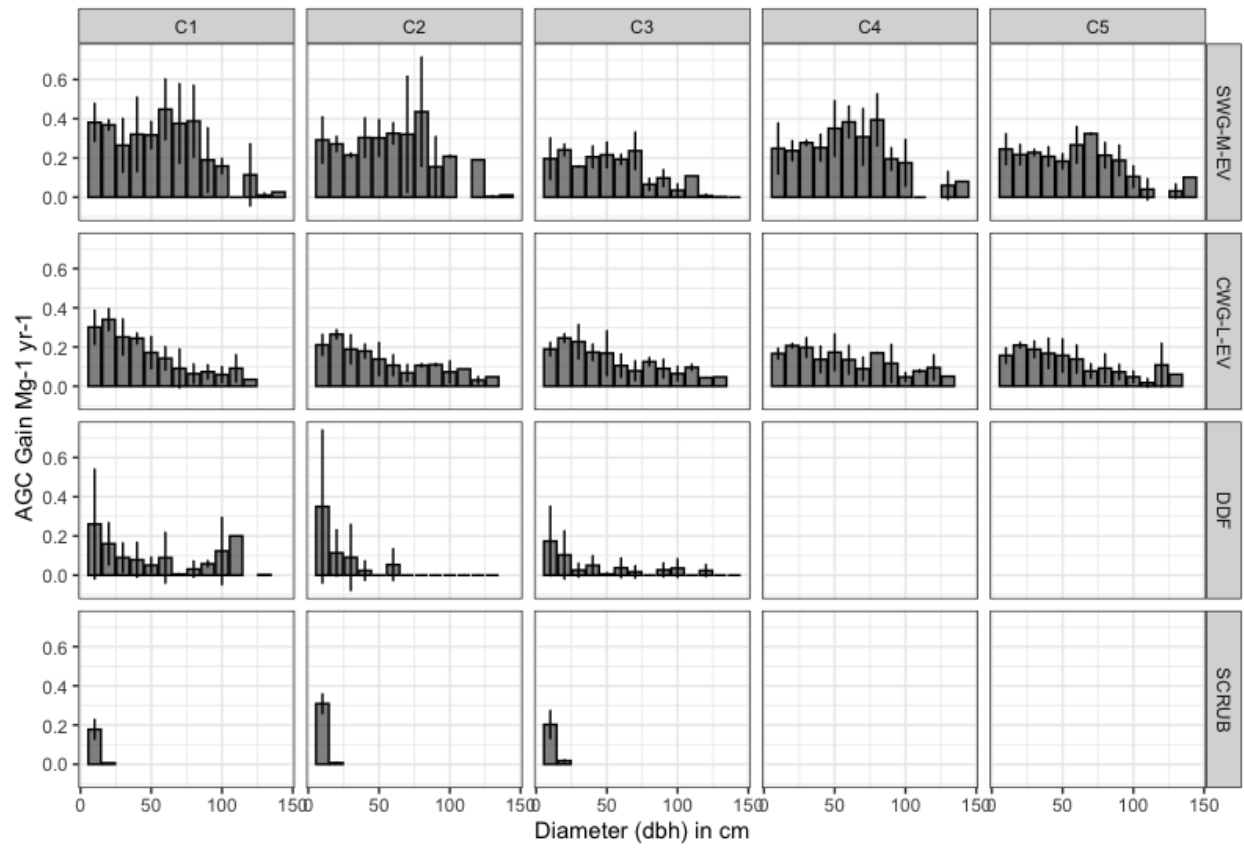


Figure 53: Annual variation in above-ground carbon (AGC; Mg ha^{-1}) accumulation across diameter at breast height (DBH) classes over census intervals C1–C5, grouped by forest type. The figure highlights both temporal dynamics and structural contributions to carbon accumulation.

CONCLUSION

This study provides a comprehensive evaluation of the ecological and evolutionary processes structuring woody plant communities in the Western Ghats, biodiversity hotspot, by integrating three complementary perspectives: phylogenetic community assembly, environmental and phenological filtering, and aboveground carbon (AGC) dynamics. Together, these analyses demonstrate that community structure and ecosystem functioning are jointly shaped by deep evolutionary history, contemporary environmental gradients, functional trait trade-offs, and the disproportionate roles of rare and dominant species.

Across forest strata and biogeographic subregions, phylogenetic analyses revealed consistent vertical stratification in community assembly, with the understorey and emergent strata showing the strongest clustering across both basal (SESMPD) and terminal (SESMNTD) divergence. These strata are dominated by ancient shade- and stress-tolerant lineages, reflecting long-term evolutionary conservatism. In contrast, canopy and liana assemblages exhibited weaker or inconsistent signals, suggesting greater evolutionary lability and ecological stochasticity in lineages occupying these strata. Importantly, abundance weighting consistently weakened clustering signals, underscoring the critical role of rare and evolutionarily distinct taxa in maintaining evolutionary breadth, while dominant clades often drive ecological convergence.

Environmental drivers further reinforced the scale- and stratum-dependence of assembly. Rainfall promoted divergence by enabling the coexistence of distantly related lineages, while climatic water deficit (CWD) enforced clustering, particularly in the understorey and lianas, through strong drought filtering. Elevation had contrasting effects, promoting divergence in emergent but clustering in canopy assemblages at montane sites. The influence of deciduous phenology was especially striking: higher proportions of deciduous species consistently intensified phylogenetic clustering across strata, acting primarily on deep lineages. These findings show that environmental stressors and phenological strategies impose powerful evolutionary filters, constraining communities toward narrower sets of conserved clades while reducing evolutionary distinctiveness under increasing seasonality and drought.

Linking these assembly processes with ecosystem functioning, the analysis of AGC stocks and accumulation highlighted how trait trade-offs, faunal interactions, and evolutionary relationships underpin carbon dynamics. Communities dominated by dense-wood species exhibited lower AGC accumulation, reflecting a trade-off between structural investment for drought and fire survival and reduced biomass turnover. In contrast, communities dominated by species with larger seed diaspores, such as *Cullenia exarillata* and *Palaquium ellipticum*, stored significantly higher carbon stocks, reflecting their tall stature, longevity, and reliance on large-bodied dispersers like the lion-tailed macaque. This finding highlights the cascading role of defaunation in undermining carbon storage through disrupted dispersal networks. Furthermore, phylogenetic diversity particularly when weighted by abundance or carbon was a strong predictor of AGC accumulation, reinforcing that evolutionary distinctiveness and complementarity among dominant species enhance resource partitioning, productivity, and ecosystem resilience.

Collectively, these findings advance three overarching conclusions. First, community assembly in the Western Ghats is hierarchically filtered, with vertical stratification, environmental stress, and phenological strategies exerting differential effects on deep and tip-level evolutionary scales. Second, rare and evolutionarily distinct taxa disproportionately sustain evolutionary breadth, while dominant clades determine biomass accumulation and carbon storage, highlighting complementary roles in biodiversity and ecosystem function. Third, functional traits and phylogenetic diversity jointly regulate carbon dynamics, with trait trade-offs, faunal interactions, and evolutionary complementarity shaping AGC stocks and accumulation rates across forest types.

These insights carry urgent implications for conservation and restoration. Increasing deciduousness, intensifying drought stress, and defaunation threaten to drive communities toward convergence on fewer, stress-tolerant clades, reducing both evolutionary potential and carbon storage capacity. Conservation strategies must therefore prioritize the protection of rare, evolutionarily distinct taxa alongside dominant carbon-accumulating species, safeguard faunal dispersers that maintain seed dispersal networks, and preserve evergreen refugia as buffers against climate change. Restoration programs should integrate phylogenetic and functional perspectives, emphasizing species combinations that maximize evolutionary breadth, functional complementarity, and long-term carbon sequestration potential.

In conclusion, this study integrates phylogenetic structure, environmental filtering, and carbon dynamics, and it provides a robust framework for conservation and management that moves beyond species counts to encompass the evolutionary and functional dimensions of biodiversity. Such an approach is vital for ensuring the resilience, productivity, and carbon storage potential of tropical forests under accelerating anthropogenic impacts and climatic change.

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