Mountains as Climate Change Refugia in the Tropical Dry Forests of Central India: Inference from Phylogenetic Diversity and Structure

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ABSTRACT

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The tropical dry forests of central India are drought-prone communities that experience frequent wildfire and anthropogenic disturbances due to agricultural activity. We analysed patterns in the species diversity and phylogenetic structure of 117 tree species assemblages distributed across a ~230 m to ~940 m elevational gradient within the Central Indian state of Madhya Pradesh. We explore how these axes of diversity varied with elevation, precipitation, temperature, and climatic stress and infer possible assembly structuring mechanisms.

Species richness, phylogenetic diversity (PD), and basal area were all positively correlated with elevation, which trended towards cooler temperatures, higher precipitation, and lower Chave's E—a measure of environmental stress that compounds temperature and precipitation variability with drought intensity. High elevation assemblages tended to be phylogenetically dispersed, while the strength of dispersion diminished as plots became drier and more stressful (Chave's E). Phylogenetic turnover was strongest across gradients in elevation, followed by stress and precipitation.

Our findings indicate that precipitation deficits along with increased temperature and precipitation seasonality at low elevations may act as a selective filter on plant lineages by imposing physiological constraints on species. High elevation sites may thus provide a refuge for tree species maladapted to the harsh drought conditions present throughout low elevations in the Central Indian landscape. We suggest that high elevation habitats may become increasingly important as refugia for species if current climate warming trends continue.

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INTRODUCTION

Understanding the mechanisms that shape the distribution of species diversity across space and time remains a central area of investigation in community ecology. Large-scale environmental gradients have provided opportunities to test hypotheses on the nature of community assembly and species turnover. Elevation gradients are particularly suitable for exploring the influence of environmental variables on biodiversity, given the wide range of abiotic changes that occur across relatively narrow geographical distances (Körner, 2007; Lomolino, 2001). The unique topographical and geomorphic complexity of montane regions that drives these abiotic changes can also lead to sites of relative climatic stability at high elevations (Dobrowski, 2011; Weber et al., 2014). These sites may act as climate refugia (Ashcroft et al., 2012), harbouring relict taxa that have become range-restricted as the climate warmed following the last glacial maxima (Hewitt, 2004; Stewart et al., 2010). Relict taxa may be phylogenetically distinct from the regional community (Provan & Bennett, 2008) due to their unique evolutionary histories (Stewart et al., 2010) and thus contribute disproportionately to community phylogenetic diversity and structure. By exploring community patterns across elevations, phylogenetic approaches can therefore help to identify potential climate refugia harbouring relict taxa (Shooner et al., 2018). Identifying such sites may be important for establishing conservation targets in the wake of contemporary climate change, as many species' ranges are projected to shift upward in elevation with increased warming (Chen et al., 2011; Lenoir & Svenning, 2015).

Phylogenetic approaches can also offer insights into the ecological processes structuring community assembly (Cavender-Bares et al., 2009; Mayfield & Lavine, 2010; Webb et al., 2002). Regional community assemblages are structured by the combined influence of niche-based, neutral, and historical processes (Cavender-Bares et al., 2009). Niche-based processes are rooted in the competitive exclusion paradigm, which states that species with high degrees of ecological similarity cannot coexist due to increased competition for limited resources (Hutchinson, 1959; MacArthur & Levins, 1967). Given that species with shared evolutionary histories are expected to have more similar traits and ecological requirements, competition is expected to be strongest amongst closely related species and weaker between distant relatives. Therefore, the phylogenetic relationships of species can provide a useful proxy for ecological similarity, assuming that traits are conserved amongst evolutionary lineages (Webb, 2000; Webb et al., 2002). When assessing the influence of niche-based assembly processes, decreased species relatedness (i.e., increased phylogenetic dispersion) is expected in communities structured by competition, while increased relatedness (phylogenetic clustering) is expected under environments that select for specific physiological tolerances or traits (Elton, 1946; Simberloff, 1970; Webb et al., 2002; Williams, 1947). However, patterns of phylogenetic clustering may also result from competition if traits that provide greater competitive ability (fitness) within an environment are phylogenetically conserved (Cahill et al., 2008; Davies, 2021; Freckleton & Jetz, 2008; Mayfield & Lavine, 2010; Venail et al., 2014). It is challenging, therefore, to identify community structuring processes from phylogenetic pattern alone (Davies, 2021).

Considering axes of beta diversity alongside measures of phylogenetic community structure may improve inferences about the processes structuring community assembly (Fine & Kembel, 2011; Myers et al., 2012; Zhang et al., 2013). Taxonomic beta diversity (i.e., species turnover) measures differences in the species composition of assemblages across spatial, environmental, or temporal gradients (Whittaker, 1960), while phylogenetic beta diversity reflects how species phylogenetic relationships change across sites (i.e., phylogenetic turnover). These composition changes can be linked to ecological or evolutionary processes structuring diversity in the regional landscape (Graham & Fine, 2008; Swenson, 2011). For example, patterns of high taxonomic turnover and low phylogenetic turnover may reflect habitat partitioning among close relatives due to competitive exclusion or adaptive radiation. In contrast, a pattern of high taxonomic and phylogenetic turnover would be consistent with a tendency for phylogenetically distinct species to have small ranges and low geographical overlap and/or for more distantly related species to differ in their habitat or environmental preferences (Graham & Fine, 2008).

Here, we examined the taxonomic and phylogenetic diversity patterns of tree assemblages distributed across 117 plots located throughout the central Indian state of Madhya Pradesh (Fig. 1). This region is characterised by tropical dry deciduous forests (TDFs), which are common to the Indian subcontinent—accounting for approximately 35% of total forest cover (Reddy et al., 2015). Anthropogenic disturbances remain a significant threat to TDFs worldwide (Miles et al., 2006) and are frequent within Indian TDFs. Common disturbances include fires of anthropogenic origin, grazing from livestock, and the collection of forest products by local people. Much of the research surrounding central Indian forests has focused on the conservation of large megafauna, while information regarding plant diversity and assembly is currently limited. An increased understanding of forest community dynamics and diversity in Indian TDFs could help establish conservation priorities and direct restoration and management strategies within the region. Here we evaluate patterns of phylogenetic diversity, structure, and turnover in response to local environmental gradients to identify key habitats and ecological processes which may be important for maintaining the region's rich floristic diversity.

METHODS

Study Location & Data Collection

We surveyed 117 50x50 m (0.25 ha) plots randomly distributed throughout the natural forests of Madhya Pradesh (Figure 1). Each plot was subdivided into twenty-five 10x10 m grids for ease of sampling. All woody plants encountered within plots with heights ≥ 1.3m were counted and identified to the species level. Additionally, the stem diameter of each individual was recorded at the height of 1.3m. Specimens were prepared and identified at the Department of Botany, Dr. Harisingh Gour Central University, Sagar. GPS coordinates and elevation were recorded through a handheld GPS (Garmin-750), while Mean annual temperature and precipitation were assigned to each plot from the WorldClim dataset (https://www.worldclim.org/) using *sp* and *raster* packages in R (Bivand, Pebesma & Gomez-Rubio, 2013; Pebesma & Bivand, 2005; Hijmans, 2021). We used Chave's stress index (Chave's E) to quantify the environmental stress of each plot (Chave et al., 2014). Chave's E is a covariable commonly used to determine the diameter-height relationships of tropical trees and is defined by:

$$E = (0.178 \, x \, TS - 0.938 \, x \, CWD - 6.61 \, x \, PS) \, x \, 10^{-3}$$

where *TS* is the temperature seasonality, *CWD* is the climate water deficit (mm/yr), and *PS* is precipitation seasonality as defined in the WorldClim dataset. Plots with high Chave's E are therefore indicative of dry sites with large annual variations in temperature and precipitation.

Phylogeny Reconstruction

A species-level phylogeny of all tree species identified in plots (110 angiosperm species) was generated using the R package *V.PhyloMaker*, which utilises the time-calibrated mega tree, *GBOTB.extended.tre* (Jin & Qian, 2019; Figure 1A). The *GBOTB.extended.tre* tree combines

Smith and Brown's (2018) phylogeny of seed plants (*GBOTB*) and Zanne *et al.*'s (2014) phylogeny for pteridophytes, with corrections, updates, and expansions (Jin & Qian, 2019). We utilised the *GBOTB.exteded.tre* phylogeny as a backbone for phylogenetic reconstruction. All 34 families and 83 genera from our study were present on the backbone tree; however, 20 of the 110 regional species were absent. These species were added as tip polytomies by binding them to a close relative present within the backbone tree using the *bind.relative* function (see Table 1A for a list of relatives).

Community & Statistical Analysis

Indices of phylogenetic structure were calculated using the R packages *picante* (Kembel *et al.*, 2010). To assess the total phylogenetic diversity within plots, we used Faith's phylogenetic diversity (PD), which is calculated by summing the total phylogenetic branch lengths connecting all taxa present within an assemblage (Faith, 1992).

We used the standardised effect size of mean pairwise distance (ses.MPD) and mean nearest taxon distance (ses.MNTD) to characterise plot level community structure (Kembel et al., 2010; Webb et al., 2002). These two phylogenetic distance metrics are independent of species richness and reflect divergence in the phylogenetic structure of assemblages at different evolutionary depths. MPD measures the mean phylogenetic distance between all species in an assemblage and is therefore influenced by more ancient evolutionary divergence events (basal branching in the tree). Conversely, MNTD measures the extent of terminal clustering present within an assemblage by taking the average of phylogenetic distances between each taxon and its nearest neighbour in the phylogeny. MNTD, therefore, ignores deeper branching structures, emphasising more recent speciation events at the tips of the tree (Webb et al., 2002). Both MPD and MNTD can therefore provide unique yet complementary information about the phylogenetic structure of assemblages, which, when used together, can aid in the detecting ecological processes operating at different evolutionary depths (Mazel et al., 2016). To account for species abundances, we also estimated the abundance-weighted metrics of MPD and MNTD ($\mathrm{MPD}_{\mathrm{ab}}$ and $\mathrm{MNTD}_{\mathrm{ab}}$, respectively) as:

$$\frac{\sum_{i=1}^{S_p}(m_i \cdot n_i)}{\sum_{i=1}^{S_p} n_i}$$

Where S_p is the number of taxa in a given plot, p, m_i is the distance of a given taxon to its nearest neighbour ($\mathrm{MNTD_{ab}}$) or its mean phylogenetic distance to other members in the assemblage ($\mathrm{MPD_{ab}}$), and n_i is the abundance of species i. By emphasising the contribution of abundant taxa, abundance-weighted metrics are less sensitive to bias from rare taxa. To infer community assembly processes, each phylogenetic structure metric (MPD, $\mathrm{MPD_{ab}}$, MNTD, and $\mathrm{MNTD_{ab}}$) was expressed as a standardised effect size (ses.MPD, $\mathrm{ses.MPD_{ab}}$, ses.MNTD, and $\mathrm{ses.MNTD_{ab}}$) by comparing them to a null distribution of random community assembly generated by randomly swapping the tips of the phylogeny with taxa from the regional species pool (defined by all species identified in plots) 999 times (Kembel et al., 2010). The standardised effect sizes are represented as z-scores, with positive z-scores indicating community assemblages that are phylogenetically over-dispersed relative to null expectations; conversely, negative z-scores indicate communities that are phylogenetically clustered.

We used linear regression to explore the relationships between species richness, PD, phylogenetic structure, and environmental gradients, including elevation, mean annual temperature, mean annual precipitation, and Chave's E. A central assumption of regression is that observations are independent; however, clustered sampling designs in ecological studies could violate these assumptions due to spatial autocorrelation, inflating type I errors (Peres-Neto & Legendre, 2010). To assess if spatial autocorrelation influenced the significance of regression, we generated Moran's eigenvector maps (MEMs; Dray et al., 2006), using the function *quickMEM* (see Appendix for a description; Borcard et al., 2018). MEMs translate spatial relationships between data points into explanatory variables, which describe positive spatial correlation at different spatial scales (Peres-Neto & Legendre, 2010). We found two significant MEMs that we then added to our regression model scheme along with explanatory (species data) and predictor variables (environmental data) to assess whether spatial autocorrelation biased estimated regression parameters. The relationships between stem density and basal area with environmental variables were also explored through linear and partial regression.

We calculated beta-diversity using the taxonomic pairwise dissimilarity measure *Bray-Curtis dissimilarity* (Bray & Curtis, 1957) and the phylogenetic measure *weighted UniFrac* (Lozupone et al., 2006; Lozupone & Knight, 2005). These measures were calculated using the *vegdist* function from the R package *vegan* (Oksanen *et al.*, 2020) and the *UniFrac* function from the R package *phyloseq* (McMurdie & Holmes, 2013), respectively. Both measures were abundance weighted. We used partial mantel tests, using the *mantel* function in *vegan* (Oksanen *et al*., 2020), to assess the relationship between environment and taxonomic and phylogenetic turnover, correcting for the geographical distance between plots. Additionally, we performed a Mantel test on the Bray-Curtis dissimilarity and weighted UniFrac distances to explore the relationship between both metrics. All statistical analyses were conducted using the R statistical programming software, version 4.0.5 (R Core Team, 2021).

RESULTS

Alpha Diversity & Phylogenetic Structure

High elevation sites tended to be cooler, wetter, and associated with lower environmental stress (Figure 2A). Elevation was negatively correlated with temperature ($r^2 = -0.70$, $p < 0.001$) and Chave's E ($r^2 = -0.69$, $p < 0.001$), but was positively correlated with precipitation ($r^2 = 0.65$, $p < 0.001$). Precipitation decreased with increasing temperature ($r^2 = -0.74$, $p < 0.001$), while Chave's E increased with temperature ($r^2 = 0.70$, $p < 0.001$) and decreased with precipitation ($r^2 = -0.74$, $p < 0.001$).

Species richness and phylogenetic diversity had a significant positive relationship with elevation and precipitation, while a significant negative relationship was apparent with temperature and Chave's E (Figure 2 & Table 1). Although the relationships were weaker, correlations between the basal area of assemblages and environmental variables followed similar patterns to species richness and PD. We also found stem density to correlate positively with precipitation, but relationships with other environmental variables were not significant. We identified two significant MEMs (MEM2 and MEM4), suggesting positive spatial autocorrelation between plots. However, partial regression, including MEMs, did not qualitatively shift the relationships between species richness, PD, stem density, or basal area relationships with environmental variables (Table 2A).

Phylogenetic structure metrics indicated that the tree assemblages of plots were, on average, phylogenetically over-dispersed, although some individual plots showed evidence of phylogenetic clustering (Figure 3A). Partial regression with MEMs influenced the relationships between phylogenetic structure and environment (Table 3A); therefore, we report results controlling for spatial autocorrelation, including MEM2 and MEM4 in the regressions. Both ses.MNTD and ses.MNTD$_{ab}$ suggested a trend towards increased phylogenetic overdispersion with higher precipitation and reduced phylogenetic dispersion with Chave's E (Figure 3 & Table 2). Metrics of MPD did not correlate with environment after correcting for spatial autocorrelation.

Taxonomic & Phylogenetic Turnover

Taxonomic (Bray-Curtis) and Phylogenetic (weighted UniFrac) pairwise beta-diversity metrics were significantly correlated (mantel $r = 0.49$, $P < 0.001$; Figure 5A). Mantel tests indicated a significant correlation between both taxonomic and phylogenetic beta-diversity and elevation (Table 3). Weaker correlations were detected between taxonomic beta diversity, temperature, and precipitation, while no significant correlation was detected between taxonomic beta diversity and Chave's E. Phylogenetic beta-diversity was weakly correlated with precipitation and Chave's E, but not with temperature. Partial Mantel tests were used to correct for differences in the geographical distance of plots; however, these corrections did not influence the significance of relationships. Geographical distance had a larger effect on phylogenetic turnover than taxonomic turnover.

DISCUSSION

We assessed the phylogenetic diversity, structure, and turnover of forest communities throughout the Central Indian state of Madhya Pradesh. High elevation sites, characterised by milder, more abiotically favourable conditions, supported a greater species richness, PD, and basal area of trees, compared to lower elevation sites, which were drier, hotter, and had increased precipitation and temperature seasonality (Chave's E). We hypothesise that these community patterns reflect the importance of high elevation habitats as climate refugia for species that are unable to persist under the harsher climatic conditions of low elevations. At lower elevations, physiological stress imposed by harsher abiotic environments resulted in lower species richness and greater phylogenetic clustering, as species are filtered more strongly along a gradient of precipitation and seasonality. Species and phylogenetic turnover were strongest across gradients in elevation, consistent with species filtering along this environmental axis. High elevation assemblages are therefore compositionally distinct, phylogenetically diverse and tend to be more phylogenetically dispersed than low elevation assemblages, which may indicate the presence of relictual taxa. We suggest that high elevation habitats will become increasingly important refuges for forest species if warming trends continue and as plants respond by shifting their distributions towards higher elevations (Chen et al., 2011; Lenoir & Svenning, 2015).

Temperature and precipitation are among the most important factors influencing plant productivity globally (Bernacchi & VanLoocke, 2015; Madani et al., 2017; Nemani et al., 2003). In arid regions—such as the tropical dry forests of India—water is often a limiting factor (Noy-Meir, 1973). High ambient temperatures can further increase aridity and lead to sharp declines in species' photosynthetic capacity if temperatures exceed species' optimum thresholds for photosynthesis (Huang et al., 2019). Therefore, by imposing physiological constraints on species, climate may act as a selective filter that drives regional diversity gradients (Chu et al., 2019; Givnish, 2001). Our findings suggest a climatic stress gradient exists across the elevational range of Madhya Pradesh, characterised by hotter, drier, and more variable precipitation and temperature conditions at low elevations (Chave's E). Greater species richness, PD, and basal area in higher elevation sites indicate that high elevation habitats may possess more favourable growing conditions for tree species and likely act as a refuge from the harsher climates of low elevations. The increasing basal area of trees with elevation might also reflect increased canopy cover, which could further moderate high elevation microclimates. By limiting light penetration to the forest floor, canopy cover could lead to reductions in temperature, solar radiation, and increased moisture (Elliott et al., 1998; Karna et al., 2020; von Arx et al., 2013), leading to more favourable micro-habitats for seedling establishment (von Arx et al., 2013). The topographical complexity of montane regions could also enhance the persistence of unique microclimates (Dobrowski, 2011; Weber et al., 2014), important for maintaining plant diversity. High elevation habitats thus may have provided critical refugia for relict taxa adapted to the cooler climate conditions that immediately followed the last glacial maxima (Hewitt, 2004; Stewart et al., 2010).

Community phylogenetic dispersion and turnover provide further support for high elevation refugia. We found that the strength of phylogenetic overdispersion decreased as plots became drier and Chave's E increased. Species that lack trait adaptations necessary to persist under drier and more climatically seasonal environments are therefore confined to more abiotically favourable habitats, such as those found at high elevations. Our analyses and previous findings indicate a general trend towards increased phylogenetic clustering and reduced overdispersion as precipitation becomes more limited in Indian forests (Bose et al., 2019; Divya, Ramesh, & Karanth, 2021; Shivaprakash et al., 2018). Additionally, we found that community turnover was correlated with elevation; thus, high elevation sites are not only more diverse but also compositionally distinct from low elevations. This distinctiveness is consistent with high elevation habitats acting as refugia for species lost in the harsher environments of low elevations. The lower turnover in phylogenetic branches than species membership, and more pronounced phylogenetic signal in our tip-level metrics of phylogenetic clustering, indicates that most of the divergence in habitat preferences is relatively shallow on the phylogeny, suggesting that differences in abiotic tolerances among species evolved relatively recently. We detected only moderate differences between weighted and unweighted metrics of phylogenetic structure, indicating that our results are not biased by the presence of rare species in assemblages.

Greater phylogenetic dispersion at higher elevation sites is also consistent with the presence of evolutionarily distinct lineages in these habitats. Because relict taxa may belong to once more diverse clades with relatively higher extinction rates, they may tend to be phylogenetically distinct from the broader regional community (Provan & Bennett, 2008), and can thus add to the apparent phylogenetic dispersion of communities (Shooner et al., 2018). Therefore, the greater phylogenetic dispersion and PD of high elevation sites could reflect the presence of once more widespread relictual taxa that have become confined to high elevation refugia more closely resembling the conditions under which they evolved. Although communities tended to be more phylogenetically dispersed at high elevations, relationships between dispersion and elevation were weak and non-significant when adjusting for spatial co-predictors. However, we observed a stronger relationship between phylogenetic dispersion and both precipitation and climatic stability (lower Chave’s E), consistent with the recruitment of evolutionarily distinct lineages to more abiotically favourable sites.

By reducing site accessibility, elevation may also provide refuge from anthropogenic disturbance regimes (Sousa, 1984; Zhang et al., 2014). Indian TDFs are prone to anthropogenic disturbance due to their suitability for agriculture and abundance of tangible forest products (Schmerbeck & Fiener, 2015; Schmerbeck & Seeland, 2007). Livestock grazing, in particular, is common throughout Madhya Pradesh and may influence both taxonomic diversity (Oldén et al., 2017; Schulz et al., 2019) and the phylogenetic structure of forest communities (Salgado-Luarte et al., 2019; Zhu et al., 2020). Anthropogenic forest fires are regarded as one of the principal factors leading to the degradation of TDFs in Madhya Pradesh (Chandra & Bhardwaj, 2015), with previous studies demonstrating a reduction in the taxonomic diversity of forests exposed to recurrent burn events (Kodandapani et al., 2008; Sathya & Jayakumar, 2017; Verma & Jayakumar, 2015). Further, fire may select for species with fire-tolerant traits such as thickened bark and resprouting, shifting community composition towards fire-tolerant species (Saha & Howe, 2003; Sathya & Jayakumar, 2017; Verma & Jayakumar, 2015). If traits for fire tolerance are phylogenetically conserved, fire may also alter the phylogenetic structure of communities (Nóbrega et al., 2019). In addition, fire may influence forest canopy structure (Karna et al., 2020), favouring the recruitment of pyrophytic grass species, which increase the susceptibility of sites to future burn events (D'antonio & Vitousek, 1992). It is likely that the increased aridity, temperature, and seasonality that we detected in low elevation sites could increase the frequency and intensity of forest fires, for example, by influencing fuel load and flammability (Mondal & Sukumar, 2016).

As regional climates shift, species may respond by adapting to novel conditions or by shifting their range distributions to regions with climates that more closely reflect the conditions under which they evolved (Hewitt, 2004; Stewart et al., 2010). Our analysis indicates that increased abiotic stress at low elevation sites throughout Madhya Pradesh favours an increased recruitment of tree species to the wetter, cooler, and more stable conditions of high elevations. We also suggest that many species found in high elevation habitats today might belong to relictual populations of once more widespread species, and that current warming trends will make these high-elevation refuges increasingly critical in the future. High elevation habitats may therefore be important conservation targets for the TDFs of Madhya Pradesh. Future work should look to better incorporate ecological niche and trait-based approaches to strengthen inferences about the assembly processes structuring Central Indian TDFs, and evaluate the impacts of anthropogenic disturbances, such as grazing, fire, and agriculture, across the abiotic stress gradients we identify.

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TABLES AND FIGURES

Figure 1. Map of plot locations throughout Madhya Pradesh, central India. Numbers on points indicate the number of 0.25 ha plots within the given area. Darker shades represent lower elevation sites. Elevation ranges from 200 to 800m above sea level.

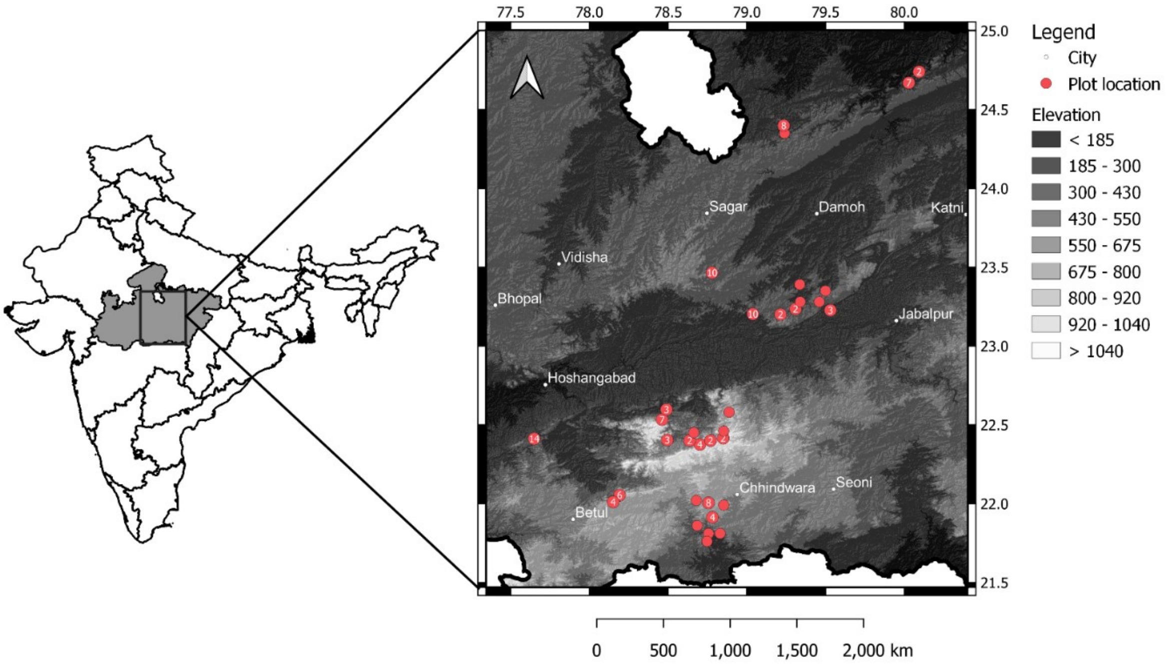

Figure 2. Correlations in diversity and density metrics with gradients in elevation, temperature, precipitation, and Chave's E. Regression lines and 95% confidence intervals are displayed.

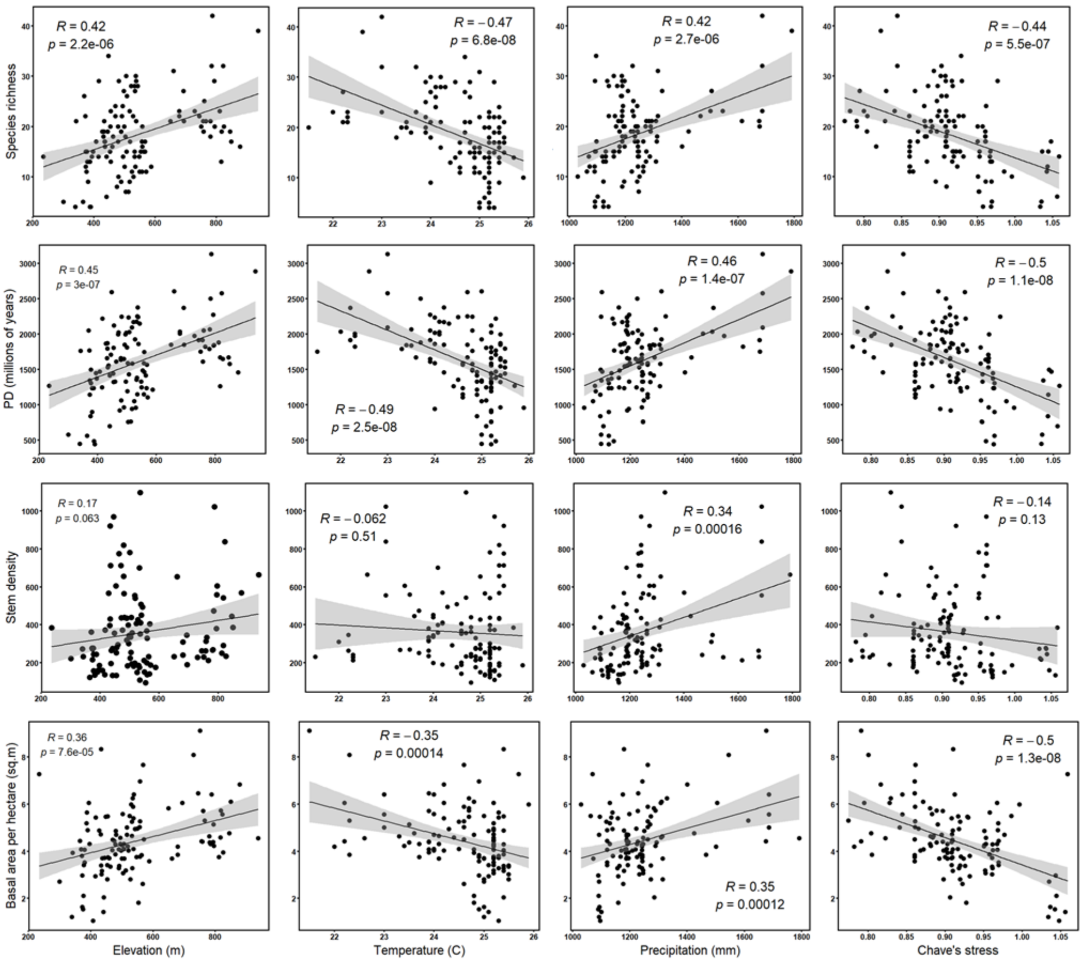

Table 1. Pearson's correlation coefficients between alpha diversity, density, basal area, and environmental variables. Asterisks indicate levels of significance (*p < 0.05; **p < 0.01).

Indices	Elevation	Temperature	Precipitation	Chave's E
Species Richness	0.42**	-0.47**	0.42**	-0.44**
Phylogenetic Diversity (PD)	0.45**	-0.49**	0.46**	-0.50**
Stem Density	0.17	-0.062	0.34**	-0.14
Basal Area	0.36**	-0.35**	0.35**	-0.50**

Figure 3. Correlations in terminal phylogenetic structure metrics with gradients in elevation, temperature, precipitation, and Chave's E. Regression lines and 95% confidence intervals are displayed.

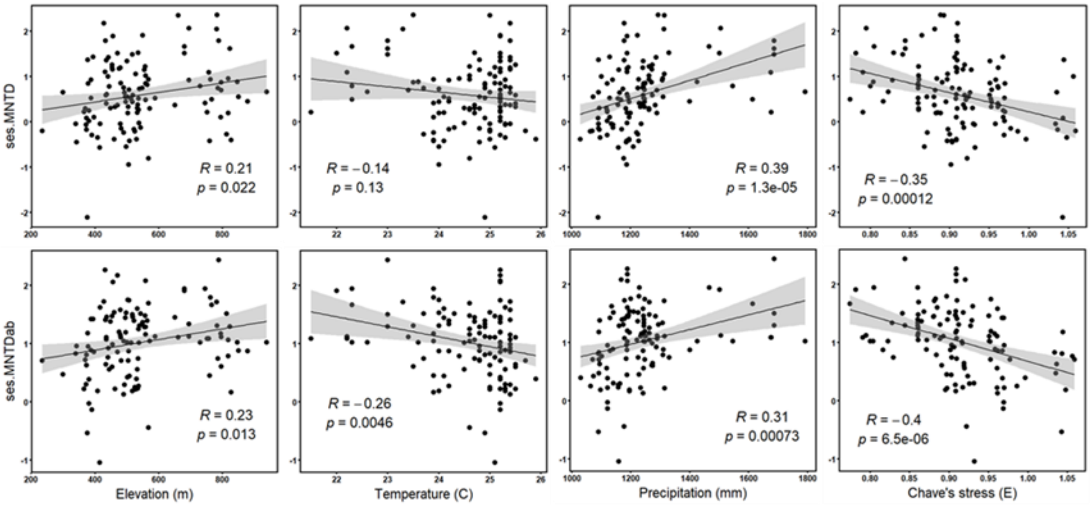

Table 2. Pearson's correlation and partial regression coefficients between terminal phylogenetic structure metrics, environmental variables, and Moran's eigenvector maps (MEMs). Asterisks indicate levels of significance (*p < 0.05; **p < 0.01).

Indices	Elevation	Temperature	Precipitation	Chave's E
ses.MNTD	0.21*	-0.14	0.39**	-0.35**
ses.MNTD – MEM2	0.13	-0.067	0.34**	-0.26**
ses.MNTD – MEM4	0.21*	-0.12	0.29**	-0.35**
ses.MNTD$_{ab}$	0.23*	-0.26**	0.31**	-0.40**
ses.MNTD$_{ab}$ *– MEM2*	0.098	-0.16	0.20*	-0.24**
ses.MNTD$_{ab}$ *– MEM4*	0.23*	-0.25**	0.24**	-0.40**

Table 3. Mantel and partial mantel tests for phylogenetic (weighted UniFrac) and taxonomic (Bray-Curtis) changes in beta-diversity with environmental variables and geographical distance. Environmental factors and distance represent the pairwise differences between plots. Significant correlations are bolded.

Distance metric:	**Bray-Curtis**		**Weighted UniFrac**	
Model	**Mantel r**	**p**	**Mantel r**	**p**
Elevation	**0.28**	**<0.01**	**0.25**	**<0.01**
Elevation + Distance	**0.27**	**<0.01**	**0.30**	**<0.01**
Temperature	**0.10**	**0.02**	0.07	0.06
Temperature + Distance	**0.13**	**<0.01**	0.07	0.08
Precipitation	**0.11**	**0.02**	**0.11**	**0.02**
Precipitation + Distance	**0.15**	**<0.01**	**0.12**	**0.01**
Stress	<0.01	0.43	**0.16**	**<0.01**
Stress + Distance	0.06	0.08	**0.27**	**<0.01**
Distance	**0.11**	**<0.01**	**0.32**	**<0.01**

APPENDIX

We computed distance-based Moran's eigenvector maps (MEMs; Dray et al., 2006)—previously referred to as PCNM eigenvectors (Borcard & Legendre 2002)—to assess if spatial autocorrelation influenced the significance of relationships between species and environmental data. MEMs are proportional to Moran's I correlation coefficient, which measures spatial autocorrelation. MEMs translate spatial autocorrelation into variables that describe community spatial structure at different spatial scales. These variables can then be applied through partial regression or partial canonical analysis to control for type I errors that may result from spatial non-independence in community data (Peres-Neto & Legendre 2010). We used the function quickMEM (Borcard et al., 2018), which computes MEMs as described by Dray et al. (2006). This function computes MEMs with positive eigenvalues (positive autocorrelation) from a list of geographical coordinates corresponding to plot locations. A spatial weighting matrix is generated based on the maximum distance in a minimum spanning tree that maintains links between all sites. MEMs are then built through principal coordinates analysis. The MEMs generated represent positive spatial structure from broad to fine scales. Our analysis generated ten MEMs with positive spatial correlation (MEM1 to MEM10). A global RDA is then performed with all MEMs. If significant MEMs are present, a forward selection is applied with Blanchet et al. (2008) double stopping criterion. An additional RDA is then run with the forward selected MEMs, and axes are tested for significance. Significant axes represent MEMs that describe positive spatial autocorrelations in community data. Two significant MEMs were retained in our analysis (MEM2 & MEM4) which were used in partial regression with community metrics and environmental variables to test if spatial autocorrelation influenced the significance of results (Table 2A & Table 3A).

APPENDIX REFERENCES

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APPENDIX TABLES AND FIGURES

Table 1A. Taxa used for phylogenetic reconstruction of central Indian tropical dry deciduous forest communities in Madhya Pradesh, India. Bolded taxa were not present in the backbone and are represented by a closely related species relative.

Species	**Genus**	**Family**	**species.relative**
Acacia catechu	***Acacia***	***Fabaceae***	***Acacia mearnsii***
Acacia donaldii	***Acacia***	***Fabaceae***	***Acacia farnesiana***
Acacia leucophloea	***Acacia***	***Fabaceae***	***Acacia auriculiformis***
Acacia nilotica	*Acacia*	*Fabaceae*	
Acacia pennata	***Acacia***	***Fabaceae***	***Acacia senegal***
Adina cordifolia	***Adina***	***Rubiaceae***	***Haldina cordifolia***
Aegle marmelos	*Aegle*	*Rutaceae*	
Ailanthus excelsa	***Ailanthus***	***Simaroubaceae***	***Ailanthus triphysa***
Albizia lebbeck	*Albizia*	*Fabaceae*	
Albizia odoratissima	*Albizia*	*Fabaceae*	
Albizia procera	*Albizia*	*Fabaceae*	
Ampelocissus latifolia	*Ampelocissus*	*Vitaceae*	
Annona squamosa	*Annona*	*Annonaceae*	
Anogeissus latifolia	*Anogeissus*	*Combretaceae*	

Anogeissus pendula	*Anogeissus*	*Combretaceae*	
Antidesma acidum	*Antidesma*	*Phyllanthaceae*	
Azadirachta indica	*Azadirachta*	*Meliaceae*	
Bauhinia malabarica	***Bauhinia***	***Fabaceae***	***Bauhinia tomentosa***
Bauhinia racemosa	*Bauhinia*	*Fabaceae*	
Bauhinia roxburghiana	***Bauhinia***	***Fabaceae***	***Bauhinia phoenicea***
Bauhinia vahlii	*Bauhinia*	*Fabaceae*	
Bauhinia variegata	*Bauhinia*	*Fabaceae*	
Bombax ceiba	*Bombax*	*Malvaceae*	
Boswellia serrata	*Boswellia*	*Burseraceae*	
Bridelia retusa	*Bridelia*	*Phyllanthaceae*	
Buchanania cochinchinensis	*Buchanania*	*Anacardiaceae*	
Butea monosperma	*Butea*	*Fabaceae*	
Butea superba	*Butea*	*Fabaceae*	
Careya arborea	*Careya*	*Lecythidaceae*	
Carissa spinarum	*Carissa*	*Apocynaceae*	
Casearia graveolens	***Casearia***	***Salicaceae***	***Casearia gladiiformis***
Casearia tomentosa	***Casearia***	***Salicaceae***	***Casearia velutina***
Cassia fistula	*Cassia*	*Fabaceae*	
Catunaregam spinosa	*Catunaregam*	*Rubiaceae*	
Celastrus paniculatus	*Celastrus*	*Celastraceae*	
Ceriscoides turgida	*Ceriscoides*	*Rubiaceae*	
Chloroxylon swietenia	***Chloroxylon***	***Rutaceae***	***Chloroxylon faho***
Cochlospermum religiosum	***Cochlospermum***	***Bixaceae***	***Cochlospermum vitifolium***
Cordia myxa	*Cordia*	*Boraginaceae*	
Dalbergia lanceolaria	*Dalbergia*	*Fabaceae*	
Dalbergia latifolia	*Dalbergia*	*Fabaceae*	
Desmodium oojeinense	*Desmodium*	*Fabaceae*	
Dioscorea bulbifera	*Dioscorea*	*Dioscoreaceae*	
Diospyros melanoxylon	*Diospyros*	*Ebenaceae*	
Dodonaea viscosa	*Dodonaea*	*Sapindaceae*	
Ehretia laevis	*Ehretia*	*Boraginaceae*	
Elaeodendron glaucum	*Elaeodendron*	*Celastraceae*	
Eriolaena hookeriana	*Eriolaena*	*Malvaceae*	
Erythrina stricta	*Erythrina*	*Fabaceae*	
Ficus benghalensis	*Ficus*	*Moraceae*	
Ficus racemosa	*Ficus*	*Moraceae*	
Ficus religiosa	*Ficus*	*Moraceae*	
Ficus virens	*Ficus*	*Moraceae*	
Flacourtia indica	*Flacourtia*	*Salicaceae*	
Gardenia latifolia	*Gardenia*	*Rubiaceae*	
Garuga pinnata	*Garuga*	*Burseraceae*	
Gmelina arborea	*Gmelina*	*Lamiaceae*	
Grewia hirsuta	***Grewia***	***Malvaceae***	***Grewia nervosa***

Grewia tiliifolia	***Grewia***	***Malvaceae***	***Grewia occidentalis***
Gymnosporia emarginata	*Gymnosporia*	*Celastraceae*	
Gymnosporia senegalensis	*Gymnosporia*	*Celastraceae*	
Hardwickia binata	*Hardwickia*	*Fabaceae*	
Helicteres isora	*Helicteres*	*Malvaceae*	
Holarrhena pubescens	*Holarrhena*	*Apocynaceae*	
Holoptelea integrifolia	*Holoptelea*	*Ulmaceae*	
Ichnocarpus frutescens	*Ichnocarpus*	*Apocynaceae*	
Ixora pavetta	*Ixora*	*Rubiaceae*	
Kydia calycina	*Kydia*	*Malvaceae*	
Lagerstroemia parviflora	*Lagerstroemia*	*Lythraceae*	
Lannea coromandelica	*Lannea*	*Anacardiaceae*	
Limonia acidissima	*Limonia*	*Rutaceae*	
Litsea glutinosa	*Litsea*	*Lauraceae*	
Madhuca longifolia	*Madhuca*	*Sapotaceae*	
Mallotus philippensis	*Mallotus*	*Euphorbiaceae*	
Mangifera indica	*Mangifera*	*Anacardiaceae*	
Manilkara hexandra	*Manilkara*	*Sapotaceae*	
Miliusa tomentosa	*Miliusa*	*Annonaceae*	
Millettia extensa	*Millettia*	*Fabaceae*	
Mitragyna diversifolia	*Mitragyna*	*Rubiaceae*	
Mitragyna parvifolia	*Mitragyna*	*Rubiaceae*	
Nyctanthes arbor-tristis	*Nyctanthes*	*Oleaceae*	
Phoenix sylvestris	*Phoenix*	*Arecaceae*	
Phyllanthus emblica	*Phyllanthus*	*Phyllanthaceae*	
Pongamia pinnata	*Pongamia*	*Fabaceae*	
Pterocarpus marsupium	*Pterocarpus*	*Fabaceae*	
Radermachera xylocarpa	*Radermachera*	*Bignoniaceae*	
Schleichera oleosa	*Schleichera*	*Sapindaceae*	
Schrebera swietenioides	*Schrebera*	*Oleaceae*	
Searsia parviflora	*Searsia*	*Anacardiaceae*	
Semecarpus anacardium	*Semecarpus*	*Anacardiaceae*	
Shorea robusta	*Shorea*	*Dipterocarpaceae*	
Soymida febrifuga	*Soymida*	*Meliaceae*	
Sterculia urens	*Sterculia*	*Malvaceae*	
Stereospermum chelonoides	*Stereospermum*	*Bignoniaceae*	
Syzygium cumini	*Syzygium*	*Myrtaceae*	
Tamarindus indica	*Tamarindus*	*Fabaceae*	
Tectona grandis	*Tectona*	*Lamiaceae*	
Terminalia arjuna	*Terminalia*	*Combretaceae*	
Terminalia bellirica	*Terminalia*	*Combretaceae*	
Terminalia chebula	*Terminalia*	*Combretaceae*	
Terminalia coriacea	***Terminalia***	***Combretaceae***	***Terminalia tomentosa***
Vallaris solanacea	*Vallaris*	*Apocynaceae*	
Ventilago denticulata	*Ventilago*	*Rhamnaceae*	

Wendlandia heynei	*Wendlandia*	*Rubiaceae*	
Wrightia arborea	*Wrightia*	*Apocynaceae*	
Wrightia tinctoria	***Wrightia***	***Apocynaceae***	***Wrightia religiosa***
Ziziphus mauritiana	***Ziziphus***	***Rhamnaceae***	***Ziziphus jujuba***
Ziziphus oenoplia	***Ziziphus***	***Rhamnaceae***	***Ziziphus mucronata***
Ziziphus rugosa	***Ziziphus***	***Rhamnaceae***	***Ziziphus glabrata***
Ziziphus xylopyrus	***Ziziphus***	***Rhamnaceae***	***Ziziphus ornata***

Figure 1A. Phylogenetic relationships between tree species in plot locations sampled within Madhya Pradesh, India.

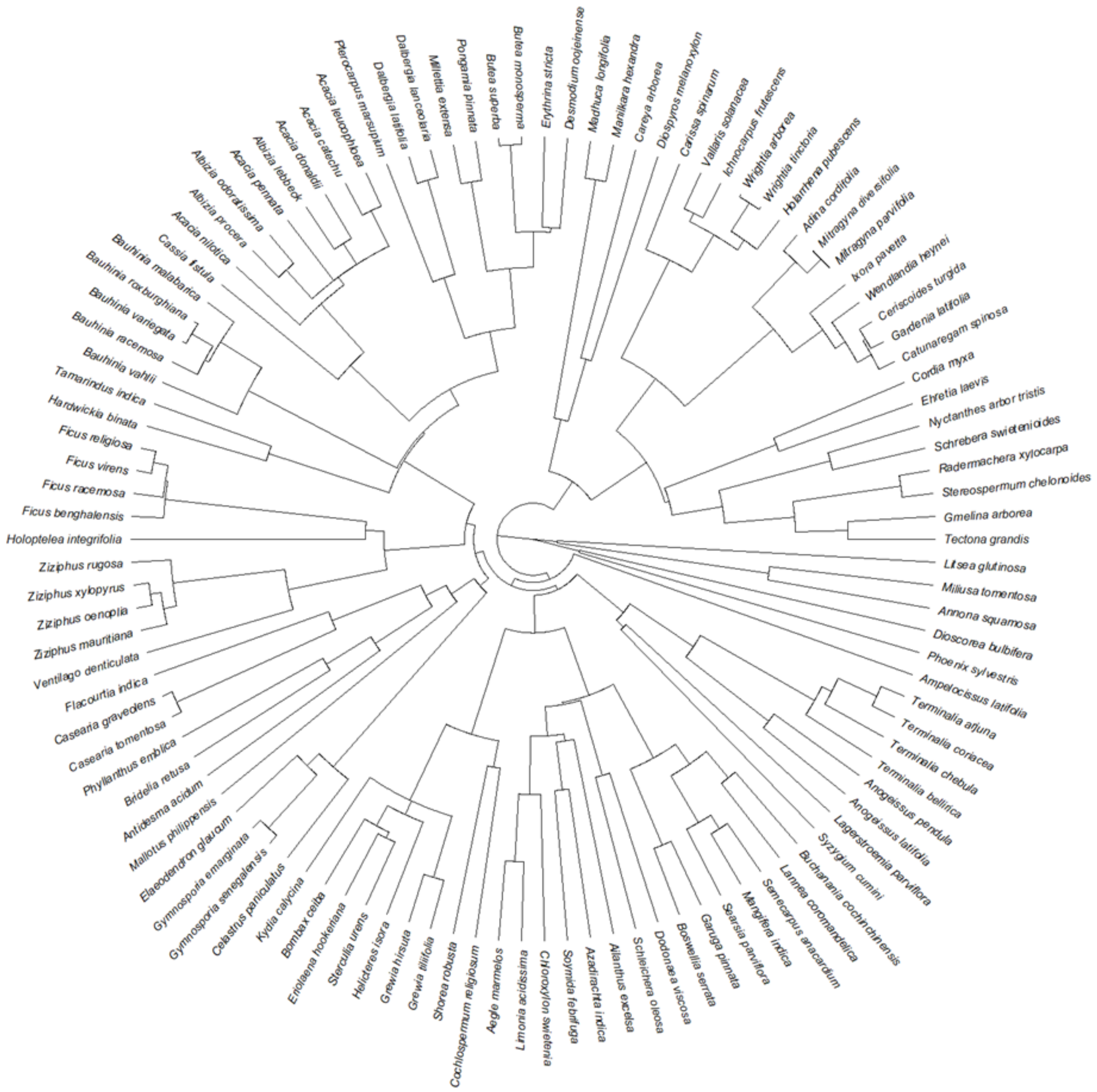

Figure 2A. Pearson's correlation between environmental variables. Regression lines and 95% confidence intervals are displayed.

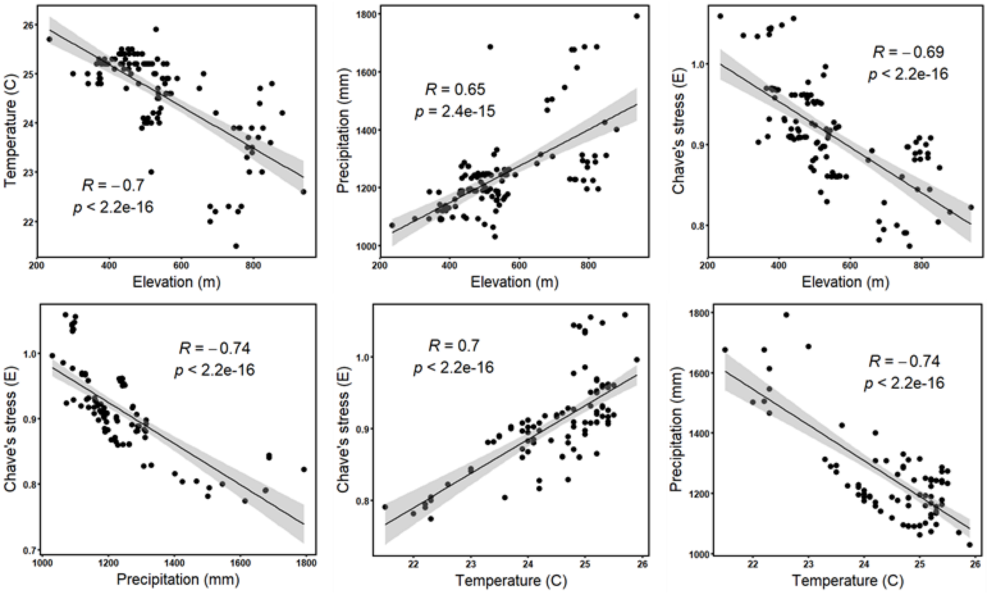

Figure 3A. Average phylogenetic structure of assemblages. Values represent the number of standard deviations from null expectation. Positive values indicate phylogenetic over-dispersion, while negative values represent phylogenetic clustering.

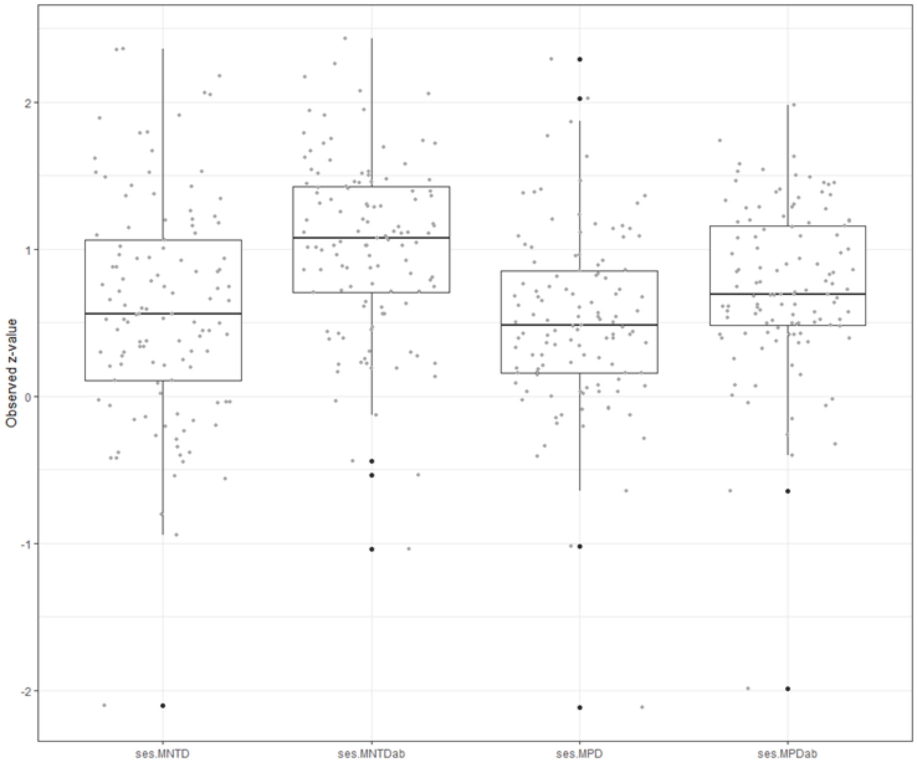

Table 2A. Pearson's correlation and partial regression coefficients between alpha diversity, density, environmental variables, and Moran's eigenvector maps (MEMs). Asterisks indicate levels of significance (*p < 0.05; **p < 0.01).

Indices	Elevation	Temperature	Precipitation	Chave's E	MEM2	MEM4
Species richness	**0.42****	**-0.47****	**0.42****	**-0.44****	**0.43****	**0.0014**
Species richness – MEM2	0.30**	-0.39**	0.31**	-0.21*		
Species richness – MEM4	0.42**	-0.48**	0.46**	-0.44**		
PD	**0.45****	**-0.49****	**0.46****	**-0.50****	**0.48****	**0.056**
PD – MEM2	0.32**	-0.40**	0.45**	-0.24**		
PD – MEM4	0.45**	-0.49**	0.48**	-0.50**		
Stem density	**0.17**	**-0.062**	**0.34****	**-0.14**	**0.055**	**0.16**
Stem density – MEM2	0.16	-0.047	0.35**	-0.15		
Stem density – MEM4	0.17	-0.048	0.31**	-0.13		
Basal area	**0.36****	**-0.35****	**0.35****	**-0.50****	**0.33****	**0.040**
Basal area – MEM2	0.26**	-0.27**	0.26**	-0.40**		
Basal area – MEM4	0.36**	-0.34**	0.36**	-0.49**		

Table 3A. Pearson's correlation and partial regression coefficients between phylogenetic structure metrics, environmental variables, and Moran's eigenvector maps (MEMs). Asterisks indicate levels of significance (*p < 0.05; **p < 0.01).

Indices	Elevation	Temperature	Precipitation	Chave's E	MEM2	MEM4
ses.MPD	**0.15**	**-0.15**	**0.19***	**-0.23***	**0.16**	**0.092**
ses.MPD – MEM2	0.088	-0.11	0.15	-0.16		
ses.MPD -MEM4	0.14	-0.15	0.17	-0.22*		
ses.MPD$_{ab}$	**0.012**	**-0.12**	**0.089**	**-0.11**	**0.10**	**0.023**
ses.MPD$_{ab}$ *– MEM2*	-0.032	-0.092	0.057	-0.052		
ses.MPD$_{ab}$ *– MEM4*	0.011	-0.12	0.087	-0.11		
ses.MNTD	**0.21***	**-0.14**	**0.39****	**-0.35****	**0.24****	**0.37****
ses.MNTD – MEM2	0.13	-0.067	0.34**	-0.26**		
ses.MNTD – MEM4	0.21*	-0.12	0.29**	-0.35**		
ses.MNTD$_{ab}$	**0.23***	**-0.26****	**0.31****	**-0.40****	**0.36****	**0.23***
ses.MNTD$_{ab}$ *– MEM2*	0.098	-0.16	0.20*	-0.24*		
ses.MNTD$_{ab}$ *– MEM4*	0.23*	-0.25**	0.24**	-0.40**		

Figure 4A. Correlations in phylogenetic structure metrics with gradients in elevation, temperature, precipitation, and Chave's E. Regression lines and 95% confidence intervals are displayed.

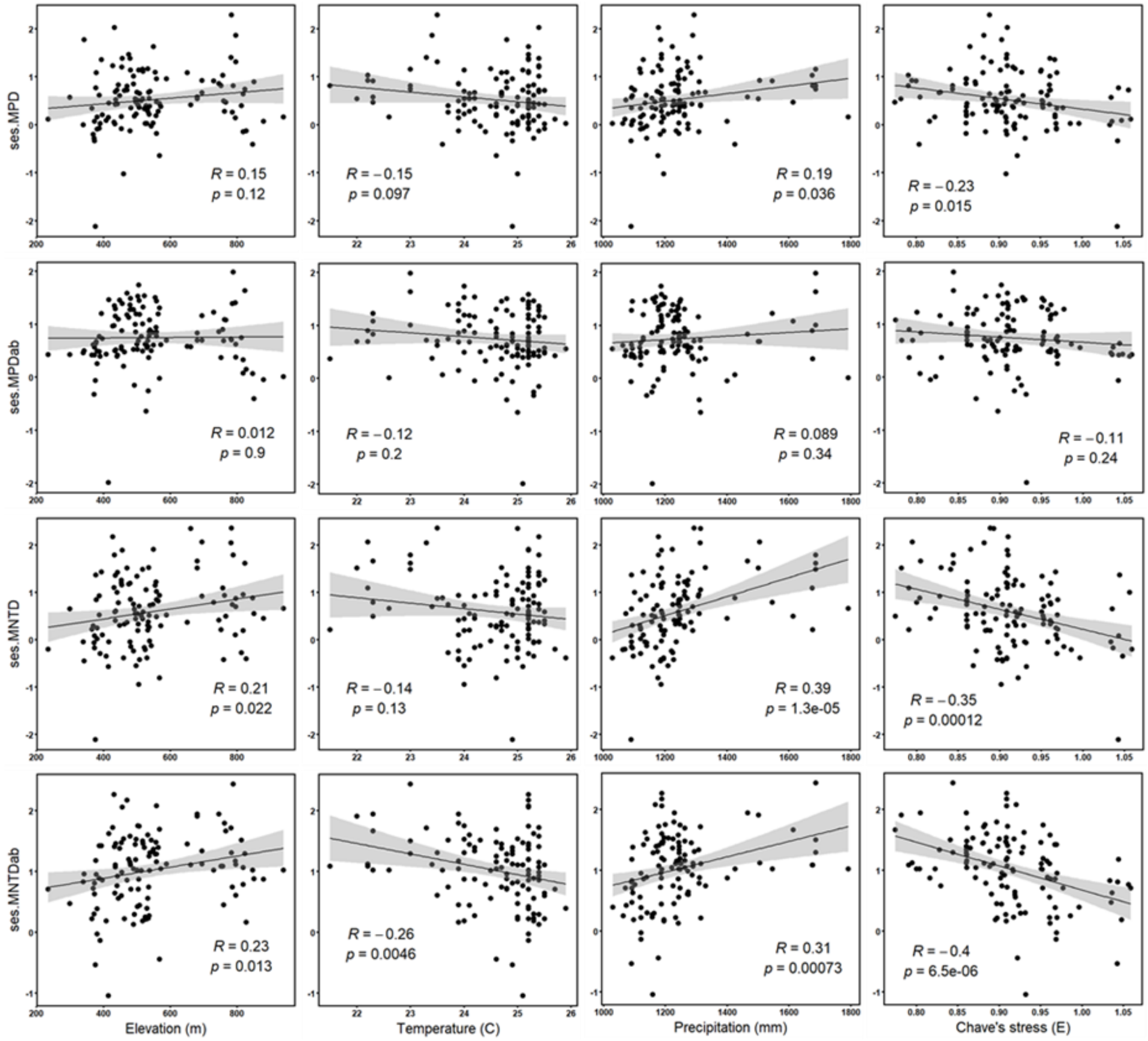

Figure 5A. Relationship between phylogenetic beta-diversity (weighted UniFrac) and taxonomic beta-diversity (Bray-Curtis). The level of overlap in similarity reduces as values approach 1.