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Phylogenetic diversity in the Western Ghats biodiversity hotspot reflects environmental filtering and past niche diversification of trees

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Abstract

Aim: We examined how contrasted climatic conditions influenced the ecological and phylogenetic diversity of tropical trees at the regional scale. Beyond the basic expectation of greater environmental filtering in currently stressful contexts, we addressed how biogeographic history and past climates contributed to shaping the distribution and diversity of extant taxa.

Location: Evergreen forests of Western Ghats, India.

Methods: We evaluated the relative importance of niche-based, historical, and spatial processes on community phylogenetic structure and turnover in 297 plots including 459 species. If niche conservatism prevails, we expected greater phylogenetic clustering under harsher or historically less stable climates, and overdispersion in opposite conditions. To test the role of environmental filtering in shaping local communities, we assessed species' climatic niches and congruence between niche and phylogenetic diversity. To assess the imprint of ancient versus recent evolutionary constraints, we calculated mean pair-wise (MPD) and nearest-taxon (MNTD) phylogenetic distances, respectively.

Results: We found non-random phylogenetic structure depending on both current and past climatic variation. Basal community phylogenetic structure (MPD) was related to niche diversity and varied according to hydric stress: (a) northern environments filtered more closely related species, while (b) phylogenetic overdispersion suggested greater niche differentiation in stable, least-seasonal southern habitats and at high elevations. Terminal phylogenetic structure (MNTD) did not show overdispersion. Phylogenetic turnover was driven by current abiotic factors, not space.

Main conclusions: The patterns of ecological and phylogenetic diversity likely reflect the Miocene climate shift to increasing seasonality northwards. Phylogenetic clustering under hydric stress or historical instability suggests the influence of functional conservatism, whereas overdispersion in southern forests supports the persistence of old lineages in an ancient rain forest refugium as an evolutionary museum. Overdispersion in fragmented montane forests reflects a mixture of biogeographically distinct species pools, both tropical and temperate, that characterise environmentally contrasted cores and fringes. Low phylogenetic turnover along the

seasonality gradient suggests recent ecological diversification across forests with contrasted rainfall seasonality.

KEYWORDS

biogeography, community phylogenetics, ecological niche, evolutionary time-scale, India, rain forest refugia

1 | INTRODUCTION

To understand the origins of high diversity and endemism in biodiversity hotspots, we need to address the combined influence of evolutionary and ecological dynamics (Myers, Mittermeier, Mittermeier, da Fonseca, & Kent, 2000). Environmental filtering is expected to drive species turnover and the variation of ecological strategies along environmental gradients (Ackerly & Cornwell, 2007). In addition, past diversification and adaptations determine the pattern of ecological strategies in the phylogeny of extant taxa. The phylogenetic diversity of coexisting organisms then reflects the influence of both adaptations inherited over time and present environmental constraints (Fine, 2015; Gerhold, Cahill, Winter, Bartish, & Prinzing, 2015).

Under an assumption of phylogenetic niche conservatism (Wiens & Graham, 2005), closely related species are likely to be ecologically similar, so that shared ancestry in assemblages can provide a surrogate for ecological similarity among co-occurring species (Webb, Ackerly, McPeck, & Donoghue, 2002). The phylogenetic structure of extant assemblages is thus expected to reflect present niche-based species dynamics: biotic interactions can entail niche differentiation and phylogenetic overdispersion, while competitive hierarchy (Kunstler et al., 2012; Mayfield & Levine, 2010) or facilitation among close relatives (Sargent & Ackerly, 2008) can yield functional and phylogenetic clustering. At larger habitat scales, environmental filtering can also lead to such clustering (e.g., Carboni et al., 2016).

However, niche conservatism is not the rule (Pavoine & Bonsall, 2011), and phylogenetic diversity cannot be reduced to a proxy of present niche diversity. Similar traits among co-occurring distantly related species can arise from adaptation to similar climatic conditions (convergence, Freckleton & Jetz, 2009). Phylogenetic patterns can then convey signatures of past evolutionary dynamics that conferred extant adaptations, as well as the historical biogeography of lineages (Bartish et al., 2016; Hardy & Senterre, 2007). Past events of allopatric speciation and colonisation dynamics can imply less co-occurrence of close relatives, even in the absence of competition and niche evolution (Warren, Cardillo, Rosauer, & Bolnick, 2014). Phylogenetic patterns thus also reflect the diversification and migration events that defined regional biota (Fine & Kembel, 2011). In this regard, more than simply being static proxies of community assembly mechanisms, phylogenetic patterns can be used to infer evolutionary and biogeographic processes (Gerhold et al., 2015). We addressed here the relative contributions of current niche-based dynamics and

past biogeography on the phylogenetic structure of highly diverse rain forests in India.

Sharp environmental gradients and a long and complex evolutionary, geomorphologic and biogeographic history in the Western Ghats (WG) of India provide an ideal context for such a study. Marked variations in rainfall, seasonality, and temperature are major drivers of species turnover (e.g., Pascal, 1988). The monsoon regime was established after the Himalayan uplift at mid-Miocene (Guo et al., 2008), and generated a south to north gradient of seasonality (Gunnell, 1997; Patnaik et al., 2012) within the WG. A south-north decrease in species diversity and endemism (Barboni, Bonnefille, Prasad, & Ramesh, 2003; Ramesh & Pascal, 1997) may reflect a historical gradient of climate stability, such that southernmost forests with least seasonality and more stable climatic conditions could have served as recurrent refugia over millennia (Prasad, Farooqui, Tripathi, Garg, & Thakur, 2009). However, the influence of the past and present environmental variations on the phylogenetic structure of tree species across the WG has been little studied (but see Hardy, Coutheron, Munoz, Ramesh, & Pélissier, 2012).

We addressed two basic hypotheses on the biogeography of climatic niches and the influence of current environmental filters on the phylogenetic diversity of trees in WG forests: (a) a stress-gradient hypothesis (Weiher & Keddy, 1995) and (b) a historical stability hypothesis (Jablonski, Roy, & Valentine, 2006; Kissling et al., 2012). According to the first hypothesis, environmental conditions constrain the range of ecological adaptations of trees in more stressful sites (environmental filtering, Kraft et al., 2015). In WG forests, high seasonality and low rainfall conditions may represent ecophysiological limits. Tree growth and respiration can also be constrained by lower temperature at higher elevations. Assemblages of closely related taxa have recently been reported in environmentally constraining contexts such as in high elevation (Qian, Hao, & Zhang, 2014) and seasonally dry (Moro et al., 2015) areas. Our study comprises an extensive breath of both environmental gradients.

If niches are conserved in the phylogeny, constraints on tree adaptations translate into phylogenetic clustering, i.e., only specific lineages with inherited adaptations can occur locally (Kraft, Cornwell, Webb, & Ackerly, 2007; Webb et al., 2002). Conversely, conditions of lower seasonality and a diversity of resources should entail greater niche differentiation and limiting similarity due to competition in southern WG (Abrams, 1983). A greater diversity of lineages with a broader range of adaptations should then be found and lead to phylogenetic overdispersion.



The assumption of niche conservatism can still be challenged, which can reverse the above predictions (Cavender-Bares, Ackerly, Baum, & Bazzaz, 2004). To decipher the joint contributions of niche structuring in phylogeny and current environmental constraints, we compared the ecological diversity of climatic niches and the phylogenetic patterns in tree communities. We expected congruence between the two, i.e., a high (low) diversity of niches in assemblages displaying phylogenetic overdispersion (clustering) when niches are conserved, and incongruence if they are not (see Table 1).

According to the stability hypothesis, species are differentially excluded from areas experiencing greater historical climate fluctuation, while stability enhances persistence and diversification over geological time-scales (Jablonski et al., 2006; Svenning, Eiserhardt, Normand, Ordonez, & Sandel, 2015). Palaeoclimatic instability can also decrease diversity depending on species dispersal from refugia (Ordonez & Svenning, 2015). Thus less stable northern areas of the WG should harbour assemblages of survivors or species able to re-colonise these areas after local extinction (Kissling et al., 2012), resulting in phylogenetic clustering when niches are conserved. Conversely, older, more stable rain forest regions as in southern WG should comprise a mixture of distantly related lineages, which could both persist better through evolutionary time ("museum") and diversify over a broad ecological spectrum ("cradle"). The hierarchy of evolutionary and biogeographic influences over time is expected to affect the phylogenetic structure differently depending on clade age: Koenen, Clarkson, Pennington, and Chatrou (2015) suggest that rain

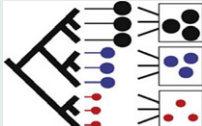
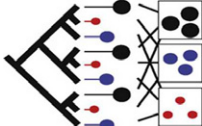
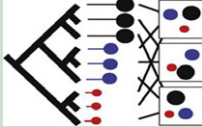
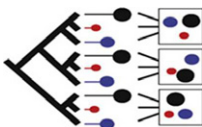
forests are museums for higher level taxa with diverse traits, which provide a stock for ecological diversification over more recent clades.

To address the temporal hierarchy of biogeographic processes, we considered alternative metrics of phylogenetic diversity either sensitive to basal (ancient evolutionary dynamics) or terminal (recent dynamics) branching in the phylogeny (Mazel et al., 2015). For instance, environmental filtering and niche conservatism consistently operating at large and fine evolutionary time-scales would lead to both basal and terminal phylogenetic clustering in communities. Conversely, environmental filtering can concern niches conserved over the long term, while niche differentiation can occur between relatives at finer time-scale (and/or colonisation of distantly related lineages from adjacent regions), resulting in basal clustering and terminal overdispersion (Hardy & Senterre, 2007); alternatively, phylogenetic overdispersion in deep nodes can reflect the legacy of ancient evolutionary differences (older lineage splits), followed by phylogenetic clustering in terminal nodes reflecting environmental filtering of clade-specific habitat preferences acquired over time (Kooyman, Rossetto, Cornwell, & Westoby, 2011).

The hypotheses on ecological and evolutionary dynamics yielded eight scenarios presented in Table 1, which combined (a) assembly rules, (b) niche conservatism versus niche convergence, and (c) phylogenetic depth, i.e., ancient versus recent evolutionary dynamics.

To complement the analysis of phylogenetic and niche composition within communities, we assessed their turnover across

TABLE 1 Hypotheses and scenarios of phylogenetic and niche diversity within communities The inset figures (adapted from Emerson & Gillespie, 2008) exemplify different cases of deep phylogenetic structure in communities. [Colour table can be viewed at wileyonlinelibrary.com]

| Hypothesis on community assembly | Ancient evolutionary dynamics and phylogenetic pattern in deep nodes | Congruence between species niches and phylogenetic relatedness | Recent evolutionary dynamics and phylogenetic pattern in terminal nodes |
|--|--|--|---|
| Harsher abiotic environment filters species with similar niches (EF) | Phylogenetic Clustering  | Niches conserved Ecological niches of co-occurring closely related species are similar | Clustering |
| | | | Overdispersion |
| | Phylogenetic Overdispersion  | Niches convergent Niches of co-occurring distantly related species are similar | Clustering |
| | | | Overdispersion |
| Biotic interactions filter species with dissimilar niches (BF) | Phylogenetic Overdispersion  | Niches conserved Niches of co-occurring distantly related species are dissimilar | Clustering |
| | | | Overdispersion |
| | Phylogenetic Clustering  | Niches divergent Niches of closely related species are dissimilar | Clustering |
| | | | Overdispersion |

communities along environmental gradients. When environmental filtering operated along gradients and concerned phylogenetically conserved niche properties, we expected higher turnover in phylogenetic composition, reflecting a change of lineages adapted to the different environmental conditions. Alternatively, when closely related species diverged in habitat preferences and occupied dissimilar environments, we expected lower phylogenetic turnover along gradients. We thus (a) quantified the phylogenetic structure and climatic niche diversity within and between 297 forest plots arrayed across the entire WG region and (b) examined how this structure varied along broad-scale environmental and historical habitat stability gradients after accounting for spatial effects.

2 | MATERIALS AND METHODS

2.1 | Assemblage composition and phylogeny

We used a dataset of 297 forest plots including 459 tree species, comprising (a) 189 plots between 8°5' and 11°5'N (Gimaret-Carpentier, 1999), (b) 12 plots between 10 and 12°5'N from Chandrashekar (2004), and (c) 96 plots between 13°3' and 15°2'N in north-central WG (Ramesh et al., 2010). For (a) and (b), species accumulation sampling methods, i.e., noting new species starting from a fixed point until no new species were encountered within a particular habitat, were used to characterise tree composition, resulting in presence/absence data covering c. 1 ha. Plots in (c) comprised complete inventories of all trees with stem diameter >10 cm within a fixed area of 1 ha, which we converted to presence/absence. We verified that species richness estimated by both sampling methods was comparable (see Supporting Information Appendix S1: Figure S1.1).

To ease interpretation, each plot was assigned to one of 16 discrete forest types (Supporting Information Appendix S1: Table S1.1) defined by Pascal (1988) based on its location, classified as southern versus northern plots to acknowledge the major ecological differentiation related to rainfall amount and seasonality above and below 13°N (Barboni et al., 2003; Pascal, 1986).

Using *PHYLOMATIC* v.3 (<http://phylodiversity.net/phyloomatic>) we matched the family and genus names of WG species to those of the time-calibrated megaphylogeny of Zanne et al. (2014) updated by Qian and Jin (2016), built from gene sequences of land plants available in GenBank, to extract a tree in which relationships followed the megaphylogeny. We then used *PHYLOMATIC* to attach 26 (out of a total of 226) additional genera randomly as polytomies within families and missing species within genus nodes, following many previous studies (e.g., Giehl & Jarenkow, 2012; Hardy et al., 2012).

2.2 | Environmental, historical, and spatial predictors

We considered variables reflecting (a) basic abiotic drivers of vegetation composition and (b) historical habitat stability in the WG, to

convey the effect of ecological filters of current climate and of its dynamics over the Quaternary. We also included (c) predictors to account for spatial variation.

For current environment, we performed a Principal Component Analysis (PCA) of 19 bioclimatic variables and altitude obtained at 30-s resolution (c. 1 km) from WorldClim (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005) including all the pixels of each raster covering the WG area. The first three PCA axes explained 90.4% of the overall variation and represented the major environmental gradients devoid of co-linearity, namely, (a) decreasing temperature with elevation gradient, (b) south to north increase in seasonal hydric stress (3–8 dry months, with rainfall <100 mm) and (c) west-east decreasing rainfall gradient (annual precipitation from 484 to 6,032 mm) (see Supporting Information Appendix S1: Figure S1.2a–c).

Historical habitat stability (Supporting Information Appendix S1: Figure S1.2d) was assessed from Last Interglacial (LIG, c. 120–140 kyr BP), following Bose, Munoz, Ramesh, and Pélissier (2016). Binary maps of potential habitat models were generated for each species under present, Last Glacial Maximum (LGM; c. 21 kyr BP) and LIG climatic conditions, and the number of species potentially occurring at all the three epochs calculated for each grid-cell. The higher this number, the greater the number of species that could persist locally over time, thus providing an index of habitat stability (see Bose et al., 2016 for details). We note that climate stability over the Quaternary also reflects the presence of longer term refugia in the more aseasonal forests of the south (Prasad et al., 2009).

Eigenvectors derived from distance-based Moran's Eigenvector Maps (dbMEM, Borcard & Legendre, 2002; Dray, Legendre, & Peres-Neto, 2006) allow assessing spatial effects on phylogenetic structure at multiple scales. Seventeen orthogonal dbMEMs were selected for the analyses (see Supporting Information Appendix S2).

2.3 | Statistical analyses

2.3.1 | Diversity and phylogenetic signal of climatic niches

We performed a canonical correspondence analysis (CCA) to study the changes in community composition depending on the abiotic and historical stability gradients (Ter Braak, 1986). The species' scores on the CCA axes represent their niche position along the basic gradients and were subsequently used as surrogates for species' climatic niches. To assess niche conservatism, we measured the phylogenetic signal of the species scores in CCA using λ (Pagel, 1999), and compared the observed value to a reference Brownian evolution model across the phylogeny (Cooper, Jetz, & Freckleton, 2010). In addition, following Soininen, Heino, Lappalainen, and Virtanen (2011), we measured the variability in species niche positions in each plot as the SD of species positions along each CCA axis. This provides an estimate of the diversity of climate niches. We then evaluated the congruence between this diversity and the phylogenetic dispersion in each plot using linear regression.



2.3.2 | Alpha phylogenetic dispersion

We used complementary metrics to represent the phylogenetic structure of tree communities at different evolutionary depths (Mazel et al., 2015), viz., mean pair-wise phylogenetic distance (MPD), sensitive to deep branching structure, and mean nearest-taxon phylogenetic distance (MNTD), reflecting the influence of more recent evolutionary events (Hardy & Senterre, 2007). To avoid inflated phylogenetic dispersion due to a few taxa connected to deep phylogenetic nodes, we excluded the single gymnosperm and the five monocot species in subsequent analyses.

We built the null distribution of each metric by randomly reshuffling the tips of the phylogeny 999 times. We then calculated the standardised effect size (SES) of MPD (denoted MPD_{SES}) and MNTD (denoted $MNTD_{SES}$) in a community to represent the deviation of the observations from the null expectation. The variation of species richness is conserved in the null model, so as not to affect the analyses (Swenson, 2014). Negative values of MPD_{SES} and $MNTD_{SES}$ indicated phylogenetic clustering, while positive values indicated overdispersion, i.e., species found in a plot were on average more (resp. less) closely related than expected by chance. The deviation from the null hypothesis was considered significant at 5%. MNTD assesses terminal relatedness among co-occurring taxa and could be affected by phylogenetic uncertainty due to unresolved terminal nodes. To assess the influence of this uncertainty, we randomly generated 100 fully resolved phylogenies based on the same communities using SUNPLIN (Martins, Carmo, Longo, Rosa, & Rangel, 2013). Unresolved and randomly resolved phylogenies provided highly correlated MNTD and $MNTD_{SES}$ values ($R^2 > 0.92$ and $R^2 > 0.8$; see Supporting Information Appendix S2), indicating that our results were robust to terminal uncertainty.

We performed a multiple regression analysis of the variation of local phylogenetic structure (MPD_{SES} and $MNTD_{SES}$) on environmental variables to assess the direction of variation along gradients. The relative contribution of current and past environmental variation and spatial process was then assessed by variation partitioning (Borcard, Legendre, & Drapeau, 1992) using dbMEMs as spatial predictors. The total percentage of variance explained was partitioned into unique and common contributions of environmental, historical, and spatial predictors and the significance of independent fractions evaluated through permutation tests.

The inference of macroevolutionary influences could be greatly improved by examining how lineage composition in communities influences community phylogenetic structure (Gerhold et al., 2015). For this, we identified clades that contributed significantly to the phylogenetic structure of local communities. The *nodesig* algorithm evaluates, for each node in the phylogeny, whether a particular clade has significantly more/less descendant taxa in a sample than predicted by a null model. The null model is a random draw of n taxa from the phylogeny, where n is the number of species in the sample (Webb, Ackerly, & Kembel, 2008).

2.3.3 | Phylogenetic turnover

We assessed the variation of phylogenetic structure among communities following Hardy et al. (2012), who analysed a part of the same community dataset. The π st metric measures the relative increase of mean phylogenetic distance between species sampled among sites versus within sites (defined as $1 - MPD_{within}/MPD_{between}$ plots, Hardy & Senterre, 2007). We estimated π st for each pair of sites ($PW\pi$ st) and tested it against the same null model as for alpha phylogenetic dispersion metrics. Values departing positively from the null hypothesis represented phylogenetic turnover between communities.

We performed variation partitioning based on a distance-based redundancy analysis (db-RDA, Legendre & Anderson, 1999) using dbMEMs to assess the relative importance of environmental and spatial components to phylogenetic turnover expressed through the adjusted R^2 statistic. The significance of independent fractions was evaluated through permutation tests for db-RDA.

All statistical analyses were performed in R; phylogenetic dispersion analyses were implemented using the 'picante' package (Kembel et al., 2010), variation partitioning and distance-based redundancy analysis using 'vegan' and phylogenetic turnover using 'spacodiR' (Eastman, Paine, & Hardy, 2011).

3 | RESULTS

Seasonality, elevation, and stability all contributed to CCA Axis 1 (50% of variance explained), and rainfall to CCA Axis 2 (30%), and thus constituted major environmental gradients driving the changes in community composition. **The phylogenetic signal of these scores was strong along the annual rainfall gradient ($\lambda = 0.46$, $p \ll 0.001$ for CCA Axis 2), indicating niche conservatism, and less marked along the seasonality gradient ($\lambda = 0.35$, $p < 0.001$ for CCA Axis 1).**

3.1 | Variations in local phylogenetic structure

We found mostly non-random phylogenetic structure in communities across the WG. Our results indicated phylogenetic clustering in drier, more seasonal, less stable northern forests (above c. 13°N) for both MPD_{SES} and $MNTD_{SES}$, in contrast to basal overdispersion in wet, less seasonal, more stable southern forest types (MPD_{SES}) (Figures 1 and 2). Both MPD_{SES} and $MNTD_{SES}$ increased from phylogenetic clustering at lower rainfall levels to overdispersion at higher rainfall (LM, $p < 0.001$). MPD_{SES} decreased with seasonality and increased with elevation ($p < 0.001$), while the variation of $MNTD_{SES}$ was less influenced by seasonality ($p < 0.05$, see Supporting Information Appendix S3: Table S3.1a). Departing from the basic north-south gradient, phylogenetic clustering was also found for MPD_{SES} in dry evergreen forests in the south-east (in orange DMM, DMMK, DMO types, in Figure 2a, see the codes in Supporting Information Appendix S1: Table S1.1), and in the southernmost low elevation evergreen forest (DKS).

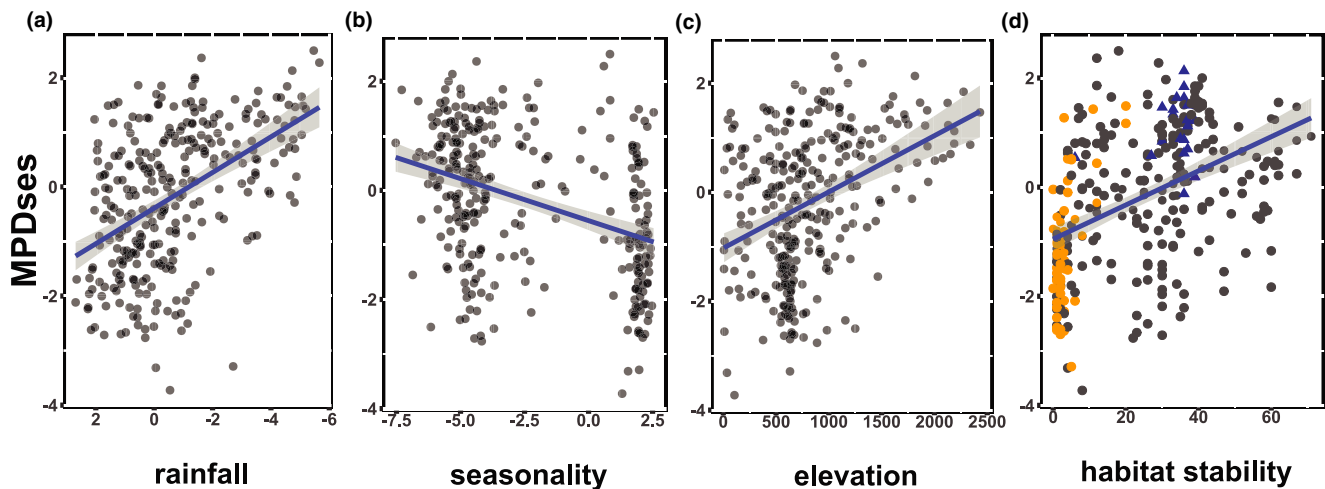


FIGURE 1 Variation of MPD_{SES} (overdispersed + MPD_{SES} , vs. clustered - MPD_{SES}) according to (a) rainfall, (b) seasonality (PCA scores on the abscissas), (c) elevation (m) and (d) historical habitat stability in the Western Ghats of India. More overdispersed and clustered plots tended to occupy extremes of the abiotic gradients. In (d) the most seasonal plots are found in areas of low stability (orange points), and high elevation plots in areas of intermediate stability (blue). Regression lines and 95% confidence intervals are shown [Colour figure can be viewed at wileyonlinelibrary.com]

Figures 3a and 4a show phylogenetic clustering (blue) and overdispersion (red) of plots along the CCA axes for MPD_{SES} and $MNTD_{SES}$, respectively. MPD_{SES} follows the north to south pattern of increasing phylogenetic dispersion, except for southern dry evergreen plots on southern leeward slopes (Figure 3b). We observed increased terminal clustering in plots that were basally overdispersed at both high elevations and in less seasonal sites ($MNTD_{SES}$, Figure 4a,b), especially in southern WG (see Supporting Information Appendix S3: Figure S3.3 for plot-wise results). We found congruence between phylogenetic dispersion (MPD_{SES}) and the diversity of climate niches for both seasonality and rainfall niches (Figure 3c,d). Conversely, there was no congruence between $MNTD_{SES}$ and climate niches related to seasonality (Figure 4c), and a weak relationship with species rainfall preferences (Figure 4d).

Variation partitioning showed that the fraction of the total variation in MPD_{SES} explained uniquely by environmental variation (18%) was larger than the spatial component (5%). The unique contribution of historical habitat stability was low (0.7%), however, a fair portion was attributed to the joint effect of current and historical predictors (12.6%, see Supporting Information Appendix S3: Figure S3.1a for details). In fact, least stable plots were also currently most seasonal, and plots of intermediate stability were located at higher elevations (Figure 1d). The total variation in $MNTD_{SES}$ was partially explained by environmental, (6%) spatial (4.6%), and the joint effect of current and historical climate variation (3.7%, see Supporting Information Appendix S3: Figure S3.1b). The variation explained by all predictors was statistically significant.

According to our evaluation of clades contributing significantly to particular plots (i.e., had significantly more/less descendant taxa in a plot) using 'nodesig', Magnoliids were more frequent in the forests of the south and at higher elevations compared to the null model, while they were significantly underrepresented at low elevations further north and in plots in the southern dry evergreen

leeward-slope forests (Supporting Information Appendix S1: Figure S1.4).

3.2 | Phylogenetic turnover according to environmental and spatial distances

Distinct species were phylogenetically closer within communities than between communities (global $\pi_{st} = 0.01$, $p < 0.001$). The proportion of variation explained by environmental variables was much larger than space (48.5% vs. 5%) in the variation partitioning based on db-RDA. Rainfall, seasonality, and temperature/elevation were significantly related to phylogenetic turnover (Figure 5), with annual rainfall having the strongest influence compared to other factors (Supporting Information Appendix S3: Figure S3.2).

Phylogenetic turnover increased monotonically with annual rainfall difference among plots, to a maximum $PW_{\pi_{st}}$ c. 0.07 (Figure 5a). However, along the seasonality gradient, phylogenetic turnover was lower (average $PW_{\pi_{st}} = 0.01$), and only increased between most contrasted plots (maximum $PW_{\pi_{st}} = 0.02$, Figure 5b). We observed low variation of $PW_{\pi_{st}}$ with increasing elevation difference for plots up to 900 m difference, while $PW_{\pi_{st}}$ abruptly increased above this difference (Figure 5c). Given the correlation between temperature and elevation in the WG, a similar trend was obtained between plots of contrasted temperature (in grey in Figure 5a).

4 | DISCUSSION

Variations in rainfall regime (annual amount and seasonality) and historical habitat instability determined the phylogenetic structure of tree communities in the WG. We found phylogenetic conservatism of species niches related to annual rainfall (species scores in CCA analysis), as noted in Hardy et al. (2012). Significant phylogenetic

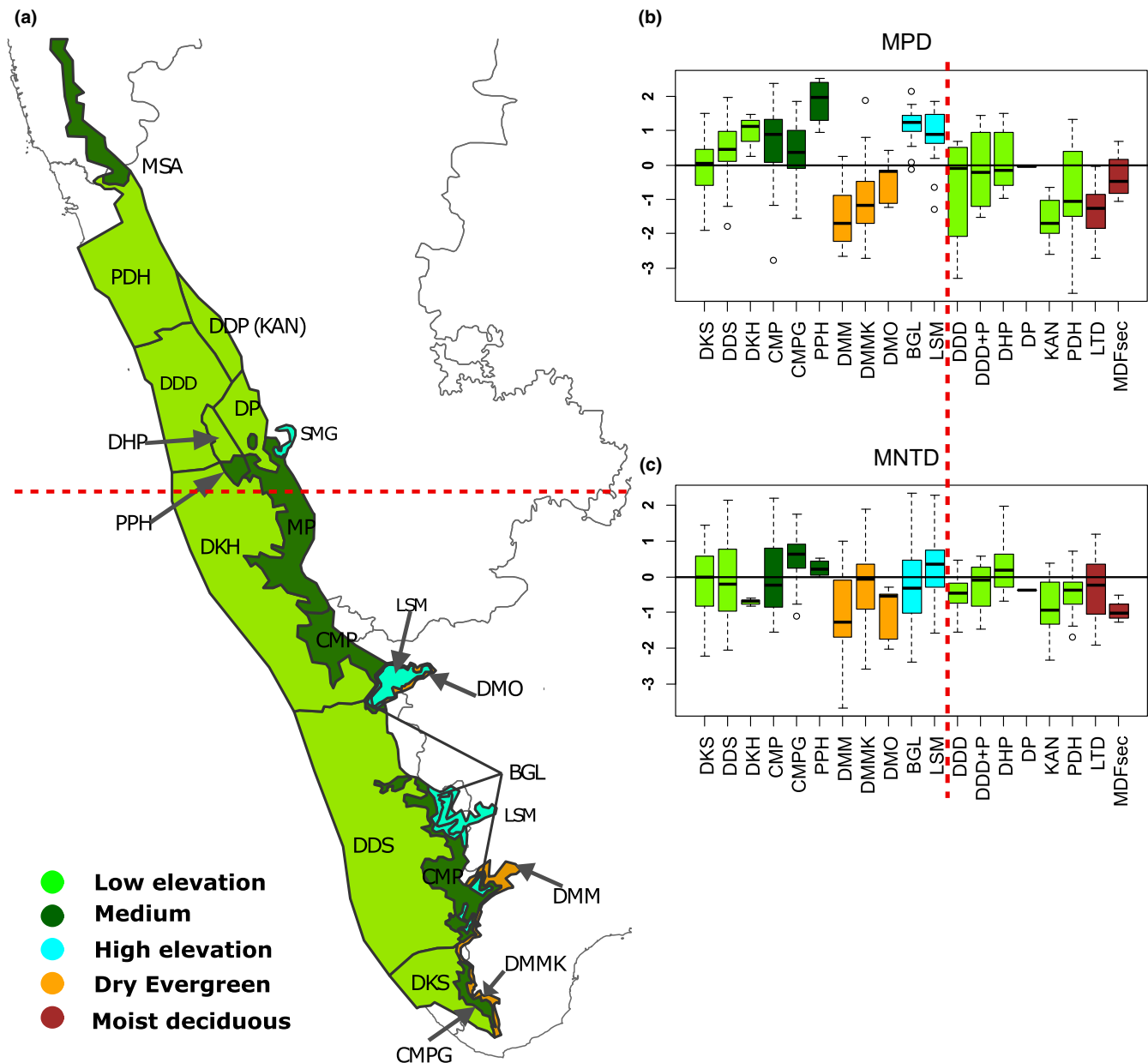


FIGURE 2 (a) Main forest types in the Western Ghats are categorised into low, medium, and high elevation wet evergreen, dry evergreen and moist or dry deciduous types (color code). The red line at 13°N separates northern and southern forest types. (b and c) Distributions of MPD_{SES} and MNTD_{SES} values in the plots per forest type. Positive and negative SES values indicate overdispersion and clustering, respectively. The red line separates southern (<13°N, left) from central (>13°N, right) types. In (b) the general trend is overdispersion in southern (+MPD_{SES}, ancient evolutionary events), and clustering (−MPD_{SES}) in north-central forests. Dry evergreen forests of the south are an exception since they are more clustered. In (c) (MNTD_{SES}, sensitive to terminal relatedness), many plots in southern forests showed less overdispersion, and more clustering [Colour figure can be viewed at wileyonlinelibrary.com]

turnover (π_{st}) supported phylogenetic sorting of species niches among communities along the rainfall gradient. Within communities, we found congruence between basal phylogenetic structure (MPD_{SES}) and climatic niche diversity (Figure 3), which indicates that the phylogenetic structure could reflect the imprint of species assembly related to climatic preferences. Conversely, terminal phylogenetic structure (MNTD_{SES}), was less sensitive to the diversity of niches related to rainfall regime (Figure 4), although it displayed some structuring within communities (Figure 2).

Local phylogenetic structure across the WG covered a broad range of MPD_{SES} and MNTD_{SES} values from clustering to overdispersion. According to our results, (a) harsher environments filter more closely related species (phylogenetic clustering) in central WG and dry evergreen formations in the south-east; (b) by contrast, in less constrained and more stable habitats of south WG, phylogenetic overdispersion (MPD) and greater climatic niche diversity suggests niche differentiation among distantly related species. Furthermore, (c) phylogenetic overdispersion at higher elevations could reflect a

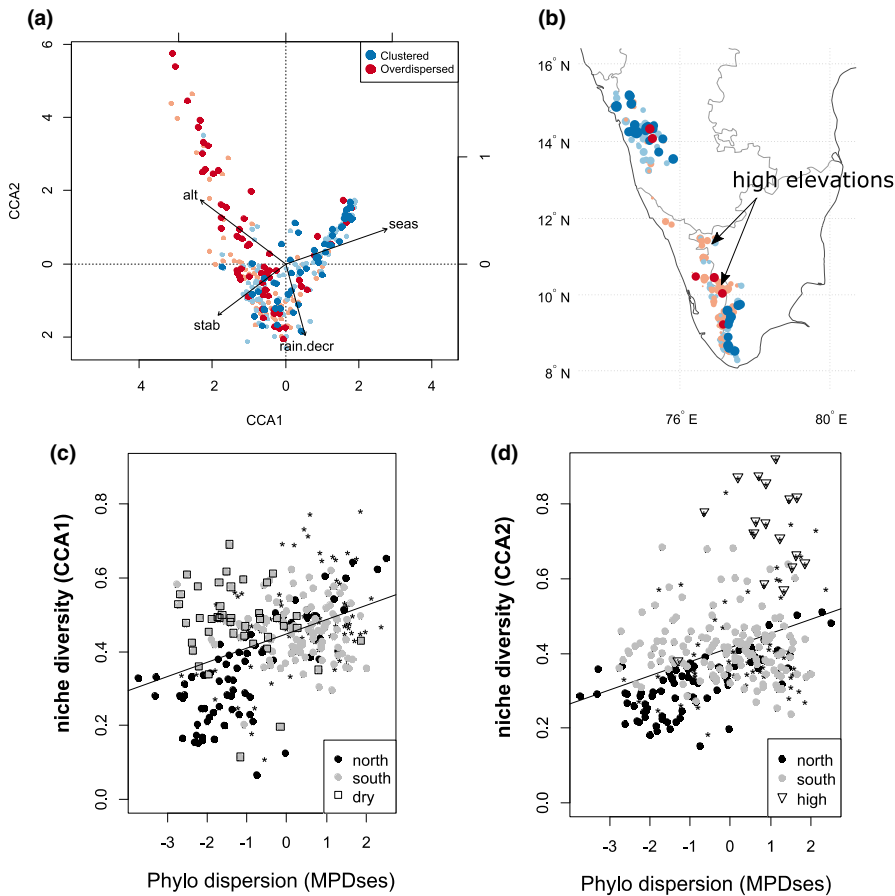


FIGURE 3 Phylogenetically clustered and overdispersed plots (MPD_{SES}) are highlighted in (a) the biplot of the CCA of floristic composition. Phylogenetic clustering (blue points) was related to higher seasonality (seas), and overdispersion (red) with lower seasonality, higher elevations (alt), and higher stability (stab). (b) Map of the plots in the Western Ghats, where blue to red color represent low to high MPD_{SES} values. Point size varies according to absolute MPD_{SES} values, and dark colors are used for significant values and light colors for non-significant. There is a positive relationship between the diversity of (c) seasonality ($p < 0.001$, $R^2 = 0.13$) and (d) rainfall niches ($p < 0.001$, $R^2 = 0.16$) niches and MPD_{SES} . Northern communities are black points, southern communities are grey points, dry evergreen southern forests are squares and high elevation communities are triangles [Colour figure can be viewed at wileyonlinelibrary.com]

mixture of low- and high-elevation species pools with distinct biogeographical and evolutionary backgrounds. Conversely, the phylogenetic structure of terminal branches (MNTD) did not show overdispersion, indicating that niche differentiation among close relatives did not contribute to their coexistence locally. These results indicate distinct evolutionary legacies and influences of environmental filtering when considering complementary metrics of phylogenetic structure sensitive to either basal or terminal branching (Mazel et al., 2015).

4.1 | Harsher and less stable environment filters more closely related species

Basal (MPD) and terminal (MNTD) phylogenetic clustering was associated with greater physiological stress and less historical stability, pointing to the fundamental influence of environmental filtering at all phylogenetic scales. In northern assemblages this is supported by the low diversity of climatic niches (functional conservatism), whereas in dry evergreen south-eastern forests the observed high diversity of climatic niches related to seasonality is consistent with recent diversifications in certain clades under novel conditions of high seasonality (Pascal, 1988).

Precipitation seasonality increases northwards and eastwards. Annual rainfall also diminishes rapidly beyond the crest of the WG, exacerbated by strong foehn effects on leeward slopes (Pascal, 1988). Limited water availability can thus explain increased

phylogenetic clustering in both central and south-eastern forest types. Specifically, central forests include an impoverished subset of southern species, and local dominance of *Poeciloneuron indicum* Bedd. (Pascal, 1988). In the south-east, populations of species having established on both sides of southern hills would have subsequently experienced contrasting conditions on the wind- and leeward slopes with the onset of the monsoon regime, potentially leading to allopatric speciation.

During the Quaternary, greater monsoon fluctuations entailed climatic instability in currently more seasonal areas ($>12^\circ\text{N}$, Bose et al., 2016), making it difficult to separate the respective roles of current and past environments. In variation partitioning, a fair amount of the variation in phylogenetic structure was attributable to their joint contribution. To test the influence of past climatic instability in terms of limited migration from refugia, additional analyses of the mismatch between potential and realised distributions would be needed (Ordóñez & Svenning, 2015).

4.2 | Distinct causes of phylogenetic overdispersion

In southern WG, where annual rainfall is high and the dry season shorter, less abiotic constraints could entail stronger influence of niche differentiation due to competitive interactions, resulting in phylogenetic overdispersion (Webb et al., 2002). This is supported by our observation of functional divergence among co-existing

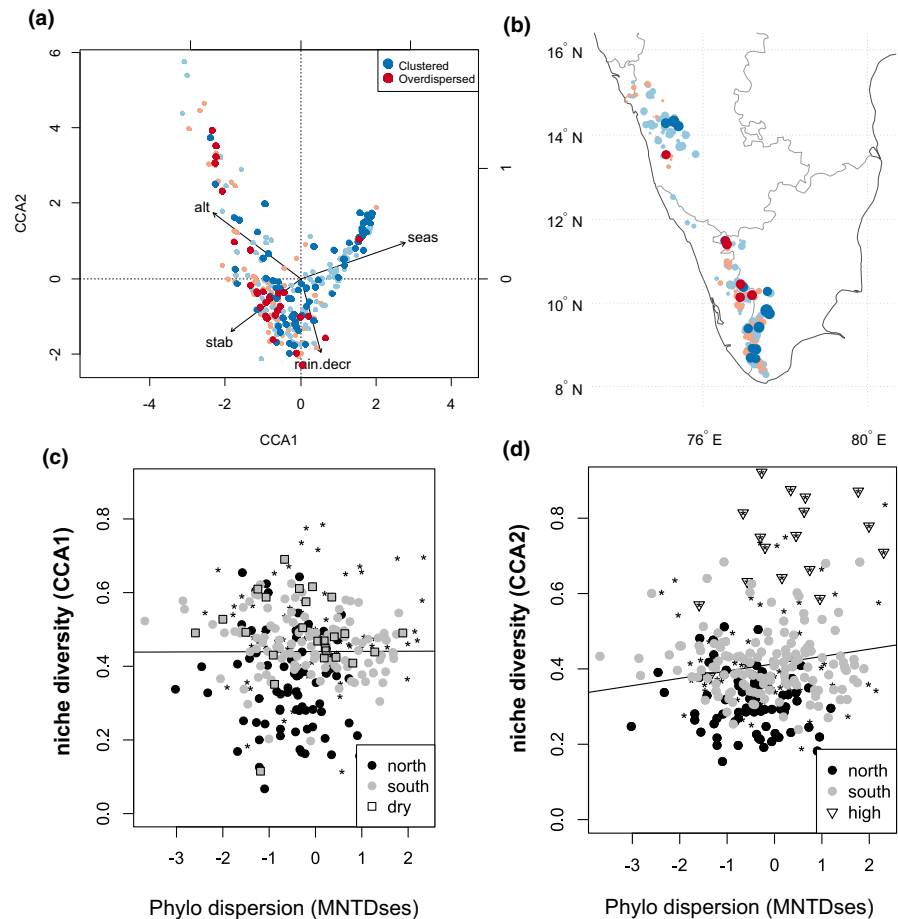


FIGURE 4 (a) Biplot of the CCA of floristic composition where the color of communities represents phylogenetic clustering (blue) and overdispersion (red) for MNTD_{SES}. (b) More southern plots are phylogenetically clustered. The north versus south pattern of low versus high niche diversity is not congruent with phylogenetic dispersion, which has no relation to (c) seasonality preferences and a weak one to (d) rainfall preferences ($p < 0.01$, CCA2, $R^2 = 0.02$) [Colour figure can be viewed at wileyonlinelibrary.com]

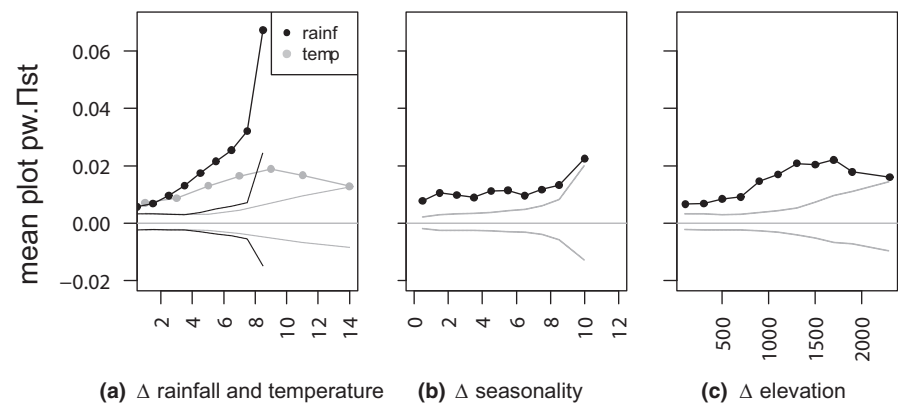


FIGURE 5 Phylogenetic turnover (mean PW_{st}) as a function of environmental distance for (a) rainfall and temperature, (b) seasonality, and (c) elevation. The dotted lines represent the 95% confidence envelopes of the null hypothesis of absence of phylogenetic constraints.

species here. Over the long term, i.e., beyond the Quaternary, the persistence of favourable conditions in this Palaeogene refuge (Prasad et al., 2009) could have maintained more diverse lineages, contributing to phylogenetic overdispersion ("museum" hypothesis, Jablonski et al., 2006; Stebbins, 1974). An exception was the southern-most evergreen forest (DKS) where communities display basal phylogenetic clustering (MPD), plausibly due to "Myristica swamps" dominated by some specific flood-tolerant trees.

At higher elevations (up to 2,700 m asl), trees endure physiological stress due to lower annual mean temperatures, for e.g., $<13.5^{\circ}\text{C}$ in upper montane LSM. Mist immersion and frost would limit the establishment and survival of many tropical species (Das, 2015).

Temperature stress at high altitudes could result in phylogenetic clustering, as reported for other taxa like birds, bees, butterflies, microbes (Qian et al., 2014 and references therein), and plants (e.g., Dossa et al., 2013). However, we found deep phylogenetic overdispersion in higher elevation forests.

We also reported greater diversity of rainfall and temperature niches in high-elevation communities (Figure 2). High-elevation forest fragments, called "shola," are embedded in a matrix of grasslands, occurring in thalwegs protected from cold winds and fire. The environmental contrast between the core and the edge of shola forests (Mohandass & Davidar, 2010) could explain the observed niche differentiation. In addition, phylogenetic turnover showed an abrupt

change among communities at 900–1,000 m difference. This trend could not reflect a gradual variation in underlying abiotic drivers, as in the case of rainfall, and points to a specific evolutionary background of higher-elevation communities.

4.3 | Mixed evolutionary background of high-elevation forests

The tree species found in WG montane forests represent a complex mixture of biogeographic origins (e.g., Das, 2015). Cold-adapted taxa at forest fringes could be immigrants of lineages adapted to distant mountains, which reached the WG by long-distance dispersal (see Mohandass & Davidar, 2010). These typically include temperate genera (*Daphniphyllum*, *Eurya*, *Viburnum*), distinct Himalayan elements (*Mahonia*, *Rhododendron*), or species of subtropical genera also occurring in eastern Himalaya or beyond. Conversely, trees of tropical origin are more restricted to less-exposed forest interiors (Meher-Homji, 1967). Therefore, distinct groups of species may have been filtered in contrasted environmental contexts generated by the complex topography of montane landscapes (e.g., Jiménez-Alfaro, Marcenó, Bueno, Gavilán, & Obeso, 2014).

The abrupt increase in phylogenetic turnover between plots at contrasting elevations is more pronounced for endemic species (result not shown). Montane forests are practically the only habitat of most species of *Ilex*, *Schefflera*, and *Vaccinium*. A number of narrow endemics occur only above 2,000 m, e.g., in *Mahonia*, *Magnolia* and *Rhododendron*, and endemics of families not well-represented in low elevation forests abound in shola interiors.

4.4 | Distinctive basal and terminal phylogenetic structure

Complementary metrics reflect the influence of deeper (MPD) or more recent (MNTD) phylogenetic structure: phylogenetic clustering was basically consistent for MPD_{SES} and MNTD_{SES}, but overdispersion found in MPD_{SES} did not translate into overdispersion of MNTD_{SES}. We found an overall tendency towards terminal clustering, although fewer plots were significantly clustered. Compared to fully resolved phylogenies in SUNPLIN, MNTD tended to be slightly underestimated in our phylogeny, and MPD_{SES} values were closer to the null expectation. This bias has been ascribed to the lack of terminal resolution by Swenson (2009) who notes, however, that if most basal nodes are bifurcating and terminal nodes are unresolved, as in our case, the loss of power is greatly minimised.

Ancient evolutionary history underlies niche differentiation as expressed by phylogenetic overdispersion in southern WG and high elevation ecosystems. It does not mean, however, that the taxa in question differentiated a long time ago in the area, but rather that present ecosystems filter ecological strategies that diversified anciently (Bartish et al., 2016). For instance, not all lineages living in wetter forests can survive in drier areas. According to our results, phylogenetically clustered forests in harsher central and southeast environments are basically devoid of Magnoliids. These taxa retained

ancestral adaptations to warm and humid periods when they diversified in a rain forest context (Carlucci et al., 2016) (see Supporting Information Appendix S1: Figure S1.2). They could also evolve over the long term and occupy higher elevation ecosystems, leading to high diversity of Lauraceae for instance, albeit with limited stress-tolerance.

A tendency towards phylogenetic clustering in terminal nodes for most plots conversely suggests that more recent diversification did not entail large niche shifts among species coexisting in local communities. In southern WG forests, while the benign environment may have favoured niche differentiation over the long term, climate stability would have limited extinction and favoured diversification more recently. These forests could thus represent both a former refuge for wet evergreen forest species (museum, basal overdispersion) and a centre of speciation (cradle, terminal clustering) at finer evolutionary time-scales (Koenen et al., 2015). Terminal clustering was also observed in montane forests, especially in BGL. Relatively recent diversification suggested by high levels of endemism (e.g., in *Cinnamomum*, *Actinodaphne*, and *Litsea*) would contribute to terminal clustering in this context. *In situ* adaptive divergence, speciation following immigration, or even allopatric diversification due to expansion and contraction over periods of climate change, can account for the diversity of particular clades in this complex mountain landscape.

Phylogenetic turnover between communities also reflect evolutionary dynamics at multiple temporal scales. Apart from the turnover of deep-branching groups such as Magnoliids along the rainfall gradient, species from the same genus can be found in wet, southern dry and more seasonal central evergreen forests, suggesting recent speciation events across habitats. α ST reached a maximum of 0.07 for annual rainfall compared to 0.02 for seasonality, and the phylogenetic signal of seasonality niches was far weaker. Our results support the hypothesis that closely related species diverged in preferences for seasonality and tend to occupy dissimilar environments along the gradient, previously coined “ecological vicariance” (De Franceschi, 1993; Pascal, 1988). A number of habitat-specific species are endemics, suggesting that ecological speciation along the seasonality gradient could be a driver of diversification in the WG. Therefore, while terminal clustering indicates little niche differentiation across close relatives in local communities, close relatives now occupying different habitats along the major environmental gradients could show niche differentiation.

5 | CONCLUSION

Southern WG represents both an evolutionary museum and a cradle of WG biodiversity. Overdispersion in these least-seasonal stable forests can be ascribed to conservation of old lineages and opportunities for their diversification by parapatric or sympatric speciation provided by high topographic and habitat heterogeneity. By contrast, greater past climatic instability and current hydric stress can jointly explain lower phylogenetic and niche diversity northward.

Overdispersion at high elevations is due to the assemblage of species pools of distinct biogeographic and evolutionary backgrounds occupying locally heterogeneous environmental contexts. Strong conservation of rainfall niches and turnover of deep-branching clades, such as Magnoliids entail phylogenetic turnover along the rainfall gradient. Conversely, seasonality niches are more labile among close relatives, especially endemics, which entails lower phylogenetic turnover along the seasonality gradient. Hydric stress due to rainfall seasonality could have become an important driver of diversification more recently, with the establishment and reinforcement of the monsoon regime.

The importance of including evolutionary processes that maintain and generate biodiversity rather than focusing solely on patterns (e.g. species rarity and richness) in conservation planning is increasingly being recognised. Our results could inform conservation strategies as we highlight and contribute to understanding the evolutionary potential of different areas of this biodiversity hotspot.

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BIOSKETCH

The authors are interested in the ecological, biogeographic and evolutionary processes involved in the dynamics of biodiversity in tropical forest tree communities. They investigate the signature of these processes on biodiversity patterns from local to regional scales, using modelling approaches.

Author contributions: R.B., F.M. and R.P. conceived the project; B.R.R. coordinated data collection; R.B. conducted the statistical analyses and wrote the paper; R.B., F.M., and R.P. revised the text.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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