



# Environmental gradients structure tropical tree assemblages at the regional scale

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## Keywords

Community assembly; Environmental filtering; Habitat classification; Indicator species; Multivariate regression trees; Niche breadth; Tropical forest; Western Ghats

## Nomenclature

Pascal and Ramesh 1987; Ramesh et al. 2010a.

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## Introduction

Environmental filtering, or the differential survival of species in response to abiotic factors, is a major driver of community assembly (Levine & HilleRisLambers 2009). After chance colonization events from a larger species pool, establishment and persistence of individuals

depends upon their ability to withstand biotic pressures and survive prevailing abiotic conditions (Kraft et al. 2008; HilleRisLambers et al. 2012). Non-random survival and growth responses to abiotic factors results in niche partitioning among species, which influences patterns of diversity (Valencia et al. 2004; Brown et al. 2013; Munoz et al. 2014).

## Abstract

**Questions:** Environmental filtering and niche differences influence assembly of tree communities at multiple spatial scales. At regional scales, determining the environmental variables that primarily influence compositional variation in species assemblages reveals ecologically relevant habitat types for conservation. Strength of species' association with these habitats and differences in species occurrence along environmental gradients lend credence to niche-based assembly and help estimate responses of tree communities to natural or human-mediated environmental change.

**Location:** Western Ghats, India.

**Methods:** We analysed an openly available data set of *ca.* 62 000 trees (>10 cm DBH) in 96 1-ha plots across a 22 000 km<sup>2</sup> landscape, using multivariate regression trees (MRT) to identify compositional groups related to combinations of temperature, rainfall and soil type. Next, we conducted indicator species analysis to assess species associations with habitats. We then compared species richness and diversity among habitats. Finally, to discern niche overlap we assessed pairwise differences between species in their abundance distributions along environmental gradients.

**Results:** Environmental gradients clearly influenced landscape-scale tree assemblages in this region. Nine ecological habitat types were identified: annual rainfall was the most important variable driving compositional differences, followed by temperature, seasonality and soils. Approximately 17% of 398 species tested were associated with single habitats. Number of species associations and local diversity varied significantly among habitats. Between 29 and 50% of species pairs showed significant differences in their distributions along environmental gradients considered.

**Conclusions:** Relating compositionally defined tree assemblages to combinations of abiotic variables allows ecologically robust recognition of habitat types for conservation planning. Compositional differences structured by annual rainfall and temperature suggests that climate change can impact species persistence and tree community composition in the Western Ghats. Specifically, future research should assess drought response of forests by examining recruitment and survival of species in different combinations of rainfall, temperature and human disturbances.

Species turnover in trees is known to be markedly higher in regions with greater environmental heterogeneity, e.g. climatic or topographic gradients, compared to more homogenous regions (Condit et al. 2002). With niche partitioning, species vary in their occurrence and abundances along environmental gradients (Potts et al. 2004). Species assemblages are determined by the extent of overlap among species' in their ranges across these gradients (Phillips et al. 2003; Pitman et al. 2008; Kanagaraj et al. 2011). Resulting compositional assemblages that correspond with subsets of environmental conditions across a landscape comprise ecologically relevant habitat types (De'ath 2002).

Environmental factors differ in their influence on community assembly. Hence, it is necessary to discern among a suite of potentially important variables what best explains compositional differences (Kanagaraj et al. 2011; Baldeck et al. 2013a,b). At meso- and macro-scales rainfall is an important driver of species turnover and community composition (Baltzer et al. 2007; Ramesh et al. 2010a), likely reflecting the influence of drought resistance on tree species' distributions across moisture gradients (Engelbrecht et al. 2007; Comita & Engelbrecht 2014). Similarly, edaphic and topographic variables structure plant communities at multiple spatial scales (Harms et al. 2001; Phillips et al. 2003; Baldeck et al. 2013a,b; Brown et al. 2013). Furthermore, plants exhibit functional differences in response to temperature (Moles et al. 2014), which influence their survival and growth (Stephenson 1998; Reich & Oleksyn 2004). However, the role of temperature gradients on compositional differences at landscape scales remains to be tested.

Realized niches – locations a species occupies given abiotic preferences, interspecific competition and natural enemies (Leibold 1995; Silvertown 2004) – can manifest as habitat associations of species at multiple spatial scales (Clark et al. 1999; Harms et al. 2001; Phillips et al. 2003; Aiba et al. 2004; Gunatilleke et al. 2006; Kanagaraj et al. 2011). Differences between pairs of species in their abundance distributions along abiotic gradients provides an indication of niche breadths and overlap, hitherto examined primarily at local scales of 1–50 ha (Potts et al. 2004; Baldeck et al. 2013a,b). Assessing strength of species associations and niche differences over larger spatial extents (meso-scales) can reveal species' environmental tolerances at scales relevant to habitat conservation (Phillips et al. 2003; Tuomisto et al. 2003; Réjou-Méchain et al. 2011).

Relating floristically defined communities to environmental conditions is crucial to identify vegetation communities at risk from anthropogenic land-use and climate change (Lindenmayer et al. 2008; Stork et al. 2009; Wiens et al. 2010; Iverson & McKenzie 2013). Further, species that are significantly more abundant in, or restricted to,

specific habitats can serve as indicators for associated environmental conditions (Dufrene & Legendre 1997; De Cáceres & Legendre 2009; De Cáceres et al. 2010). In this study, therefore, we sought to identify ecological habitat types in the biodiversity hotspot of Western Ghats in south India (Myers et al. 2000) by relating species assemblages to environmental conditions, and determine patterns of variation in abundance of individual species along relevant environmental gradients.

Previously, with the data set used here, floristic types in this region (evergreen, moist and dry deciduous) were found to broadly correspond to rainfall differences (Ramesh et al. 2010a). While the highest and lowest rainfall areas were found to be compositionally distinct, no differences were found among assemblages in intermediate rainfall areas. It was suggested that other factors such as temperature and soils may be driving compositional variation (Ramesh et al. 2010a). However, the influence of these variables on compositional variation has hitherto not been examined. Additionally, seasonality of rainfall drives species turnover here (Davidar et al. 2007), but whether this also discriminates species assemblages across the region is unknown.

In addition to land-use changes, climatic shifts in the Western Ghats are predicted to occur as changes in monsoon rainfall and temperature (Lal et al. 2001; Kumar et al. 2006). Therefore, across ca. 22 000 km<sup>2</sup> in the Western Ghats (2.5° latitude span) spanning wide gradients of climate, topography and soil types (Ramesh et al. 2010a), we asked: (1) which environmental variables best explain compositionally defined species assemblages, i.e. environmental domains which maximize inter-domain compositional variation; (2) do individual species show associations with habitats identified at this spatial scale, i.e. are there indicator species; (3) what is the extent of niche overlap between tree species in the Western Ghats, i.e. the magnitude of difference between pairs of species in their abundances along environmental gradients; and (4) do compositionally defined habitats differ in diversity and number of species associated with them?

## Methods

### Study area

The Western Ghats are a ~1600 km mountain chain along the west coast of peninsular India, starting from the southern tip of India (8° to 21° N) and covering about 160 000 km<sup>2</sup>. Most of the rainfall is from southwest monsoons. Commencing in the southern parts during the first week of June, monsoons last nearly 5 mo and move progressively north, withdrawing from the north to the south. As a result, the northern Western Ghats experience more dry months than the south. Local rainfall is also mediated

by orography, and therefore the annual rainfall does not form a clear south–north gradient. In fact, some localities in the north receive higher total annual rainfall (e.g. Agumbe: ~9000 mm) than the south. However, the duration of the dry period clearly shows a south–north gradient, and this has been proposed as a major determinant of plant diversity (Pascal 1988; Davidar et al. 2005). Mean annual temperature varies considerably with latitude and altitude (16–29 °C). In the higher altitudes of the southern escarpments (up to 2690 m) nighttime temperatures can go down to –5 °C.

Forests here have been broadly classified into evergreen, moist deciduous forest and dry deciduous tropical forests (Pascal 1988). With ~30% endemism in >5000 species of flowering plants, and 75% endemism in nearly 800 tree species, the Western Ghats is amongst the world's important biodiversity hotspots (Myers et al. 2000). See Ramesh et al. (2010a,b) and Pascal (1988) for a detailed description of the topography, orography, soils and vegetation of the study region.

#### Data source

We used openly available data from 96 forest plots established and censused by Ramesh et al. (2010a,b) across ~22 000 km<sup>2</sup> (13°13'–15°15' N, 74°15'–75°40' E) extending eastwards from the coastal plain of the Arabian Sea to the humid hill zone. Georeferenced 1-ha plots (100 m × 100 m) were laid randomly within evergreen, semi-evergreen, moist and dry deciduous forest types (Appendix 1, Fig. A1), encompassing ~1000 m variation in altitude (55–1060 m a.s.l.) and 7500 mm annual rainfall (776–8340 mm). Thus, they were ideally suited for analyses of large-scale habitat associations based on environmental gradients. All trees and lianas (≥10 cm DBH) were enumerated within plots – 61 965 individuals from 398 species were recorded. Plots were separated by at least 2 km. Species richness of woody plants varied from 60 to 350 ha<sup>-1</sup> (Ramesh et al. 2010b).

#### Environmental variables

From WorldClim Global Climate Database (1 km<sup>2</sup> spatial resolution, <http://www.worldclim.org>; Hijmans et al. 2005) we obtained mean annual precipitation, coefficient of variation in precipitation (indicating seasonality), mean precipitation of wettest, driest and warmest quarters, mean annual and maximum temperatures, mean temperatures of driest, warmest and coldest quarters. Precipitation was measured in mm; temperature is presented as °C × 10. We also included annual number of dry months provided by Ramesh et al. (2010a). For soil types, we used morpho-pedological types derived

from a geo-referenced digital version of the 1:1 000 000 scale soil map of Bourgeon (1989), as provided in Ramesh et al. (2010a), and detailed descriptions can be found therein.

#### Data analysis

##### *Compositionally defined habitat types*

We used multivariate regression tree analysis (MRT) to detect compositionally defined habitat types (De'ath 2002). MRT uses recursive partitioning to group plots based on abundances of each species in every plot. Splits are determined by a threshold value of explanatory environmental variables, chosen to maximize within-group homogeneity of the community data (De'ath 2002). Model fit is assessed by cross-validated relative error (CVRE); lower CVRE indicates better fit and higher reliability of variables explaining compositional differences (1 – CVRE gives model  $R^2$ ). We used criterion 'xv = min' which selects the tree with minimum CVRE. We chose the abundance-based Bray-Curtis measure of dissimilarity for compositional differences as recommended by De'ath (2002).

First, we assessed multicollinearity between pairs of variables within the two broad categories of temperature and precipitation using Pearson's correlation coefficient. Since CVRE decreases with increasing number of explanatory variables (De'ath 2002; Kanagaraj et al. 2011), to avoid overfitting models we used a clustering approach to group correlated variables (function: `hclustvar`, package: `ClustOfVar`; Chavent et al. 2012). We then selected variables with highest squared loadings in each category (Appendix 1, Fig. A2). Mean annual rainfall, precipitation in driest quarter, mean annual temperature, maximum temperature and temperature of driest quarter showed highest loadings within clusters. CV precipitation and number of dry months were included as they influence species turnover and are not correlated with annual rainfall in this region (Davidar et al. 2007). In addition, we included soil type in the model since soil information has been shown to improve compositional variation explained (John et al. 2007; Baldeck et al. 2013a,b).

We used the above selected variables in a global model and ran models removing one variable at a time. Further, to examine whether correlated abiotic variables together provided a more composite measure of environmental gradients, we conducted separate PCA for temperature and precipitation groups. Variables were standardized and checked for multivariate normality using an extension of the Shapiro-Wilk test (R package, 'mvnormtest'; R Foundation for Statistical Computing, Vienna, AT). The first two PCA axes explained 97% and 99% of the variation in precipitation and temperature, respectively (Appendix 1,

Fig. A2). The top three models for individual variables and the model using PCA axes are provided in Supplementary Material (Appendix 1, Fig. A3). We chose to use models with untransformed variables for further analyses since they provided a more intuitive picture of which environmental variables corresponded with species assemblages, and PCA axes did not significantly improve model fit.

#### *Indicator species in habitats*

To identify species with statistically significant associations with each habitat-type, we used indicator species analysis (Dufrene & Legendre 1997). For this, we used habitats identified with untransformed variables from the model with the lowest CVRE. Indicator value (IndVal) is the product of relative abundance and relative frequency of occurrence of the species within a habitat compared to all other habitats. For species  $i$  in habitat-type  $j$ , IndVal is defined as:

$$\text{IndVal}_{ij} = A_{ij} \cdot B_{ij}$$

where

$$A_{ij} = \frac{n_{ij}}{\sum_1^J n_{ij}}$$

$$B_{ij} = \frac{j_i}{J}$$

Here,  $A_{ij}$  = relative abundance of species  $i$  in habitat  $j$ ,  $n_{ij}$  = number of individuals of species  $i$  in habitat  $j$ ,  $B_{ij}$  = proportion of sites in which species  $i$  is present within habitat  $j$ ,  $j_i$  = number of sites with species  $i$ ,  $J$  = total number of sites in habitat  $j$ , and  $\text{IndVal}_{ij}$  = indicator value of species  $i$ .

IndVal is zero if the species is absent within a habitat, and attains a maximum value of 1 if the species occurs in all plots in a given habitat type, but is absent from other habitats. Statistical significance is determined by multiple randomizations of species occurrences across all plots and comparing observed  $\text{IndVal}_i$  with this null distribution (Dufrene & Legendre 1997; De Cáceres & Legendre 2009). Species with high  $\text{IndVal}_i$  for a habitat are regarded as strong indicators. To discern true habitat specificity we estimated species associations with single habitats and with combinations of habitats (De Cáceres & Legendre 2009), providing reasonable reflections of species' environmental ranges.

We used chi-square tests to examine difference between habitats in their number of indicators. After checking normality, ANOVA and *post-hoc* Tukey's HSD was used to examine whether the strength of species association (i.e.  $\text{IndVal}_i$  values) differed among habitats.

#### *Species niche overlap*

We used the Kolmogorov-Smirnov test (Potts et al. 2004) to test for extent of species niche overlap along environmental gradients. Being non-parametric, this test does not require variables to be normally distributed. Cumulative abundance distributions for each pair of species along temperature and rainfall gradients were compared to test if they were from the same distribution. Niche overlap was computed as the  $D$  statistic, a value between 0 and 1 that accounts for differences in central tendency, spread and skew. Higher  $D$  values imply lower niche overlap, i.e. greater niche difference between species (Potts et al. 2004; Baldeck et al. 2013a,b). We conducted K-S tests for species abundances along each abiotic variable individually, and for the first two PCA axes of temperature and precipitation. To avoid spurious results due to low sample sizes, niche overlap was calculated for 154 species with >50 individuals out of 398 total species in the data.

#### *Diversity within habitats*

For differences in local diversity among habitats, we calculated rarefied species richness ( $N = 100$  individuals per subsample) and exponential Shannon's diversity index for each habitat (Jost 2006). Since values conformed to normality assumptions, we used ANOVA and *post-hoc* Tukey's HSD to examine pair-wise differences between habitats for these measures.

R packages 'mvpart' and 'indic spp' (De Cáceres & Legendre 2009) were used for MRT and IndVal analysis, respectively, and diversity indices were computed using package 'vegan' in R v 3.0.1.

## Results

### Habitat identification

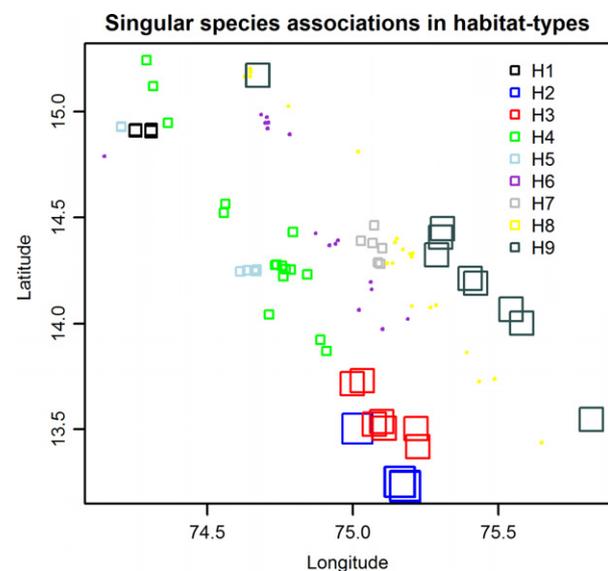
The best fit tree had a CVRE of 0.65 ( $R^2 = 0.35$ ; Appendix 1, Fig. A3) and delineated nine habitat types (Table 1). The first split based on mean annual rainfall (> or <3260 mm) explained 33% variation in community composition, followed by temperature (7%). CV precipitation differentiated intermediate rainfall plots. High rainfall plots were further segregated based on number of dry months and mean annual temperature (Table 1).

### Indicator species

Of 398 species, 194 (~49%) showed significant habitat associations. Of these, 68 species were singularly associated with their habitats, i.e. they showed affinities for one habitat only. Number of singular associations per habitat ranged from 0 (in H6, H8) to 18 species (H2; Fig. 1). Habitats

**Table 1.** Description of habitat types shown in Fig. 1 based on MRT splits of community data matrix (site  $\times$  species abundance) in relation to thresholds of abiotic factors. The environmental conditions of a habitat are the combination of abiotic variables that were most important in reducing within-group homogeneity of tree community data in relation to all other plots. Rain = mean annual rainfall, ann.tmean = mean annual temperature, DryMo = number of months with rainfall (mm)  $< 2 \times$  mean temperature ( $^{\circ}\text{C}$ ) (*sensu* Ramesh et al. 2010a), cv.prep = coefficient of variation in mean monthly precipitation.

Habitat Types	Environmental Characteristics
H1	Rain $> 3260$ mm & ann.tmean $\geq 27.2$ $^{\circ}\text{C}$
H2	Rain $> 3260$ mm & ann.tmean $< 27.2$ $^{\circ}\text{C}$ & DryMo $< 5.5$ & cv.prep $< 139.5$
H3	Rain $\geq 3260$ mm & ann.tmean $< 27.2$ $^{\circ}\text{C}$ & DryMo $< 5.5$ & cv.prep $\geq 139.5$
H4	Rain $\geq 3260$ mm & DryMo $\geq 5.5$ & ann.tmean $< 26.5$ $^{\circ}\text{C}$
H5	Rain $\geq 3260$ mm & $27.2$ $^{\circ}\text{C} < \text{ann.tmean} \geq 26.5$ $^{\circ}\text{C}$ & DryMo $\geq 5.5$
H6	Rain $< 3260$ mm & Rain $\geq 1865$ mm & cv.prep $\geq 135.5$
H7	Rain $< 1865$ mm & Rain $\geq 1248$ mm & cv.prep $\geq 135.5$
H8	Rain $< 3260$ mm & Rain $\geq 1248$ mm & cv.prep $< 135.5$
H9	Rain $< 1248$ mm



**Fig. 1.** Habitat types delineated based on compositional variation in relation to environmental variables. Each square denotes a 1-ha plot; GPS coordinates lie at centres of squares. Colours indicate different habitat types. Size of squares for a habitat is proportional to the number of indicator species significantly associated with it. Note: H6 and H8 had no singular species associations (see Appendix 2, Table A1) and dots are for representative purpose only.

differed in the number of indicator species associated with them ( $\chi^2 = 37.5$ ,  $df = 8$ ,  $P < 0.001$ ). In general, wetter habitats had more associated species; the wettest habitats

H2 and H3 having the highest number (Fig. 2). Table A1 (Appendix 2) lists species associated with each habitat and groups of habitats.

### Species niche overlap

Large  $D$  values, implying low niche overlap, were seen with respect to rainfall and temperature variables (Fig. 3). Patterns were similar with PCA axes for temperature and precipitation and individual variables (Figs 3 and S5). Between 29% and 50% of pair-wise comparisons showed significant differences in  $D$  values.

### Diversity within habitats

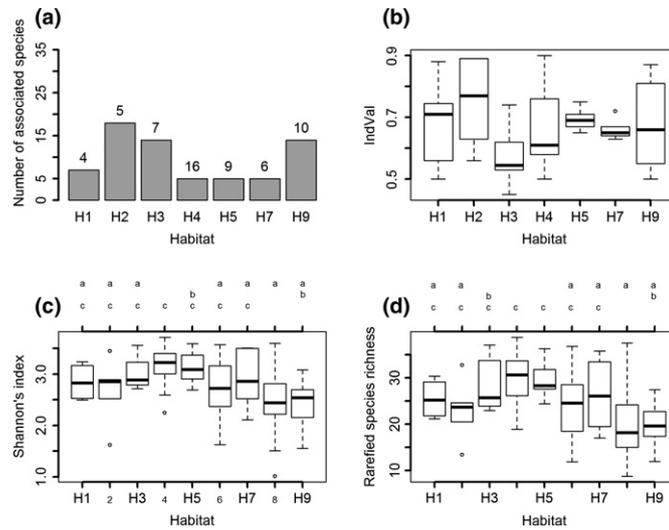
Identified habitats differed in Shannon's index (ANOVA;  $F = 3.93$ ,  $P \ll 0.001$ ), rarefied species richness ( $F = 4.97$ ,  $P \ll 0.001$ ) and observed species number ( $F = 9.6$ ,  $P \ll 0.001$ ). Wetter habitats (H3, H4 and H5) had higher richness and diversity. Tukey's HSD showed significant pair-wise differences between some habitats (Fig. 2).

### Discussion

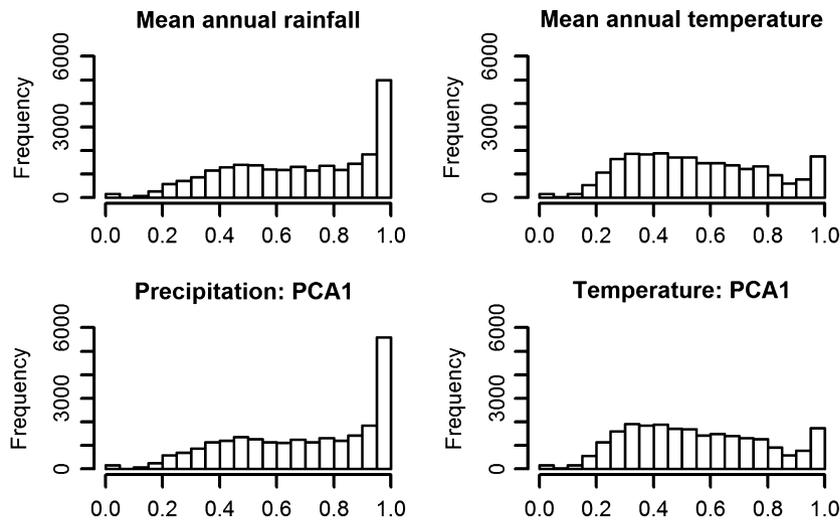
Environmental gradients were found to structure tree assemblages at landscape scales in our study region located within the Western Ghats (Karnataka, IN); rainfall being the primary differentiator. Mean annual temperature and number of dry months further separated high rainfall plots, while seasonality differentiated lower rainfall plots. Positive associations with single habitat types were observed for 68 (17%) species. Wetter, less seasonal habitats had more species associations, higher local diversity and species richness. Amongst 154 species tested, nearly 50% of species pairs differed in their abundance distributions along environmental gradients. Low niche overlap might be contributing to the observed compositional variation differentiating habitat types.

### Environmental heterogeneity drives compositional variation

Environmental filtering affects plant community assembly at multiple spatial scales (Slik et al. 2003; Baldeck et al. 2013a,b; Siefert et al. 2013; Munoz et al. 2014; Trisos et al. 2014). Although smaller-scale studies found the signature of habitat heterogeneity on compositional variation to be eroded in adults compared to seedlings and saplings (Kanagaraj et al. 2011; Baldeck et al. 2013a,b), our results indicate that environmental variation correlates with distinct species assemblages at meso-scales. These patterns corroborate previous analyses using this dataset which



**Fig. 2.** (a) Number of indicator species that showed significant associations with each habitat type. Numbers above each bar stand for number of plots in that habitat. Habitats H6 and H8 are excluded since they had no singular associations. (b) Distribution of indicator values for species within habitats. Higher values show stronger association with a habitat. (c) Shannon index of diversity. (d) Rarefied species richness within habitats. Letters denote significant pairwise differences between habitats based on *post-hoc* comparisons with Tukey's HSD test.



**Fig. 3.** Frequency distribution of *D* values, a measure of niche overlap between pairs of species, for selected variables and first axes of PCA for temperature and precipitation variables. *D* values range from 0–1, higher values implying larger niche difference. Y-axis shows number of species pairs in each category of *D* values. Niche overlaps along other abiotic axes are provided in Appendix 1, Fig A5.

found that taxonomic and phylogenetic turnover were largely explained by differences in rainfall and seasonality (Davidar et al. 2007; Swenson 2011; Hardy et al. 2012).

Previously, qualitative assignment of compositional subsets to bioclimatic types (wet evergreen, semi evergreen, moist and dry deciduous) found that the wettest and driest forests were compositionally distinct, but not communities

within intermediate rainfall sites (Ramesh et al. 2010a). Further, remotely sensed classifications identified three phenological forest types in our study region—tropical evergreen, broad-leaved and moist deciduous (Roy et al. 2015), whereas up to seven compositionally distinct assemblages have been suggested (Utkarsh et al. 1998). We show that while rainfall was the primary

differentiating factor, temperature additionally discriminated species assemblages within broad bioclimatic classifications. Explicitly relating compositional differences to environmental variables within broad-scale vegetation typology can improve the ecological basis of identifying habitats for conservation planning (Moilanen et al. 2005).

Nearly 50% of species pairs we assessed showed significant differences in their abundance distributions along temperature and precipitation gradients (Fig. 3), and this could be contributing to distinct species assemblages through niche partitioning (Munoz et al. 2014). However, compositional patterns could also arise from a combination of niche differences and dispersal limitation reducing species' range overlap (Hu et al. 2012), especially at the scales considered in our study (Pyke et al. 2001; Munoz et al. 2008). Spatial aggregation of some habitats suggests limited seed dispersal, which can substantially reduce the true extent of niche differentiation. In addition, spatial aggregation could also occur through historical contingency and biogeography, which confound accuracy of observed influence of environmental factors on species distributions. Recently developed methods that account for spatial autocorrelation due to dispersal and biogeography may offer more robust techniques to explain compositional variation at landscape scales (Wagner & Dray 2015).

While spatial distance was correlated with compositional differences in this data (Hardy et al. 2012), landscape-scale studies (~10 000 km<sup>2</sup>) of tree communities in Borneo and the Amazon found that floristic variation was better explained by environmental conditions than geographic distance (Potts et al. 2002; Phillips et al. 2003; Tuomisto et al. 2003). The limited role of space alone in explaining turnover at regional scales in this region (Davidar et al. 2007) and elsewhere (Condit et al. 2002; Phillips et al. 2003, 2004) lead us to believe that low niche overlap likely shows differences in species performance along spatially correlated environmental gradients. Additionally, human use legacies have influenced extant tree communities in the Western Ghats (Utkarsh et al. 1998; Ramesh et al. 2010a). Successional trajectories can differ based on forest type (Lohbeck et al. 2013) and management history (Bhaskar et al. 2014). Its implications for tree community assembly and composition across environmental gradients in human-altered forests of Western Ghats should be investigated further.

### Species assemblages in relation to abiotic variables

Rainfall is a well-recognized factor influencing plant species' distributions (Engelbrecht et al. 2007) and composition (Phillips et al. 2003; Baltzer et al. 2007). Accordingly, habitats were broadly divided into west (H1–H5) and east (H6–H9; Fig. 1) groups based on annual rainfall ( $\geq$  or

$<3260$  mm·yr<sup>-1</sup>, respectively; Table 1), reflecting the high species turnover along the east–west rainfall gradient in this region (Davidar et al. 2007). Within the rain shadow areas of eastern slopes (rain  $< 3260$  mm·yr<sup>-1</sup>), plots were further divided into intermediate (1865–3260 and 1248–1865 mm·yr<sup>-1</sup>) and low rainfall habitats ( $<1248$  mm·yr<sup>-1</sup>), capturing the transition into dry forests of peninsular India.

As suggested by Ramesh et al. (2010a), the inclusion of temperature better discriminated compositional variation within high rainfall sites. In fact, spatially distant plots were classified as compositionally similar based on temperature (H4 and H5). Considering that mean annual temperature and mean annual precipitation were not correlated ( $r = 0.13$ ,  $P = 0.2$ ), and temperature showed larger correlation with latitude ( $r = 0.58$ ,  $P < 0.05$ ) and altitude ( $r = -0.91$ ,  $P < 0.05$ ) than precipitation (Lat:  $r = -0.27$ ,  $P < 0.05$ ; Alt:  $r = -0.26$ ,  $P < 0.05$ ), our results suggest that temperature is driving previously observed correlations of turnover with latitude (Davidar et al. 2007). Dry months and CV precipitation further separated species assemblages within temperature categories in high rainfall habitats (Table 1).

Our findings complement a recent meta-analysis that showed temperature to be a crucial factor driving functional differences between plant species (Moles et al. 2014). Temperature and precipitation may synergistically determine realized niches of adult trees and species assemblages over intermediate to large spatial extents (Clarke & Gaston 2006). Trait-based differences in species survival along combinations of temperature and precipitation conditions are an important direction for future research (Comita & Engelbrecht 2014).

Further, soil influences tree community assembly in intermediate rainfall regions (John et al. 2007; Pitman et al. 2008). Although soil was not selected in our final model, plots classified based on CV precipitation were related to soil when PCA axes for temperature and rainfall were used in MRT, and with mean maximum temperature (Appendix 1, Fig A3). At smaller scales, adding soil information improves compositional variation explained (Baldeck et al. 2013a,b; Brown et al. 2013), suggesting scale dependency in niche partitioning related to edaphic conditions. Our results also hint at an interaction between soil type and rainfall.

### Limitations of MRT

We used MRT for habitat classification because it relates species assemblages to environmental variables without any *a priori* categorization. However, MRT habitats neither imply hard boundaries between species assemblages nor that cut offs of environmental variables represent discrete

thresholds for compositional change. In reality, species turnover and compositional differences occur along a spatial continuum with few truly discrete ‘habitats’ (e.g. arising from localized topography or soil). Communities transition gradually as abundances of individual species change over gradients, as shown by analyses of niche breadths.

Habitat classification also depends on abiotic variables used. Multiple MRT models are therefore possible and should be interpreted using biological relevance of environmental variables. While tree assemblages emerge from a combination of environmental variables, dispersal limitation and natural enemies, MRT analysis suggests that amongst a suite of abiotic factors, some may be more important than others in influencing compositional variation. Disentangling the mechanistic effects of multiple drivers on species persistence and community assembly at various scales is scope for further research.

### Species associations with habitats

Within high rainfall sites, more species associations were seen in cooler habitats (H2 and H3) (Fig. 1), which also had high local diversity and species richness (Appendix 1, Fig A4). Among low rainfall habitats, species associations in H9 was comparable to wet habitats. H9 was distinguished by (low) rainfall alone, and lies in eastern rain shadow region of the Ghats and likely has a suite of species adapted to dry hot climates. Even though species richness was low, these plots were compositionally distinct from the highest rainfall sites (Ramesh et al. 2010a). The relatively high number of associations in spatially restricted H1 could result from localized edaphic factors or land-use history.

In spite of widest spatial extents (Fig. 1), H6 and H8 had no singular associations, lower species richness and diversity compared to wetter habitats. The wide rainfall range in H6 and H8 could imply the presence of environmental generalists. In fact, species in these habitats were associated with multiple habitats (Appendix 2, Table A1). Alternatively, these may be well-dispersed species gaining competitive release from wet forest specialists. Future studies could use these results to disentangle dispersal effects from environmental tolerance of representative species.

Multiple reasons may contribute to higher diversity and species associations in wetter habitats. Increased preponderance of natural enemies creates specialized niches and limits plant species distributions in wet areas (Freckleton & Lewis 2006; Spear et al. 2014). Control of competitively dominant (common) species by host-specific pathogens (Bagchi et al. 2014) may allow competitively inferior (rare) species to persist in wetter habitats (Spear et al. 2014), resulting in higher species richness. Further, even

in moist tropical forests, seedling mortality associated with drought stress during the dry season is a strong environmental filter that excludes drought-sensitive species (Engelbrecht et al. 2007; Comita & Engelbrecht 2014). Our results might be capturing the outcome of these smaller-scale processes on composition and diversity at landscape scales. Of course, considering the low number of plots in some habitats, differences in local diversity as well as species associations with poorly represented habitats should be interpreted with caution, especially in light of dispersal limitation.

There were some evident patterns in species’ natural histories and indicator status. Surprisingly, half the species associated with H1, even though a high rainfall site (Rain > 3260 mm-yr<sup>-1</sup>), are deciduous (Appendix 2, Table A2). High mean annual temperatures (>27.2 °C) could account for this. In comparison, species in equally wet habitats H2 and H3 were all evergreen and displayed associations with cooler, aseasonal conditions (ann.tmean < 27.2 °C, DryMo < 5 mo); *Symplocos macrophylla*, *Cleistanthus malabaricus*, *Litsea stocksii*, *L. mysorensis*, *Poeciloneuron indicum* in H2 are evergreen species known to occur primarily in wet cool regions (Pascal 1988). However, indicator species in H3 (*Memecylon* spp., *Antidesma menasu*) are often associated with edges and disturbed evergreen forest. Possibly, some habitat associations reflect species affinities with human-modified conditions rather than environmental variables alone. Species in H4 and H5 are also evergreen, preferring wet climates but tolerating an extended dry period (>5.5 mo), suggesting survival differences based on seasonality. Notably, the driest habitat (H9) had 14 singularly associated species. Deciduous species like *Anogeissus latifolia*, *Albizia amara*, *Maytenus emarginata* and *Lagerstroemia parviflora* were top indicators, capturing the biome shift towards drier areas of peninsular India.

### Conclusion

Climatic changes are likely to affect species persistence, composition and diversity of tree communities (Engelbrecht et al. 2007; Gonza 2011) and predicting ecological responses and species’ range shifts poses an immense challenge for ecologists (Walther et al. 2002; Ibáñez et al. 2006; Hannah et al. 2007). Future research should examine relationships between drought tolerance, local abundance and geographic extent of tree species’ occurrence and survival (Comita & Engelbrecht 2014). Further, local co-existence depends on inter and intraspecific interactions such as density-dependent mortality (Wills et al. 2006; Comita et al. 2010; Piao et al. 2013; Lebrija-Trejos et al. 2014), herbivory (Fine et al. 2004) and resource competition (Tilman 2004). Understanding relevant

ecological processes governing community assembly at multiple spatial scales will better predict the impacts of climatic and land-use changes on plant communities in a changing world (Tilman & Lehman 2001; Lewis 2009).

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### Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Appendix S1.** Supplementary figures for results stated in the manuscript.

**Appendix S2.** Table of indicator species in habitat types.doc.

**Appendix S3.** Table of indicator species in habitat types.csv.