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Functional trait and community phylogenetic analyses reveal environmental filtering as the major determinant of assembly of tropical forest tree communities in the Western Ghats biodiversity hotspot in India

K. Nagaraju Shivaprakash^{1,2,3*}, B. R. Ramesh⁴, Ramanan Umashaanker⁵ and Selvadurai Dayanandan^{1,2}

Abstract

Background: Improved understanding of the processes shaping the assembly of tropical tree communities is crucial for gaining insights into the evolution of forest communities and biological diversity. The climate is thought to be the first order determinant of abundance and distribution patterns of tree species with contrasting traits such as evergreen and deciduous leaf phenology. However, the relative role of neutral, and niche-based processes in the evolution of these patterns remain poorly understood.

Methods: Here, we perform an integrated analysis of the data on tree species abundance, functional traits and community phylogeny from a network of 96 forest plots, each 1 ha in size, distributed along a broad environmental gradient in the central Western Ghats, India. Then, we determine the relative importance of various process in assembly and structuring of tropical forest communities with evergreen and deciduous leaf phenology.

Results: The deciduous leaf phenological trait has repeatedly evolved among multiple distantly related lineages. Tree communities in dry deciduous forests were phylogenetically clustered and showed a low range and variance of functional traits related to light harvesting, reproduction, and growth suggesting niche-based processes such as environmental filtering play a vital role in the assembly of tree communities in these forests. The external factors such as human-mediated disturbance also significantly, but to a lesser extent, influences the species and phylogenetic turnover.

Conclusions: These findings revealed that the environmental filtering plays a significant role in assembly of tree communities in the biologically diverse tropical forests in the Western Ghats biodiversity hotspot.

Keywords: Functional traits, Phylogenetic turnover, Deciduous, Evergreen, Niche-based processes, Human disturbance

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Background

Despite the efforts to understand the ecological and evolutionary processes shaping the distribution and abundance patterns of plant species in tropical forests for centuries, overall mechanisms underlying the assembly of tropical forest communities remain poorly understood (Woodward et al. 2004; Westoby and Wright 2006). In particular, the distribution and abundance patterns of tropical trees with different leaf phenology such as deciduous and evergreen have attracted considerable attention from ecologists, biogeographers, and mathematical modelers for decades (Monk 1966; Givnish 2002; Lavorel and Garnier 2002; Bowman and Prior 2005; Kikuzawa et al. 2013). The co-occurrence and different distribution and abundance pattern of evergreen and deciduous tree species across a variety of landscapes showed to be strongly influenced by environmental factors, mainly by climatic variables such as precipitation, temperature, and length of the dry season (Ramesh et al. 2010a, 2010b; Ge and Xie 2017). Thus, the climate is considered as the first-order predictor of the shift in relative composition and abundance of tree communities between evergreen and deciduous forests at both small and large spatial scales (Chabot and Hicks 1982; Reich et al. 1992; Ramesh et al. 2010a, 2010b). Also, the external factors such as anthropogenic disturbance may also lead to changes in the relative composition of evergreen and deciduous tree species. As anthropogenic disturbances modify the habitat through creating gaps in the canopy and open up areas providing opportunities to light demanding and desiccation tolerant deciduous plant species to colonize the habitat (Ramesh et al. 2010a, 2010b; González-carro et al. 2014; Ramachandra et al. 2016).

However, our current understanding of the how diversity, composition, and abundance of tropical tree assemblages influenced by different community assembly processes at a broad geographical scale covering large environmental gradients remain incomplete. Mainly, due to the interaction between ecological and evolutionary processes affecting these patterns are often ignored in many studies (Ricklefs 2006; Fine and Kembel 2011; González-carro et al. 2014). The stochastic external processes such as dispersal (Hubbell 2001) and deterministic niche based processes such as environmental filtering and interspecific competition (Kraft et al. 2008; Cornwell and Ackerly 2010) influences the spatial distribution and abundance of species across gradients at both large and small spatial scales (Harms et al. 2001; Condit et al. 2002; Fine et al. 2004; Gilbert and Lechowicz 2004; Kraft et al. 2015; Cadotte and Tucker 2017). Species with different habitat preferences occupying separate locations along an environmental gradient may have either shared (closely related species co-occur in a community) or independent (distantly related species co-occur in a community)

evolutionary history (Fine and Kembel 2011; González-carro et al. 2014). Furthermore, historical biogeographic processes such as speciation, extinction, and long-distance dispersal determine which lineages inhabit a particular region and influence the composition and turnover between communities (Ricklefs and Schluter 1993; Ricklefs 2004; ter Steege et al. 2006; Emerson and Gillespie 2008; Vamosi et al. 2009). The species in communities may also evolve converged (similar traits) or divergent (different traits) functional strategies (functional traits) which confer adaptation to different habitats occurring along the gradient (Chave et al. 2007; Hardy and Senterre 2007; Chave 2008). Thus, such processes either increase or decrease phylogenetic and functional turnover along the gradient and in different habitats (Kraft et al. 2008; Fine and Kembel 2011; González-carro et al. 2014).

The community level phylogenetic and functional trait based analyses serve as an invaluable means to test the relative importance of various community assembly mechanisms such as stochastic (dispersal limitation) and deterministic (environmental filtering, competition) processes along environmental gradients (Kraft et al. 2008; Fine and Kembel 2011; González-carro et al. 2014) as well as in distinct habitat types (Shipley et al. 2006; Kraft et al. 2008; Cornwell and Ackerly 2010). The community phylogenetic metrics such as alpha and beta phylogenetic diversity measures and functional trait metrics such as variance, range, standard deviation of nearest neighbor (SDNN), skewness and kurtosis measures can be used to detect the non-random distribution of lineages and functional trait strategies in relation to spatial and environmental gradients (Kraft et al. 2008; Fine and Kembel 2011; González-carro et al. 2014). For example, the increased or positive values of phylogenetic metrics such as net related index (NRI) and nearest taxon index (NTI) and reduced or negative values for range and variance of functional traits compared to random expectation of null model indicate clustering pattern of phylogenetic relationship and functional traits highlighting the role of environmental filtering in community assembly. In contrast, the reduced or negative values of NRI and NTI and trait metrics SDNN and kurtosis as compared to random expectation null model indicate over dispersion patterns of phylogenetic relationship and functional traits and suggest the importance of interspecific competition in assembly of the community. The congruence between observed phylogenetic and functional trait metrics with random expectation patterns indicates the crucial role of neutral or other random stochastic processes such as dispersal limitation and external factors in the assembly of the community. Thus, integrating multiple approaches is essential to gain in depth understanding of mechanisms shaping assembly of communities across environmental gradients.

In the present study, we analyzed the species composition, abundance and functional trait data of tropical tree species from 96 plots, each 1 ha in size, distributed along a broad range of environmental conditions with the varying level of human disturbance, in a phylogenetic framework, to assess the relative importance of neutral (dispersal limitation, external factors) and niche based processes (environmental filtering and interspecific competition) in assembly of forest communities along a large scale environmental gradient in the region. We specifically address following questions: (i) How does the spatial variation in environmental variables influence the relative composition, richness, abundance, phylogenetic structure and functional trait strategies of tree communities with different leaf phenology? (ii) Do the phylogenetic structure and functional trait strategies of varying forest types differ, thereby indicating the importance of niche based processes (environmental filtering and competition) in sorting of lineages into specific forest types from regional species pool? (iii) Do phylogenetic alpha and beta diversity differ among plots that experienced the different level of human disturbance and (iv) Does the phylogenetic beta diversity turnover between tree communities faster or slower between plots than that expected given the species turnover along climatic gradients? and v) Are leaf phenological traits (evergreen and deciduous) phylogenetically conserved among tree species in the Western Ghats?

Methods

Community composition and species abundance data

We used tree species abundance and stand structure data from a network of 96 plots, one hectare each in size, distributed across wet and dry environmental gradients in the central Western Ghats, India (Ramesh et al. 2010b). The study area (13°30'–15°50' N, 74°15'–75°40' E) is located within the administrative boundaries of Uttara Kannada, Shimoga and Chikmagalur districts of the State of Karnataka in south-western India (Fig. 1). The study region covers 21,970 km² area of the central Western Ghats region and extends from the coastal plain of the Arabian Sea to the humid hill zone of the Western Ghats 'great escarpment', and to the Karnataka plateau, that recedes toward the eastern upland region. These plots were established by the Karnataka Forest Department (KFD) in 1996–1997 (Ramesh et al. 2009), and the detailed description of the study area is given in (Ramesh et al. 2010a, 2010b). We recorded the diameter at breast height (dbh) of all living trees ≥10 cm in each plot along with the phenological classification of each tree as evergreen or deciduous based on existing literature (Pascal 1986) and botanists' expertise.

Finally, we calculated distribution and abundance of deciduous and evergreen tree species by summarizing

floristic data of 96 plots through a site-by-species abundance matrix. First, we classified each tree species into either evergreen or deciduous category and calculated the proportional abundance and species richness of deciduous and evergreen tree species of each plot.

Abiotic variables

We chose abiotic variables related to temperature, precipitation, evapotranspiration and aridity, which are considered as relevant factors influencing the patterns of plant species diversity and community dynamics (Wright 1983; Currie 1991). We evaluated 23 variables of which 19 were bioclimatic, 2 evapotranspiration related, one variable related to aridity and number of dry months (Additional file 1: Table S1). We removed variables with multicollinearity through forward selection and stepwise selection procedures based on Variance Inflation Factor (VIF) as implemented in Ordistep (Blanchet et al. 2008) and MASS (Ripley et al. 2011) in R statistical software packages (<http://cran.r-project.org>) and retained 12 variables for further analysis (Additional file 1: Table S1). The details of variables and their source are given in Additional file 1: Table S1. In addition to these continuous climatic variables, we used discrete habitat type variables based on precipitation seasonality and level of disturbance. These variables included three forest types, wet evergreen (rainfall > 2000 mm·yr.⁻¹), moist deciduous (rainfall 1500 to 2000 mm·yr.⁻¹) and dry deciduous (rainfall < 1500 mm·yr.⁻¹), based on precipitation seasonality and dry length season following Pascal (1982). Second, we evaluated the effect of disturbance by classifying our plots into three categories: non-disturbed forests (N); low-disturbance forests (L) where forest degradation is low; and high-disturbance forests (H) where forest degradation is severe following Ramesh et al. (2010a, 2010b).

Functional trait data

We selected a set of continuous and discrete functional traits often considered essential for the maintenance of woody plant form in both wet and dry conditions (Westoby et al. 2002). In total, we collected data on five continuous traits and two discrete traits reflecting morphology, physiology, growth and reproduction (Additional file 1: Table S2). The five continuous traits included maximum dbh (m), wood density (g·cm⁻³), leaf size (cm), seed size (mm²) and seed mass (g), and the discrete traits were seed dormancy type (orthodox and recalcitrant) and leaf phenology (deciduous and evergreen). See methods section in Supporting Information for further details on functional trait data collection.

Phylogenetic tree reconstruction

We reconstructed the dated phylogenetic hypothesis for all tree species (339 species) occurring in our study plots using three candidate loci that are frequently used in angiosperm phylogenetic studies. All three loci were from the chloroplast genome and included ribulose-bisphosphate/carboxylase Large-subunit gene (*rbcL*), the maturase-K gene (*matK*) and *psbA-trnH* intergenic region. We inferred phylogenetic relationships of tree species using maximum likelihood (ML), and Bayesian inference (BI) methods. Finally, the dated phylogenetic tree was obtained using Bayesian method (Sanderson 2002) as implemented in the program BEAST v.1.8.2 (Drummond and Rambaut 2007). All phylogenetic analyses were performed using the CIPRES Science Gateway v.3.3 (Miller et al. 2011) (<http://www.phylo.org>). See methods section in Supporting Information for further details on Phylogenetic tree reconstruction.

Phylogenetic alpha and beta diversity metrics

To evaluate the phylogenetic alpha diversity of the tree species in our plots, we calculated the two commonly used alpha diversity metrics, namely Net Relatedness Index (NRI) and Nearest Taxon Index (NTI) weighted by species abundances (Webb et al. 2008). To standardize the observed MPD and MNTD to that expected given the species richness observed, we compared each metric with null distribution of 1000 random communities constructed using the independent-swap null model (Gotelli 2000). The regional pool used in these randomizations included all the species occurring in our study plots. We multiplied the NRI and NTI results by -1 such that if the transformed values are >0 , then communities are considered as phylogenetically clustered (closely related individuals co-occurring), and if the values are negative, then communities are phylogenetically overdispersed (distantly related individuals co-occurring).

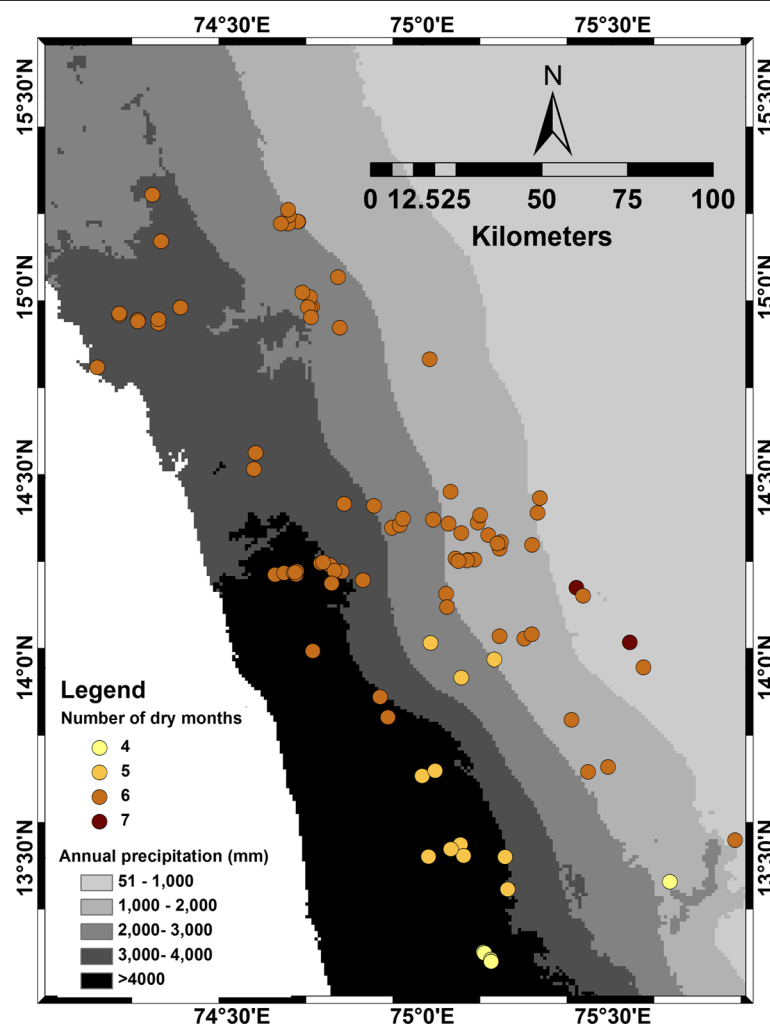


Fig. 1 Location of sampling plots across precipitation and number of dry month's gradient in the central Western Ghats region of Karnataka, India

Similarly, we quantified the phylogenetic beta diversity for tree communities in our plots based on two commonly used metrics: betaNRI and betaNTI weighed by abundance. The null models used were similar to that of alpha diversity metrics. Negative values of betaNRI and betaNTI indicate higher-than-expected phylogenetic turnover given the species turnover, meaning that each community generally contains distantly related individuals. Conversely, positive values indicate lower phylogenetic turnover than expected given the species turnover, meaning that turnover between the two communities occurs between closely related individuals. To account for phylogenetic uncertainty, both alpha and beta phylogenetic diversity measures were calculated using 1000 dated trees sampled from the Bayesian posterior distribution of BEAST. All the phylogenetic diversity measures were calculated using R package picante ver 1.6.2 (Kembel et al. 2010).

Functional trait metrics

We used four community level functional trait metrics following the method of Kraft and Ackerly (2010). Of these four metrics, the community trait range (RANGE) and variance (VAR) are sensitive to habitat filtering (Kraft and Ackerly 2010). The other two metrics, the standard deviation of nearest neighbor distance and the single direction normalized to the range (SDNDR, referred to as even spacing) and kurtosis are sensitive to niche differentiation (competition) (Cornwell and Ackerly 2009). All functional trait metrics were calculated using the R script from Kraft and Ackerly (2010). The five continuous traits were considered independently for the analysis. The species without a given trait value were excluded from that analysis.

We tested for nonrandom patterns of functional traits among plots distributed across environmental gradient and in different forest types by creating 999 null communities of equal richness to the sampled plot by drawing species at random from regional species pool (included all species occur in our study plots), weighted by plot-wide species abundance. We calculated the effect size of an observed metric by subtracting the mean metric of the simulated null communities from the observed value and dividing by the standard deviation of the simulated null communities. In this analysis, we used individual plots as our unit of a community.

We assessed the significance of each trait metric using a plot-wide Wilcoxon signed rank test with a null hypothesis that the average of the observed values of each trait metric was equal to the average of the null expectation (following Cornwell and Ackerly 2009; Kraft and Ackerly 2010). In all analyses, we used one-tailed tests based on a priori predictions of habitat filtering and niche differentiation.

Phylogenetic signal of functional traits

We quantified the degree to which phylogenetic relatedness predicts the similarity of species in functional traits by calculating phylogenetic signal for both continuous and discrete traits separately using both Blomberg's K (Blomberg et al. 2003) and Pagel's λ (Pagel 1999) statistics for continuous traits and D statistic (phylogenetic dispersion) of Fritz and Purvis (2010) for discrete traits. The analysis was performed with 1000 randomization under the expectation of no phylogenetic signal using R packages phytools (Revell 2012) and caper (Orme et al. 2012). To account for phylogenetic uncertainty, the measures were calculated using 1000 dated trees sampled from the Bayesian posterior distribution of BEAST. We used stochastic character mapping (Huelsenbeck et al. 2003) as implemented in R package phytools (Revell 2012) to reconstruct the evolutionary history of deciduous and evergreen leaf phenology in tree communities of Western Ghats, India. We used ARD (all rate different) model to map the traits. In total, we ran 1000 simulations per tree for 100 dated trees obtained from the posterior distribution of BEAST to account for phylogenetic uncertainty. The mean of the posterior probability distribution for each state (deciduous and evergreen) of the trait from 100 trees were mapped on each node of the phylogenetic tree.

Statistical analyses

We used redundancy analysis (RDA) based on bray-curtis distance to predict the important abiotic variables determining community composition and distribution pattern of deciduous and evergreen tree species across the central Western Ghats. Then, we performed single regression analysis between the chosen 12 environmental variables, richness and abundance of deciduous and evergreen tree species, phylogenetic and functional trait metrics using generalized linear modeling (GLM) (McCullagh and Nelder 1983) with log link and Poisson errors.

Since the primary goal was to identify the environmental variables with a high direct influence on species richness, abundance and phylogenetic alpha diversity of tree communities with different leaf phenology, we used hierarchical partitioning for the analysis (Chevan and Sutherland 1991). Hierarchical partitioning computes all possible regression models and estimates the increase in the fit of all possible models with a particular predictor compared to the equivalent model without that variable and averages model improvements across all hierarchies, thus permits a ranking of variables by their independent effects. Hierarchical partitioning was conducted using the R package 'hier.part' version 1.0–4 (Walsh and Mac Nally 2013). To identify non-redundant variables in the set of five most contributed variables selected from hierarchical partitioning, we conducted multiple regression

analyses using generalized linear modelling (GLM) (McCullagh and Nelder 1983) with log link and Poisson errors. All five selected variables were included in the multi-model analyses, and the best model was chosen from the 31 models representing all possible combinations of the additive variables based on the lowest AICc value (Anderson et al. 1998). If the AICc values for multiple models were nearly equal ($\Delta\text{AICc} < 1$), we used the model-averaging approach to compare them with the selected best models and assessed the relative importance of the different variables by the standardized beta coefficient (Johnson and Omland 2004). All twelve environmental variables were standardized using the center and scale function before the analysis.

We used T-test to evaluate whether phylogenetic alpha diversity and functional trait metrics significantly differed among discrete habitat variables such as forest type (wet-evergreen, moist deciduous and dry deciduous) and level of disturbance (none, low and high). Also, we calculated the percentage of NRI and NTI values and functional trait metrics that indicated significant clustering (values > 1.96) or overdispersion (values < -1.96). Finally, we used Mantel test on distance matrices available in the 'ecodist' package in R (Lichstein 2007) to evaluate the relationship between environmental variables and the phylogenetic beta diversity after controlling for spatial distance.

Results

The richness and abundance patterns of evergreen and deciduous species

The redundancy analysis grouped 96 plots into two major groups based on the bray-curtis similarity matrix accounting for species abundance. The grouping was in accordance with the evergreen and deciduous habitat of tree species (Additional file 1: Figure S2). The first two axes together explained 85.24% of variation after accounting for relevant constraining abiotic and biotic variables (Additional file 1: Figure S3). The bioclimatic variables such as precipitation of wettest month (Bio13), precipitation seasonality (Bio15), precipitation of warmest quarter and coldest quarter (Bio18 and Bio19), maximum temperature of warmest month (Bio5), global aridity index (GAI), slope, proportion abundance of evergreen species and anthropogenic disturbance significantly contributed to the grouping (Additional file 1: Figure S3). The single regression analysis suggested that, the environmental variables related to precipitation and global aridity index (GAI) positively correlated with proportion, abundance and species richness of evergreen tree species and negatively correlated with deciduous tree species, whereas environmental variables related to temperature positively correlated with proportion abundance and species richness of deciduous tree

species and negatively correlated with evergreen tree species (Additional file 1: Tables S5 and S6, Figure S3).

The hierarchical partitioning analysis suggested that the major predictors contributing to an observed pattern of both abundance and species richness of deciduous and evergreen species in Western Ghats tree communities were similar (Table 1, Fig. 2). The variables such as precipitation of wettest period (Bio13), precipitation of wettest quarter (Bio16) and annual precipitation (Bio12) showed the highest independent contribution followed by precipitation of coldest quarter (Bio19) and global aridity index (GAI) (Table 1 and Fig. 2). However, the independent effects of all predictors were statistically significant (Table 1). Further, the negative joint contribution of all predictors indicates that relationships of almost all the predictors are suppressive, not additive (Chevan and Sutherland 1991) and joint contribution of predictors explain more of the variation than the sum of the individual effects of predictors (Table 1 and Fig. 2). The multiple regression analysis retained the model with Bio13 and Bio19 as the final best model for explaining abundance pattern of deciduous and evergreen species (Table 2). The model with Bio12 and Bio16 were retained as a final best model to explain the richness pattern of evergreen and deciduous tree species (Table 2).

Phylogenetic alpha and beta diversity

The phylogenetic alpha diversity measured using net related index (NRI) and nearest taxon index (NTI) showed incongruent results in relation to the environment and discrete habitat variables (Additional file 1: Tables S7 to S9). In general, the results of single regression analyses showed that NRI was negatively correlated with precipitation variables, PET and GAI and positively correlated with temperature variables and potential evapotranspiration (Additional file 1: Table S7 and Figure S4). In other words, phylogenetic clustering of closely related species decreased with precipitation and aridity index and increased with temperature and evapotranspiration (Additional file 1: Table S7 and Figure S4).

The hierarchical partitioning analysis suggested that, the environmental variables related to precipitation (Bio15, Bio16, Bio13 and Bio12) showed highest independent contribution followed by temperature related variables (Bio3 and Bio4) and global aridity index (GAI) to explain the observed pattern of phylogenetic alpha diversity (NRI and NTI) (Table 1 and Fig. 2). Moreover, the independent effects of all predictors were statistically significant for NRI, and none of the variables showed the significant effect for NTI (Table 1). Further, the negative joint contribution of all predictors indicates that relationships of almost all the predictors are suppressive, not additive (Chevan and Sutherland 1991) and joint contribution of predictors explain more of the variation in

Table 1 Results of the randomization tests for the independent contributions of separate predictor variables in hierarchical partitioning to explain variation in the richness, abundance and phylogenetic diversity of tree communities in central Western Ghats, India (Results are expressed as Z-scores. * $p < 0.05$)

Variable	NRI		NTI		Abundance evergreen		Abundance deciduous		Richness evergreen		Richness deciduous	
	Obs. I (%)	Z-score	Obs. I (%)	Z-score	Obs. I (%)	Z-score	Obs. I (%)	Z-score	Obs. I (%)	Z-score	Obs. I (%)	Z-score
Bio2	6.752	3.55*	5.767	-0.12	6.317	11.2*	6.161	9.41*	5.461	8.37*	4.623	6.99*
Bio3	8.828	4.66*	6.728	0	4.947	7.48*	4.911	7.00*	5.187	7.38*	4.317	6.09*
Bio4	9.451	5.33*	7.118	0.05	7.025	10.72*	6.945	10.87*	6.823	10.84*	5.251	7.5*
Bio5	4.270	1.67*	5.416	-0.27	7.527	12.03*	7.581	12.55*	6.631	9.13*	8.268	13.71*
Bio7	8.228	4.48*	6.002	-0.15	6.378	10.77*	6.251	9.12*	5.937	9.24*	4.893	6.6*
Bio12	11.364	6.62*	9.750	0.45	11.070	18.81*	11.132	16.63*	11.616	18.69*	11.392	18.76*
Bio13	11.354	6.32*	11.460	0.74	11.412	19.63*	11.576	17.14*	12.134	19.98*	11.109	18.58*
Bio15	8.050	4.22*	15.661	1.61*	5.209	7.91*	5.321	7.67*	6.224	9.05*	4.617	6.6*
Bio16	11.365	6.19*	9.484	0.45	11.304	18.71*	11.379	18.11*	11.961	18.18*	11.037	16.57*
Bio19	7.075	3.31*	9.336	0.34	10.662	17.58*	10.667	13.15*	11.933	17.43*	16.570	21.91*
PET	4.658	1.71*	5.562	-0.18	7.861	11.98*	7.778	10.23*	6.422	9.21*	7.115	9.17*
GAI	8.607	3.97*	7.718	0.18	10.288	15.2*	10.298	13.35*	9.672	12.71*	10.807	13.88

Z-scores are calculated as (observed – mean (randomizations))/SD (randomizations), and statistical significance (*) is based on upper 0.95 confidence limit ($Z \geq 1.65$). The variables which contributed the most and retained for further multiple linear regression (MLR) analysis using generalized linear models (GLMs) is given in **bold**. NRI Net relatedness index; NTI Nearest taxon index; Refer Additional file 1: Table S1 for details of predictor variables abbreviation

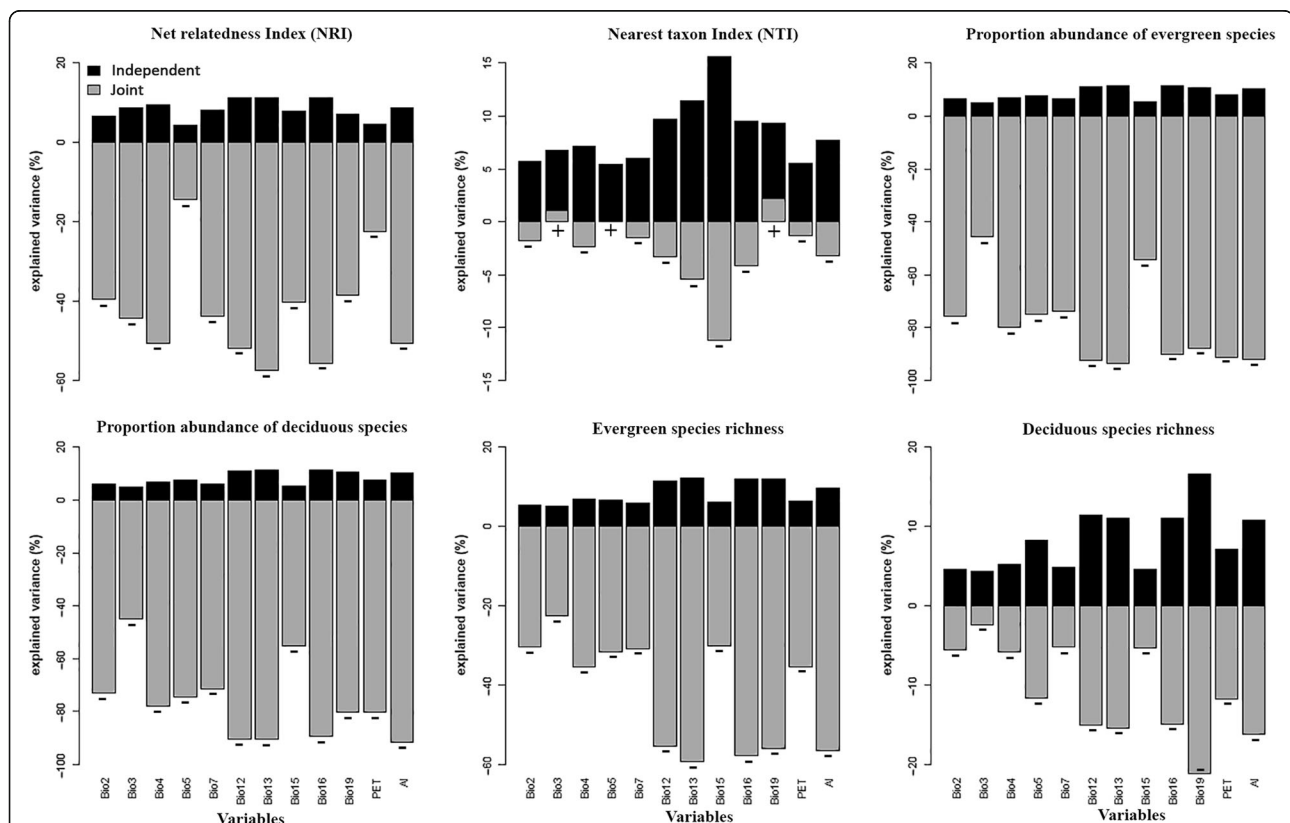
**Fig. 2** The independent and joint contributions (given as the percentage of the total explained variance) of the predictor variables for richness, abundance and phylogenetic structure of tree communities in central Western Ghats, India as estimated from hierarchical partitioning. The sign indicates the direction of variable coefficients in the full twelve-variable model. Negative grey columns indicate suppression effects

Table 2 Multiple regression analyses of abundance and richness of evergreen and deciduous species and alpha phylogenetic diversity against twelve factors for tree communities in central Western Ghats, India. Model selection (best model) for multiple regressions was based on minimizing the AICc in consideration of all 4095 models

Response variables	Standard coefficient of the best mode								Pseudo R^2	AICc
	Bio3	Bio4	Bio12	Bio13	Bio15	Bio16	Bio19	GAI		
Deciduous abundance				-0.198			-0.128		0.843	2.705
Evergreen abundance				0.197			0.128		0.640	1.707
Deciduous richness			-25.675	-11.587		36.187	-4.824		0.630	571.357
Evergreen richness			-74.094			82.971	7.947		0.651	762.358
NRI			2.362			-2.624			0.286	132.713
NTI					-0.136				0.051	175.364

Pseudo R^2 values are calculated as: (null deviance – residual deviance)/null deviance. Negative relationships are indicated by (–). *NRI* Net relatedness index; *NTI* Nearest taxon index; Refer Additional file 1: Table S1 for details of predictor variables abbreviation

phylogenetic alpha diversity than the sum of the individual effects of predictors (Table 1 and Fig. 2). Finally, multiple regression analysis retained the model with Bio12, Bio15, and Bio16 as the final best model for explaining phylogenetic alpha diversity (NRI and NTI) pattern in Western Ghats tree communities (Table 2).

We found that the NRI values of dry forests were on average more phylogenetically clustered than those in wet and moist forests, indicating that lower precipitation levels lead to the co-occurrence of closely related species (Table 3; Fig. 3). We also found that forests which were highly disturbed by humans on an average had higher phylogenetic clustering than those that are undisturbed or had the lower disturbance, indicating that human disturbance further leads to the co-occurrence of closely related species (Table 3; Fig. 3). Our results showed that NRI values were positively correlated with the increased abundance of deciduous species and negatively correlated with evergreen species, indicating cooccurring deciduous species on an average closely related to each other than cooccurring evergreen species (Additional file 1: Table S10 and Figure S5). However, none of the results were significant for nearest taxon index (NTI) (Additional file 1: Tables S8 to S10). The phylogenetic beta diversity measures (betaNRI and betaNTI) did

not show significant correlation either with spatial distance or with environmental distance, indicating that the phylogenetic turnover between two plots is not influenced either by dispersal limitation or by environmental variables (Additional file 1: Table S11 and Figure S6).

Phylogenetic signal in functional traits of wet and dry forest communities

The evaluation of phylogenetic signal in five continuous and two discrete traits (Additional file 1: Table S12 and Figure S8) showed that except for maximum DBH and seed size all other continuous traits showed significant phylogenetic signal and among discrete traits, only seed dormancy type showed significant phylogenetic signal (Additional file 1: Table S12 and Figure S7). The trait spacing analysis showed strong evidence for niche-based processes (habitat filtering) in determining assembly and dominance of tree communities in wet and dry forests (Table 4 and Additional file 1: Table S13, Fig. 4). The values of RANGE and VAR for leaf size, seed size, and wood density significantly differed among three forests (wet evergreen, moist deciduous and dry deciduous) types (Table 4 and Additional file 1: Table S13, Fig. 4). The RANGE and VAR for leaf size and wood density

Table 3 The results of the *t*-tests between NRI values and forest types and levels of disturbance

Variable	Comparison	Mean	<i>t</i>	DF	<i>P</i> value	Clustered (%)	Overdispersed (%)
Forest type	EVG/MD	-0.017	3.177	74	0.002	17	6.5
	MD/DD	0.619	2.81	38	0.007	25	0
	DD/EVG	0.141	5.671	74	0.0001	55	0
Level of Human disturbance	None/low	-0.373	8.238	63	0.0001	2.3	14
	Low/high	0.823	1.097	52	0.278	12	0
	High/none	1.001	9.326	71	0.0001	58	0

Percentage values are the proportion of sites that were significantly clustered and overdispersed assemblages per category. Bold numbers represent the statistically significant results. *DF* degrees of freedom; *EVG* evergreen; *DEC* deciduous; *MD* moist deciduous; *DD* dry deciduous. The formula for *t*-test used is $t = (\bar{x}_1 - \bar{x}_2) / \sqrt{((N_1 - 1)s_1^2 + (N_2 - 1)s_2^2) / (N_1 + N_2 - 2) (1/N_1 + 1/N_2)}$, where \bar{x}_1 and \bar{x}_2 represent means of two different forest types or disturbance level; N_1 and N_2 are sample size and s_1^2 and s_2^2 are an estimator of the common variance of the two samples. Significant results are indicated in bold

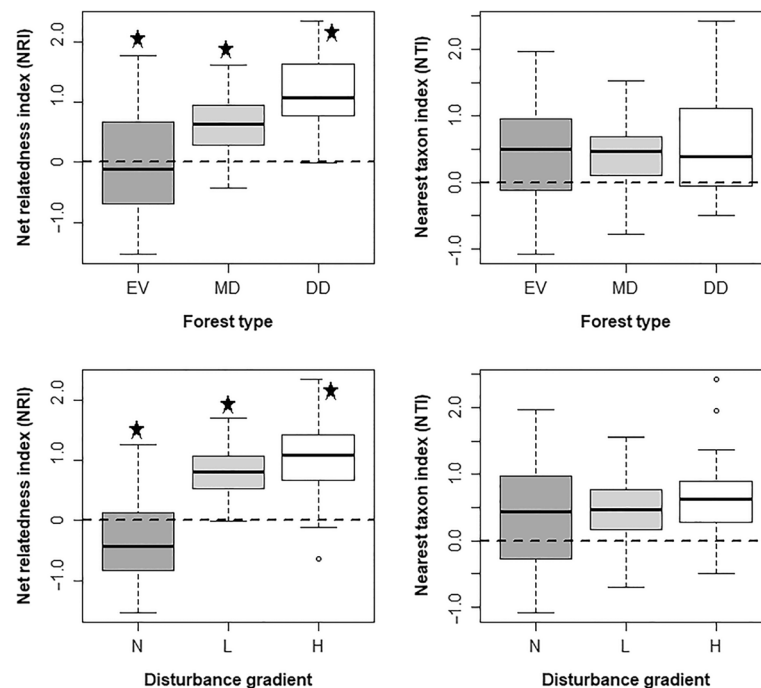


Fig. 3 The boxplot of phylogenetic alpha diversity indexes (NRI and NTI) distributed among discrete habitat variables (forest type and human disturbance). Asterisks represent result significant among groups. Habitat variable abbreviations: EV = evergreen, MD = moist deciduous, DD = dry deciduous, H = high disturbance, L = low disturbance, N = no disturbance

were significantly reduced and negative for tree communities in dry deciduous forests, whereas it was positive and increased for tree communities in moist deciduous and evergreen forests (Table 4 and Additional file 1: Table S13, Fig. 4). Conversely, seed size showed the different pattern, and we found that the RANGE and VAR were positive and increased for tree communities in dry deciduous forests, whereas it was negative and reduced for tree communities in moist deciduous and evergreen forest (Table 4 and Additional file 1: Table S13, Fig. 4).

The effect size of both VAR and RANGE for few of the traits (leaf size and seed mass) were significantly correlated with the proportion of the abundance of deciduous and evergreen tree species (Additional file 1: Table S14 and Figure S8). The communities dominated by deciduous species had lower negative VAR and RANGE, whereas communities dominated by evergreen tree species had higher and positive VAR and RANGE (Additional file 1: Table S14 and Figure S8). Although we predicted that if niche differentiation processes such as competition determine the assembly of species in wet and dry forests, the traits should be more evenly distributed and should have smaller kurtosis values than null model expectation, we did not find evidence for this prediction in any of the five functional traits. The contrasting pattern of functional trait metrics among tree communities in different forest types suggests that the distribution and dominance of tree species with contrasting leaf phenology (deciduous and

evergreen) in these habitats is strongly determined by habitat filtering.

Evolutionary history of deciduous and evergreen leaf phenology

The stochastic mapping of leaf phenological traits of deciduous and evergreen nature of 393 tree species on the dated phylogenetic tree suggested that deciduous leaf phenology has evolved multiple times independently in distantly related lineages (Fig. 5). These results indicate the convergent evolution of deciduous leaf phenology among tree species in the Western Ghats. This finding is further supported by the weak phylogenetic signal in leaf phenology traits (Additional file 1: Tables S12 and Figure S7). Furthermore, we found no significant difference between the chronology of the evolution of deciduous and evergreen leaf phenology in tree species in the Western Ghats (Fig. 5).

Discussion

The present study, to the best of our knowledge, represents one of the first to quantitatively assess the historical, ecological and evolutionary determinants of tropical tree community assembly along a broad scale spatial and environmental gradient in the Western Ghats biodiversity hotspot in India. This study investigated the taxonomic turnover, functional trait strategies and phylogenetic structure of tree communities distributed across a broad

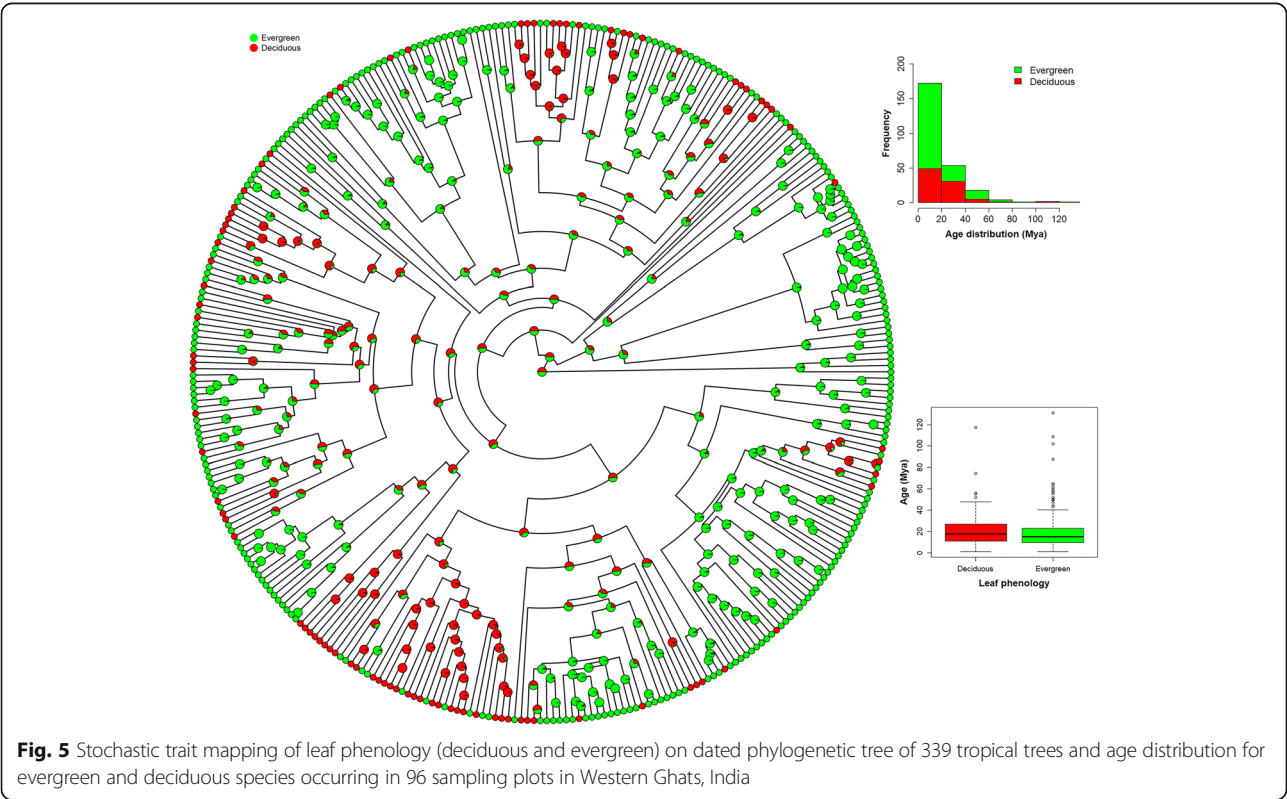
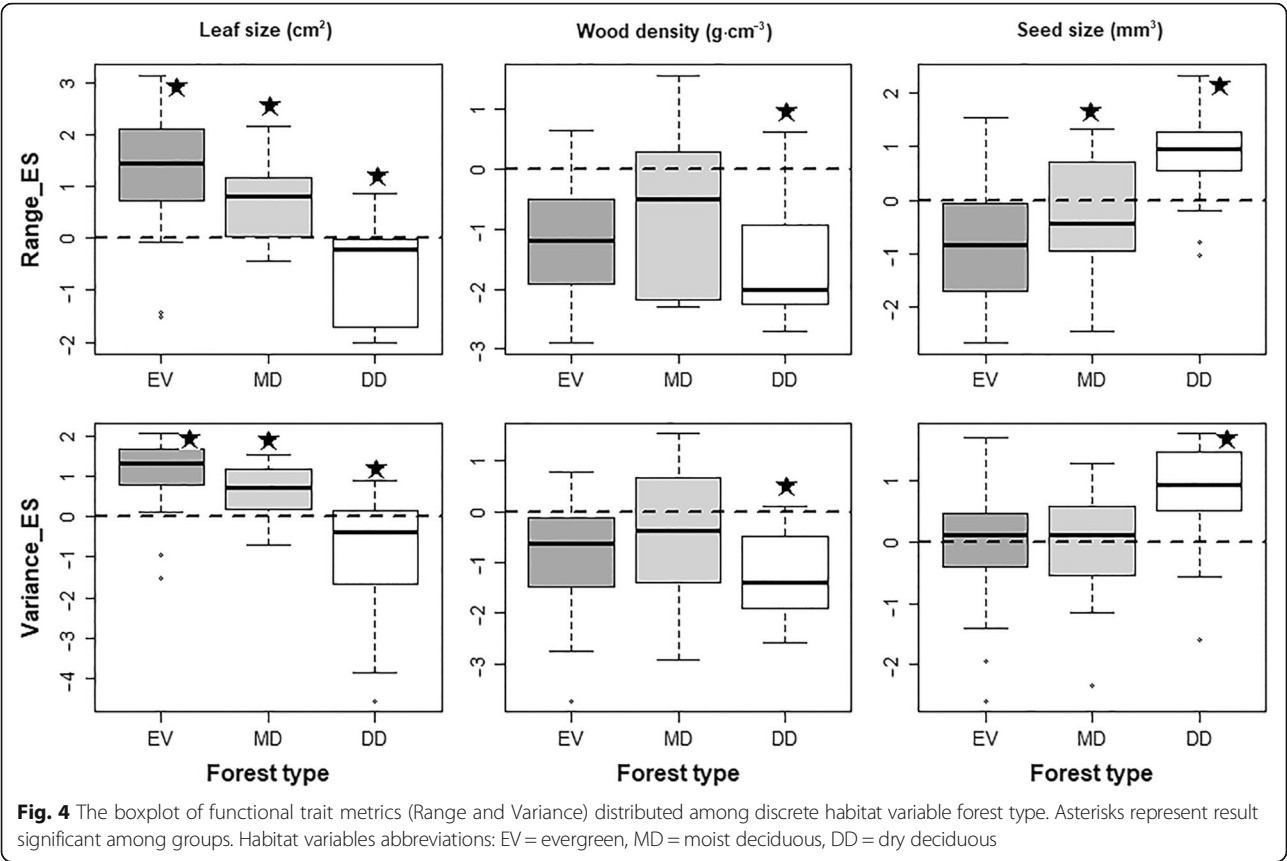
Table 4 The results of the *t*-tests between functional trait metrics (Range and Variance) and forest types

Variable	Comparison	Mean	<i>T</i>	<i>P</i> value	Clustered (%)	Overdispersed (%)
Leaf size (Range)						
Forest type	EVG/MD	1.364	2.740	0.007	4	66
	MD/DD	0.692	4.890	0.0001	0	35
	DD/EVG	−0.650	7.881	0.0001	40	0
Leaf size (Variance)						
Forest type	EVG/MD	1.162	3.132	0.002	2	57
	MD/DD	0.606	4.0382	0.0003	0	30
	DD/EVG	−0.960	8.042	0.0001	35	0
Wood density (Range)						
Forest type	EVG/MD	−1.14	1.343	0.183	57	0
	MD/DD	−0.794	2.214	0.0329	45	5
	DD/EVG	−1.583	1.878	0.064	75	0
Wood density (Variance)						
Forest type	EVG/MD	−0.839	1.236	0.219	41	0
	MD/DD	−0.483	2.201	0.0339	40	0
	DD/EVG	−1.245	1.558	0.124	60	0
Seed size (Range)						
Forest type	EVG/MD	−0.809	1.635	0.125	45	7
	MD/DD	−0.301	3.976	0.0003	25	10
	DD/EVG	0.839	6.242	0.0001	50	10
Seed size (Variance)						
Forest type	EVG/MD	0.0280	−0.156	0.876	12.5	11
	MD/DD	−0.006	2.924	0.006	15	10
	DD/EVG	0.796	3.510	0.0008	5	45

Percentage values represent the proportion of sites that were significantly clustered and overdispersed assemblages per category. Bold numbers represent the statistically significant results. *EVG* evergreen; *DEC* deciduous; *MD* moist deciduous; *DD* dry deciduous. The formula for *t*-test used is $t = (\bar{x}_1 - \bar{x}_2) / \sqrt{((N_1 - 1)s_1^2 + (N_2 - 1)s_2^2) / (N_1 + N_2 - 2)} \cdot \sqrt{(1/N_1 + 1/N_2)}$, where \bar{x}_1 and \bar{x}_2 represent means of two different forest types; N_1 and N_2 are sample size and s_1^2 and s_2^2 are an estimator of the common variance of the two samples. Significant results are indicated in bold.

spatial scale of environmental gradients to gain insights into the ecological and evolutionary determinants of distribution and abundance pattern of tree species with contrasting leaf phenology (evergreen and deciduous). Also, this study investigated the role of human disturbance on community assembly and phylogenetic structure of tree species with different leaf phenology. Although, a few studies have evaluated the role of historical and environmental factors underlying the composition, distribution and abundance pattern of tropical tree species with contrasting leaf phenology. They have not integrated the ecologically important traits and evolutionary relationship of co-occurring species in an integrated ecological analysis (Ramesh et al. 2010a, 2010b; Joseph et al. 2012; Van Ommen Kloeke et al. 2012; González-Caro et al. 2014; Lohbeck et al. 2015; Krishnadas et al. 2016; Ge and Xie 2017). Our results show that taxonomic turnover and phylogenetic structure of tree communities in the study region is best predicted by precipitation gradient followed

by temperature related variables and aridity index. The human-induced disturbance gradient also significantly correlated with taxonomic turnover and community phylogenetic structure. Furthermore, the tree communities distributed among wet and dry forests showed divergent functional trait strategies. Overall our findings highlight the crucial role of niche based processes such as environmental filtering in the assembly of tropical tree communities. Also, our results also highlight the role of historical factors such as human disturbance in the assembly of tropical tree communities possibly through altering ecological and evolutionary processes. The evidence for convergent evolution of leaf phenological traits (evergreen and deciduous) early in the evolution of angiosperms highlights the importance of the evolutionary history of ecologically important traits in the assembly of tree communities along wet and dry climatic gradients.



Environmental determinants and human disturbance influence on taxonomic turnover and phylogenetic structure of tree communities

We found that variables related to precipitation, water deficit (aridity index) and temperature strongly associated with the patterns of taxonomic turnover (species composition, species richness and directional shift in abundance) and phylogenetic structure of tropical tree species with contrasting leaf phenology (deciduous and evergreen) across forests in Western Ghats, India (Tables 1, 2 and Fig. 2). These findings corroborate the quantitative analyses reported in earlier empirical studies that showed contrasting patterns of taxonomic turnover and phylogenetic structure of tropical tree species differing in leaf phenology (evergreen and deciduous), which was primarily influenced by precipitation, and water deficit (aridity index) associated with length of dry season and temperature (Ramesh et al. 2010a, 2010b; Joseph et al. 2012; González-Caro et al. 2014). Several processes may explain the observed pattern of taxonomic turnover and phylogenetic structure of tree communities in relation to environmental variables in the study region. First, the ability of a species to survive under limited moisture conditions and competition between tree species with different leaf types could be the possible physiological mechanism driving this pattern. Thus, an evergreen–deciduous trade-off between water availability and competitive ability exists, and greater tolerance to the limited water supply can result in the reduced competitive ability for either leaf type in a given climatic regime (Chabot and Hicks 1982; Reich et al. 1992; van Ommen Kloeke et al. 2012). The tropical forests in the Western Ghats occur along broad scale precipitation gradient (< 1000 mm to > 5000 mm) with varying length of dry season ranging from 3 to 7 months (Davidar et al. 2007; Ramesh et al. 2010a, 2010b). The evergreen broad-leaved tree species adapted to high rainfall of > 5000 mm with < 3 months of the dry season in lower altitudes seldom thrive and fail to reproduce in low rainfall areas with the prolonged dry season of > 3 months (van Ommen Kloeke et al. 2012; Lu et al. 2017). On the other hand, deciduous broad-leaved trees appear to possess a competitive advantage over evergreen trees at lower precipitation with prolonged dry season of over 3 to 7 months, owing to their ability to fix sufficient carbon within a short photosynthetically active period (van Ommen Kloeke et al. 2012; Lu et al. 2017). Therefore, we assumed that relative composition, the directional shift in abundance and different distribution pattern of tropical tree species differing in leaf types (deciduous and evergreen) strongly controlled by precipitation and water deficit (aridity index) associated with the length of the dry season. Further, the limited water availability (lower rainfall) and increased water deficit (lower aridity index)

represent strong habitat filters. Such demanding and stressful environment conditions are known to filter closely related lineages to colonize the habitat from regional species pool (Fine and Kembel 2011). Secondly, the niche differentiation processes such as competition may avoid closely related lineages to cooccur in stress free habitat with sufficient availability of resources (Kraft et al. 2008). Though, the environmental variables related to temperature gradient also play a fundamental role in shaping taxonomic turnover within tropical forests of Western Ghats (Ramesh et al. 2010a, 2010b). In our study, the temperature related variables were less important compared to precipitation associated variables.

Further, our results suggested that environmental variables interacted in complex ways to drive the taxonomic turnover and phylogenetic structure of tropical tree species differing in leaf phenology (evergreen and deciduous) (Tables 1 to 2 and Fig. 2). Previous studies have shown that multiple simultaneously occurring environmental variables can synergistically interact (Stephenson 1990; O'Brien 2006). In the present study, the interaction between precipitation related variables was much stronger than any other combinations of climatic variables in explaining the richness, relative dominance and phylogenetic structure of evergreen and deciduous tropical tree species (Additional file 1: Tables S5 to S6 and Figure S2). Specifically, the precipitation related variables such as Bio12, Bio13, Bio15, Bio16, and Bio19 interacted to become the most important determinants of taxonomic turnover and phylogenetic structure of tree communities in the tropical forest of Western Ghats, India.

Furthermore, the present study revealed that historical human disturbance significantly influenced the taxonomic turnover (species richness, relative composition, and proportion abundance) and phylogenetic structure of tropical tree species differing in leaf phenology (evergreen and deciduous) in the region. The studies from other tropical areas also confirms that, historical factors such as human disturbance strongly influence the taxonomic turnover and phylogenetic structure of plant assemblages (Verdú and Pausas 2007; Knapp et al. 2008; Norden et al. 2009; Helmus et al. 2010; Letcher 2010; Ding et al. 2012; González-Caro et al. 2014). Increased anthropogenic disturbance favor deciduous tree species over evergreen species irrespective of the influence of climatic variables, due to competitive ability of deciduous species over evergreen species in disturbed habitats. In our study sites, we observed that the deciduous species usually dominated over evergreen species in disturbed forests in high rainfall areas, but not vice versa. Moreover, this result is consistent with previous research and the expectation that disturbance filters out all but a few lineages that can tolerate disturbed conditions (Verdú and Pausas 2007; Knapp et al. 2008; Norden

et al. 2009; Helmus et al. 2010; Letcher 2010; Ding et al. 2012; González-Caro et al. 2014). Overall these results highlight the crucial role of environmental and historical factors in shaping taxonomic turnover and phylogenetic structure of plant assemblages in tropical forest habitats.

Finally, our findings suggested that either environmental gradient or geographic distance was not able to explain the between plot turnover of phylogenetic structure. Instead, we observed the random pattern of phylogenetic turnover (betaNRI and betaNTI) with both spatial and environmental distances (Additional file 1: Table S11 and Figure S6). This pattern may emerge due to the mix of lineages among plots due to historical human-induced disturbance. In our study region, many plots have experienced the high level of human disturbance (logging) and forest degradation leading to mixing of lineages from different habitats (wet and dry).

The phylogenetic structure and functional traits associated niche based processes in community assembly

Our study revealed significantly different and non-random patterns of phylogenetic structure (alphaNRI) among the three forest types (wet evergreen (WE), moist deciduous (MD) and dry deciduous (DD)) distributed across precipitation and dryness gradient (Table 3 and Fig. 3). The observed pattern among different forest types may have emerged due to strong abiotic filtering mechanism. With the limited water availability and prolonged period of dryness in dry and moist deciduous forests poses substantial hydraulic challenges for tree species and are expected to filter out many lineages not adapted to such stressful habitat types with limited water availability enabling the species that can tolerate the abiotic limitation to colonize and radiate. In other tropical forest ecosystems, abiotic filtering due to harsh environmental conditions has been shown to produce phylogenetic clustering (Kembel and Hubbell 2006; Fine and Kembel 2011; González-Caro et al. 2014). For example, in broad-leaved subtropical forests in China (González-Caro et al. 2014) and Western Amazonian tropical forest (Kembel and Hubbell 2006), tree communities in stressful habitats such as dry deciduous forest and white sand forest showed phylogenetic clustering. Similarly, in Barro Colorado Island, Panama, the dry plateaus act as environmental filters and select for species with drought-tolerant traits due to the low soil moisture during the dry season in these environments (Kembel and Hubbell 2006).

Furthermore, the habitat specialization and environmental filtering can also lead to phylogenetic clustering when traits that provide an advantage in a given environment are phylogenetically conserved. For example, the significant phylogenetic clustering of individuals in dry deciduous forests could result from environmental filtering of lineages that possess traits that lead to dominance

in deciduous habitats such as desiccation tolerant seeds, leaf with shortest life span, heavier wood or other specialized adaptations to counter the extreme dryness and limited water availability (Kembel and Hubbell 2006; Cornwell and Ackerly 2010; Lohbeck 2015). In our study, dry deciduous forests were dominated by individuals with shortly lived leaves (deciduous leaf) and individuals were phylogenetically clustered (Additional file 1: Figure S4). Alternatively, if traits that promote habitat specialization evolve convergently or independently, one would expect environmental filtering to cause phylogenetic evenness. For example, dry forest communities exhibited significantly nonrandom patterns of phylogenetic evenness toward the tips (NTI, Fig. 3). The traits that may provide an advantage in deciduous forests, which may also be phylogenetically convergent, and could interact with environmental filtering to produce these patterns (Fine and Kembel 2011). The mapping of short-lived (deciduous) and long-lived (evergreen) leaf types on dated phylogenetic tree of tree species in the Western Ghats suggest that, short-lived and long-lived leaves have independently evolved (Fig. 5). Thus, convergent evolution of leaf traits may be interacting with environmental filtering to produce phylogenetic evenness towards the tips in dry deciduous forest tree communities (Fig. 3).

We hypothesized that tree communities distributed among contrasting habitat types (WE, MD and DD) show non-random pattern of the significant shift in community level functional trait metrics sensitive to niche based processes such as habitat filtering (RANGE and VAR) and competition (SDNDR and Kurtosis). As expected the functional traits such as leaf size, wood density, and seed size showed the significant difference in these functional trait metrics between tree communities of wet evergreen, moist deciduous and dry deciduous forest (Table 3 and Fig. 4). Specifically, the RANGE and VAR of leaf size and wood density were reduced and negative for tree communities in a dry deciduous forest, whereas tree communities of wet evergreen and moist deciduous forest had significantly higher and positive values for the metrics. This indicated that dry and wet forest species face different filters for different traits. Similarly, RANGE and VAR of seed size showed opposite pattern. However, none of the functional traits showed the significant pattern for metrics (SDNDR and kurtosis) sensitive to niche differentiation processes such as competition. These findings are consistent with the prediction that environmental filtering is the fundamental driver of tree community assembly in wet and dry tropical forest habitat in the Western Ghats.

Associations of different functional trait strategies between different habitat conditions (wet and dry) may be influenced by evolutionary history, where the presence

of particular clades with contrasting characteristics could confound their ecological interpretation (Ackerly and Reich 1999). Our phylogenetic analyses showed that most of the traits which showed the shift in traits metrics also showed significant phylogenetic signal (Additional file 1: Table S13), indicating the conservative evolution of leaf, wood, and reproductive traits influence the assembly of tree communities among wet and dry tropical forest. Moreover, the congruent pattern of functional trait metrics and phylogenetic structure between wet and dry habitat tree communities further support the above argument.

The leaf, wood, and seed related functional traits are linked to the fundamental ecological strategies of species in wet and dry habitat (Cornwell and Ackerly 2010; Lohbeck et al. 2015) and directly influence species interactions and assembly across wet and dry environmental gradient (Cornwell and Ackerly 2010; Lohbeck et al. 2015). For example; species with high wood densities are abundant in dry sites while those with low wood densities are abundant at wet sites. This contrasting pattern is not surprising given the role of wood density in hydraulic strategies. Higher wood density is associated with higher hydraulic safety but reduced conductive efficiency (Hacke et al. 2001; Pratt et al. 2007). This physiological trade-off explains why species with higher wood densities those capable of tolerating lower water potentials are found in dry sites (Preston et al. 2006). This pattern must be driven by community assembly processes such as habitat filtering which selects species with very dense wood at dry sites and the very lighter wood at wet sites (Cornwell and Ackerly 2009).

Evolutionary history of long (evergreen) and short (deciduous) lived leaf types in tropical plant species

The ancestral reconstruction of leaf types of evergreen (long-lived) and deciduous (short-lived) on dated phylogenetic tree of the 339 tropical tree species from the Western Ghats showed multiple origins of deciduous leaf type in distantly related lineages suggesting the origin of deciduous or short-lived leaf type in angiosperms appears to be a result of convergent evolution (Fig. 5). It was further supported by low or weak phylogenetic signal in leaf phenological traits (evergreen and deciduous) (Additional file 1: Table S13). However, within lineages (family) deciduous leaf habitat is conserved. Earlier studies also suggest similar trend at the family level (Lavin et al. 2003, 2004; Lavin 2006; Pennington et al. 2009). Our result also suggests that deciduous habit in tropical tree species evolved early in the angiosperm evolutionary history and there is no significant difference in age between deciduous and evergreen tree species (Fig. 5). Moreover, the high number of deciduous lineages with young age (0 to 20 Ma) suggest that plant clades with

adaptations to dry forest habitats are the result of recent evolutionary radiations. Pennington et al. (2009) also suggested the similar pattern for neotropical plant clades adapted to dry forest habitat. Fossil and climate data indicate that both tropical evergreen and dry deciduous forest are old biomes and evolved around late Eocene to early Miocene around 54 to 33 Mya (Pennington et al. 2009) and in agreement with the age estimates based on the phylogenetic tree of the present study. Overall these results suggest that both evergreen and deciduous species in the Western Ghats are geologically old lineages and both types of the leaf have evolved early in the evolutionary history of angiosperms. However, the deciduous habit may have evolved convergently among tree species in the Western Ghats.

Conclusions

There is a distinct compositional and evolutionary imprint in tropical tree communities distributed across the broad-scale environmental gradient in the Western Ghats, and environmental variables and historical human disturbance mainly influence this imprint. These imprints can be detected through the integration of functional trait data and phylogenetic relationship of co-occurring species. The distinct phylogenetic structure and different trait strategies among tree communities of wet and dry forests suggest that niche-based processes such as habitat filtering plays a predominant role in the assembly and structuring tropical tree communities. The present study highlights that, in addition to environmental variables, historical factors such as human-mediated disturbance may also influence assembly of communities and contribute to structuring and composition patterns of tropical forests.

Additional file

Additional file 1: Forest Ecosystems. (DOC 6721 kb)

Abbreviations

AIC: Akaike information criterion; AICc: Corrected Akaike information criterion; BIO: Bioclim; DBH: Diameter at breast height (outside bark at 1.3 m above ground); GAI: Global aridity index; GLM: Generalized linear modelling; KFD: Karnataka Forest Department; NRI: Net related index; NTI: Nearest taxon index; RDA: Redundancy analysis; SDNN: Standard deviation of nearest neighbor; VIF: Variance inflation factor

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Availability of data and materials

After acceptance data will be made publicly available as an additional file.

Authors' contributions

Conceived and designed the experiments: KNS, SD and BRR. Analyzed the data: KNS. Contributed analysis tools: SD. Wrote the paper: KNS, RUS, SD, BRR. Performed the experiments, fieldwork BRR. All authors read and approved the final manuscript.

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Ethics approval and consent to participate

Not applicable

Competing interests

The authors declare that they have no competing interests.

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