

# The flooded habitat adaptation, niche differentiation, and evolution of Myristicaceae trees in the Western Ghats biodiversity hotspot in India

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## Abstract

Environmental heterogeneity is considered as one of the main drivers of habitat specialization and niche evolution among tropical plant lineages, and local-scale habitat specialization promotes niche differentiation among sister taxa. In this study, we examined the degree to which habitat specialization leads to niche differentiation across the distribution range of a given species using five species of the family Myristicaceae native to Western Ghats, India, as an example. In the Western Ghats, Myristicaceae species occur in two main habitat types, namely, freshwater swamps (flooded habitat) and terra firme forest (non-flooded habitat), distributed across a seasonal flooding gradient. First, we reconstructed the evolutionary history of flooded habitat specialization among global and Western Ghats Myristicaceae by mapping flooded habitat association and traits conferring flood tolerance (e.g., aerial roots) on a dated phylogeny. Then, we investigated climatic niche differences among lineages occupying flooded and terra firme habitats using occurrence data and environmental variables. Our analysis revealed swampy habitat occurrence as the probable ancestral state with subsequent speciation events leading to adaptation to non-swampy habitats. We also show that traits conferring flood tolerance have evolved independently several times during the evolution of Myristicaceae. Furthermore, phylogenetically distantly related Myristicaceae taxa occupying different habitats (flooded and terra firme habitat) in Western Ghats show significant niche divergence. Overall, the repeated gain of swampy habitat specialization and associated morphological traits and evidence for habitat-associated climatic niche divergence among Myristicaceae taxa suggest that seasonal flooding may have been an important driver of ecological diversification in this primitive plant family.

## KEYWORDS

adventitious roots, comparative phylogenetics, flooded habitat, habitat association, habitat specialist, niche evolution

## 1 | INTRODUCTION

The environmental heterogeneity at small spatial scales may act as a local habitat filter and restrict the co-occurrence of subsets of species under given abiotic conditions. Such niche differentiation at small spatial scales due to local habitat heterogeneity could lead to habitat specialization giving rise to regional distributional patterns of species diversity (Baraloto et al., 2007; Chase & Leibold, 2003; Kneitel & Chase, 2004; MacArthur & Levins, 1964). Plants often exhibit habitat specialization as evident in strong association of species turnover and abundance with abiotic conditions including altitude, soil type, rainfall gradient, and seasonal flooding (Baraloto et al., 2007; Clark et al., 1998; Fine et al., 2005; Gentry, 1986, 1988; Potts et al., 2002; Pyke et al., 2001; Ruokolainen et al., 1997; Svenning, 2001; Tuomisto et al., 1995; Webb & Peart, 2000). However, the hypothesis of local environmental heterogeneity leading to habitat specialization and thereby ecological speciation in tropical plants has not been rigorously tested. The niche specialization at local scale can also influence niche specialization across the distributional range of the species, and as a result, local habitat specialization is associated with range-wide climatic niche evolution. Only a few studies have tested this premise (Emery et al., 2012). Inferring evolutionary history of traits explicitly in a phylogenetic framework will provide insights into adaptive evolution and niche assembly (Ackerly, 2003; Webb et al., 2002). Thus, studies integrating analysis of data on climate, habitat association, and key morphological traits conferring specialization to a given habitat are needed to rigorously test the above hypotheses. Such analyses are crucial for inferring association between local habitat specialization and range-wide niche evolution among sister lineages (Emery et al., 2012; Fine et al., 2005) and gaining insights into the role of ecological selection on speciation and the evolutionary basis of habitat specialization (Ricklefs & Schluter, 1993).

Although earlier studies have addressed the evolutionary basis of edaphic habitat specialization of tropical trees (Fine et al., 2005; Harms et al., 2001; Palmiotto et al., 2004; Potts et al., 2002; Russo et al., 2005), little is known about the evolution of forest trees subject to seasonal variation in edaphic conditions. The seasonal flooding during heavy rains creates heterogeneous landscape of seasonally flooded and non-flooded highland habitats, generally referred to as “freshwater swamps” and “terra firme,” respectively, in lowland tropical rain forests. Relatively little attention has been paid to understand how habitats with differences in seasonal flooding and associated physiological stress promote habitat specialization of tree species and limit their distribution at both small- and large-spatial scales (Lopez & Kursar, 2003; Parolin et al., 2004; Prance, 1979).

In the forests of Western Ghats in India, seven recognized species of the pantropical plant family Myristicaceae dominate heterogeneous landscape comprising low lying seasonally flooded and higher ground and non-flooded, terra firme habitats (Banik et al., 2017;

Chetana & Ganesh, 2013; Govind & Dan, 2020; Govind et al., 2020). Interestingly, congeneric and conspecific pairs of Myristicaceae members occurring in these divergent habitats show unique morphological and physiological adaptation to respective habitats and show contrasting patterns of distribution across their geographic range. We therefore chose this plant group in the Western Ghats to investigate the evolution of flooded habitat specialization and its role in ecological speciation and range-wide niche evolution. We first investigated the degree to which each of the five chosen Myristicaceae species could be classified as flooded (swamp) and non-flooded (terra firme) habitat specialists by surveying lowland tropical forests in 42 locations (Figure S1) across the Western Ghats, India. Second, we reconstructed a dated molecular phylogeny of global Myristicaceae species and mapped flooded and non-flooded (terra firme) habitat association and traits such as aerial roots that confer flood tolerance on to the phylogenetic tree to evaluate the role of local environmental heterogeneity (flooding gradient) in ecological speciation of this group. If flooding gradient is not a driver of ecological diversification in Myristicaceae, we expect phylogenetic clustering of flooded habitat specialization, that is, flooded habitat specialization has evolved among phylogenetically closely related taxa. This evidence supports the idea that evolution of flooded habitat specialization is limited by strong phylogenetic constraints and lineages are exhibiting phylogenetic niche conservatism. Alternatively, if we find that swampy habitat specialization is not clustered, or it is randomly distributed on phylogeny, that is, flooded habitat specialization has evolved among phylogenetically distantly related taxa, this evidence supports the idea that swampy habitat specialization has evolved repeatedly and independently. This would be consistent with the idea that local environmental heterogeneity (flooding gradient) plays a key role in ecological speciation in this group (Emery et al., 2012). Finally, we performed comparative niche evolution analysis (McCormack et al., 2010; Wooten et al., 2013) among Myristicaceae in the Western Ghats to test the hypothesis that local habitat specialization is associated with range-wide climatic niche evolution. Myristicaceae members distributed across flooding gradient (i.e., flooded and non-flooded (terra firme) habitat) in Western Ghats shown to occupy different climatic niche across their distribution range (Priti et al., 2016) and also differ in functional traits conferring adaptation to flooded habitat. Thus, we specifically tested the prediction that sister lineages of Myristicaceae occupying different habitats of flooded and terra firme have significantly diverged in their range-wide climatic niche and the niche divergence is not constrained by their phylogeny. We did this in two ways. 1) Given that, recently diverged sister lineages of these species are parapatrically distributed, we tested for niche overlap against a null distribution of background environmental differences between all parapatric pairs with direct species–species comparisons following McCormack et al., 2010 and 2) We compared niche overlap to phylogenetic distance between species to test niche comparison in phylogenetic context and tested for niche conservatism and divergence among these study species.

## 2 | METHODS

### 2.1 | Habitat association test, and trait data

We surveyed 42 locations (Figure S1) spanning 8° N to 15° N latitudinal gradient in lowland tropical rain forest of Western Ghats to examine flooded and non-flooded habitat specificity of five selected Myristicaceae species (Table S1). See Appendix S1: supplemental methods section in Supporting Information for study organism details. The rainfall in the study region ranges from 1200 to 4000 mm and temperature ranges from 20°C to 24°C. The elevation of the study region ranges from 20 to 650 m. Based on the depth of water availability in wet and dry seasons, the study sites were divided into two types of habitats: seasonally flooded (swamp) forest and terra firme (non-swamp) forest. We laid 42 and 29 plots of 0.1 ha respectively in seasonally flooded and terra firme forest habitats and recorded all trees of >10 cm diameter at breast height (dbh) and seedlings of the Myristicaceae members. To test for associations between trees and seedlings in flooded vs. non-flooded forest habitats, we used a modified version of the torus translation method (Baraloto et al., 2007; Harms et al., 2001). This method accounts for spatial aggregation by permuting rotations of habitat coordinates relative to those of trees. We also calculated absolute density and density ratios as the relative density of stems in seasonally flooded vs. terra firme forest.

We collected data on the presence of adventitious or aerial roots (roots above the ground or above the anoxic zone or above the level of the water) of Myristicaceae species at global and local (Western Ghats) scales from descriptions in literature (Nair et al., 2007; Rao et al., 2014) and our own field survey. The aerial roots such as stilt root, knee root, and floating water roots confer flood tolerance and thereby are regarded as adaptation of plants to flood-prone environment (Kozłowski, 1984; Parolin, 2012). In total, we collected habitat and aerial root data for 455 Myristicaceae species, covering 55.4% of species in the family (Table S2). Of which, 119 species were associated with swampy or riparian habitats, and 78 species had aerial roots (stilt roots and knee roots). The Asian endemic genera such as *Gymnacranthera*, *Myristica*, *Horsfieldia*, and *Knema* had higher number of species with swampy habitat association and presence of aerial roots compared to other genera in the family (Table S2).

### 2.2 | Comparative phylogenetic analysis

We reconstructed dated phylogenetic tree of Myristicaceae that included five species from Western Ghats, India and 71 species from other regions using DNA sequences of 10 genes retrieved from GenBank, which included both nuclear and chloroplast genomes (Table S2–S4). In addition, we sequenced two chloroplast genes (*matK* and *psbA-trnH*) for 19 individuals of five Myristicaceae species in the Western Ghats (Table S1) and submitted them to GenBank (Table S4). We inferred phylogenetic relationships of species using maximum likelihood (ML) (Zwickl, 2006) and Bayesian inference (BI) (Ronquist et al., 2012) methods. All phylogenetic

analyses were performed using the CIPRES Science Gateway v.3.3 (Miller et al., 2012) (<http://www.phylo.org>). The dated phylogenetic tree was reconstructed using Bayesian method (Sanderson, 2002) as implemented in the program BEAST v.1.8.2 (Drummond & Rambaut, 2007). Our phylogeny represented 11% of known species diversity of Myristicaceae, and of which 13 species used in our phylogenetic analyses represented swampy habitat association and aerial roots as compared to 119 and 78 species with swampy habitat association and aerial roots respectively in our database (Table S2). Thus, underrepresentation of species with swampy habitat association and aerial roots data in our global species-level phylogeny can strongly influence comparative phylogenetic analysis results of swampy habitat specialization among Myristicaceae species at the global scale. Therefore, we focused our comparative phylogenetic analysis at the genus level to understand the evolution of swampy habitat specialization within Myristicaceae family. We used pruned species-level phylogenetic trees to investigate the evolution of swampy habitat specialization among Western Ghats Myristicaceae taxa.

To determine the influence of phylogenetic constraint on evolution of flooded habitat specialization and associated morphological traits in global and Western Ghats Myristicaceae members, we tested for phylogenetic signal in habitat affinity and aerial roots using two alternative methods that included D statistic (phylogenetic dispersion) (Fritz & Purvis, 2010) and Pagel's lambda ( $\lambda$ ) (Pagel, 1999) as implemented in the R package Caper (Orne et al., 2013) and Phytools (Revell, 2012). Then, to determine the evolution of swampy habitat specialization and aerial roots among global and Western Ghats Myristicaceae members, we mapped flooded (swampy) and non-flooded (non-swampy/terra firme) habitat affinity and presence or absence of different types of aerial roots (stilt root and knee root) on dated phylogenetic tree using four different types of ancestral state reconstruction methods: maximum parsimony in Mesquite v. 2.75 (Maddison & Maddison, 2011), maximum likelihood (ML) and Bayesian Markov Chain Monte Carlo (MCMC) in BayesTraits v. 2.0 (Pagel & Meade, 2006) and stochastic character mapping (SIMMAP; Bollback, 2006) using the package "phytools" (Revell, 2012) implemented in R (R Core Development Team, 2013). We assumed transition rates to be variable for all analyses. MCMC analyses were run for  $2 \times 10^6$  iterations with the first  $1 \times 10^5$  iterations discarded as a burn-in, and a reversible-jump hyperprior with exponential distribution (Pagel & Meade, 2006). For SIMMAP analyses, we ran 10000 simulations. See Appendix S1: supplemental methods section in Supporting Information for further details on Phylogenetic tree reconstruction and comparative phylogenetic methods.

### 2.3 | Niche conservatism and divergence analysis

To test the prediction that sister lineages of Myristicaceae occupying different habitats (flooded (swampy) and non-flooded (non-swampy/terra firme) across seasonal flooding gradient in Western Ghats have significantly diverged in their range-wide climatic niche and the niche divergence is not constrained by their phylogenetic relationship,

we first built ecological niche models (ENMs) for five species of Myristicaceae based on occurrence records and 20 environmental variables (Table S5) using the program Maxent version 3.2 (Phillips et al., 2006). Second, we used ENMTools (Warren et al., 2021) to test for niche overlap among all pairwise combinations of Myristicaceae species in the Western Ghats using two test statistics, namely, Schoener's D (Schoener, 1968) and the I statistic (Warren et al., 2008). Then, we used Mantel test to evaluate the null hypothesis that the niche overlap (measured using Schoener's D and I statistic) between two species is not related to their phylogenetic distance. We also fitted separate multiple regressions on distance matrices (MRM; Lichstein, 2007) between phylogenetic distance and niche overlap matrices (obtained using Schoener's D and I statistic) to understand the effect of phylogenetic distance over niche overlap. MRM analysis was conducted with 10,000 permutations in the R package ecodist (Goslee & Urban, 2015). Finally, we used two approaches to test for niche conservatism and divergence among five Myristicaceae species in Western Ghats, first through ENMtools (Warren et al., 2021) and second through multivariate methods (McCormack et al., 2010). Both methods use data from species occurrence points and background points. See Appendix S1: supplemental methods section in Supporting Information for further details on these methods.

### 3 | RESULTS

#### 3.1 | Habitat preferences of Myristicaceae among seasonally flooded (swampy) and terra firme (non-swampy) habitat

We found strong evidence for contrasting association with seasonally flooded forest and/or terra firme (non-flooded) forest in both congeneric (*Gymnacranthera*, *Knema*, and *Myristica*) and

conspecific (*M. fatua*, *M. malabarica*, and *M. beddomei*) pairs of Myristicaceae in the Western Ghats (Table 1, Table S6). Modified version of torus translation test for habitat association indicated significant positive association for *G. canarica* and *M. fatua* and significant negative association for *K. attenuata*, *M. beddomei*, and *M. malabarica* with seasonally flooded habitat. The strength of association was strong at both adult and seedling stages ( $p < 0.0001$ , Table 1). The two species, *G. canarica* (Adults (median): 1077 (24/plot); Seedlings (median): 1362 (31/plot) and *M. fatua* (Adults (mean): 1152 (43/plot); Seedlings (median): 1885 (52/plot) had higher absolute density (Figure S2a) and density ratios (Figure S2b) for both adults and seedlings compared to community average in seasonally flooded habitat. (Table 1, Table S6). Conversely, the other three species such as *K. attenuata* (Adults (median): 30 (2/plot); Seedlings (median): 9 (1/plot), *M. malabarica* (Adults (median): 13 (1.2/plot); Seedlings (median): 5 (0.55/plot) and *M. beddomei* (Adults (median): 11 (0.95/plot); Seedlings (median): 14 (1.32/plot) had lower absolute density (Figure S1a) and density ratios (Figure S1b) than the community average at both tree and seedling stages (Table 1, Table S6).

#### 3.2 | Ancestral state of habitat affinity and associated morphological traits

The dated phylogenetic trees supported the monophyly of Myristicaceae members within South America, Africa, and Asia (Figure 1). See Appendix S1: supplemental results section in Supporting Information for further details on phylogenetic relationship. The mapping of habitat affinity on genus-level dated phylogenetic tree of global Myristicaceae revealed that flooded habitat affinity originated early in the evolution of Myristicaceae (Figure 2). We found flooded habitat association to be the most

TABLE 1 Habitat association test for trees (>10 cm dbh) and seedlings of five species of Myristicaceae in Western Ghats, India

| Species                        | Stage    | Seasonally flooded forest (swamp)<br>N = 42 |       |                    | Terra firme forest (non-swamp)<br>N = 29 |       |                    |
|--------------------------------|----------|---|-------|--------------------|--|-------|--------------------|
|                                |          | N   | p     | Association        | N  | p     | Association        |
| <i>Gymnacranthera canarica</i> | Adult    | 1077  | 1.000 | (+) <sup>***</sup> | 2  | 0.000 | (-) <sup>***</sup> |
|                                | Seedling | 1362  | 1.000 | (+) <sup>***</sup> | 1  | 0.000 | (-) <sup>***</sup> |
| <i>Knema attenuata</i>         | Adult    | 30  | 0.042 | (-) <sup>*</sup>   | 253                                      | 0.986 | (+) <sup>*</sup>   |
|                                | Seedling | 9   | 0.000 | (-) <sup>***</sup> | 300                                      | 1.000 | (+) <sup>***</sup> |
| <i>Myristica malabarica</i>    | Adult    | 13  | 0.032 | (-) <sup>*</sup>   | 168                                      | 0.991 | (+) <sup>**</sup>  |
|                                | Seedling | 5   | 0.000 | (-) <sup>***</sup> | 258                                      | 1.000 | (+) <sup>***</sup> |
| <i>Myristica beddomei</i>      | Adult    | 11  | 0.002 | (-) <sup>**</sup>  | 126                                      | 0.975 | (+) <sup>*</sup>   |
|                                | Seedling | 14  | 0.012 | (-) <sup>*</sup>   | 187                                      | 0.970 | (+) <sup>*</sup>   |
| <i>Myristica fatua</i>         | Adult    | 1152  | 1.000 | (+) <sup>***</sup> | 0  | 0.000 | (-) <sup>***</sup> |
|                                | Seedling | 1885  | 1.000 | (+) <sup>***</sup> | 0  | 0.000 | (-) <sup>***</sup> |

Note: The table reports the total number of stems censused (N), the proportion of permutations with lower relative density within that category (p), and the corresponding positive (+) or negative (-) association.

\*p, 0.05; \*\*p, 0.01; \*\*\*p, 0.001 (one-tailed); and NS, not significant.

probable ancestral state in the group based on all ancestral state estimates analyzed (probability: flooded habitat = 0.65 to 1, non-swamp = 0 to 0.35; Table 2, Table S7). The pattern was similar for Western Ghats Myristicaceae, except stochastic mapping results suggested equal probability for both swampy and non-swampy habitat association to be the ancestral state (probability: flooded habitat = 0.55 to 1, non-swamp = 0 to 0.45; Figure 3, Table 2). Our analysis also suggested that Asian Myristicaceae members gained swampy habitat specialization more frequently than African and South American clades (Figure 2).

We found opposite pattern for aerial root evolution (Table 2, Figures 2-3). Mainly we found that the absence of aerial roots was the most probable ancestral state, indicating ancestors of Myristicaceae lacked aerial roots and members have evolved aerial roots such as knee root and stilt roots independently both among global (probability: the presence of aerial roots = 0 to 0.3, aerial roots absent = 0.7 to 1.0) and Western Ghats (probability: the presence of aerial roots = 0 to 0.4, aerial roots absent = 0.6 to 1.0) Myristicaceae species (Table 2, Figures 2-3). Further we found

weak phylogenetic signal in both habitat association (Global-D: 0.631,  $p_{\text{random}} = 0.250$ ;  $\lambda: 0.152$ ,  $p = 0.132$ , Western Ghats-D: 0.712,  $p_{\text{random}} = 0.421$ ;  $\lambda: 0.230$ ,  $p = 0.190$ ) and aerial root traits (Global-D: 0.520,  $p_{\text{random}} = 0.312$ ;  $\lambda: 0.090$ ,  $p = 0.230$ , Western Ghats-D: 0.620,  $p_{\text{random}} = 0.271$ ;  $\lambda: 0.121$ ,  $p = 0.200$ ) (Table 3). Ancestral state analysis also suggested that both global and Western Ghats Myristicaceae have evolved swampy habitat specialization and aerial roots repeatedly and independently multiple times and aerial roots have evolved more frequently in lineages associated with flooded (swampy) habitat than in lineages associated with terrestrial or non-flooded (non-swampy) habitats (Figures 2-3, Table 2). The parsimony analysis-based matrix of changes (gains and losses) from one habitat to another (swampy and non-swampy) and aerial root evolution in global and Western Ghats Myristicaceae is given in Table S8. The general trend shows that there is repeated loss of non-flooded habitat association and gain of flooded habitat association (global: 3 to 4 times; Western Ghats: 2 times). Similarly, there is repeated gain of aerial roots (global: 4 to 6 times; Western Ghats: 2 times) (Table S8).

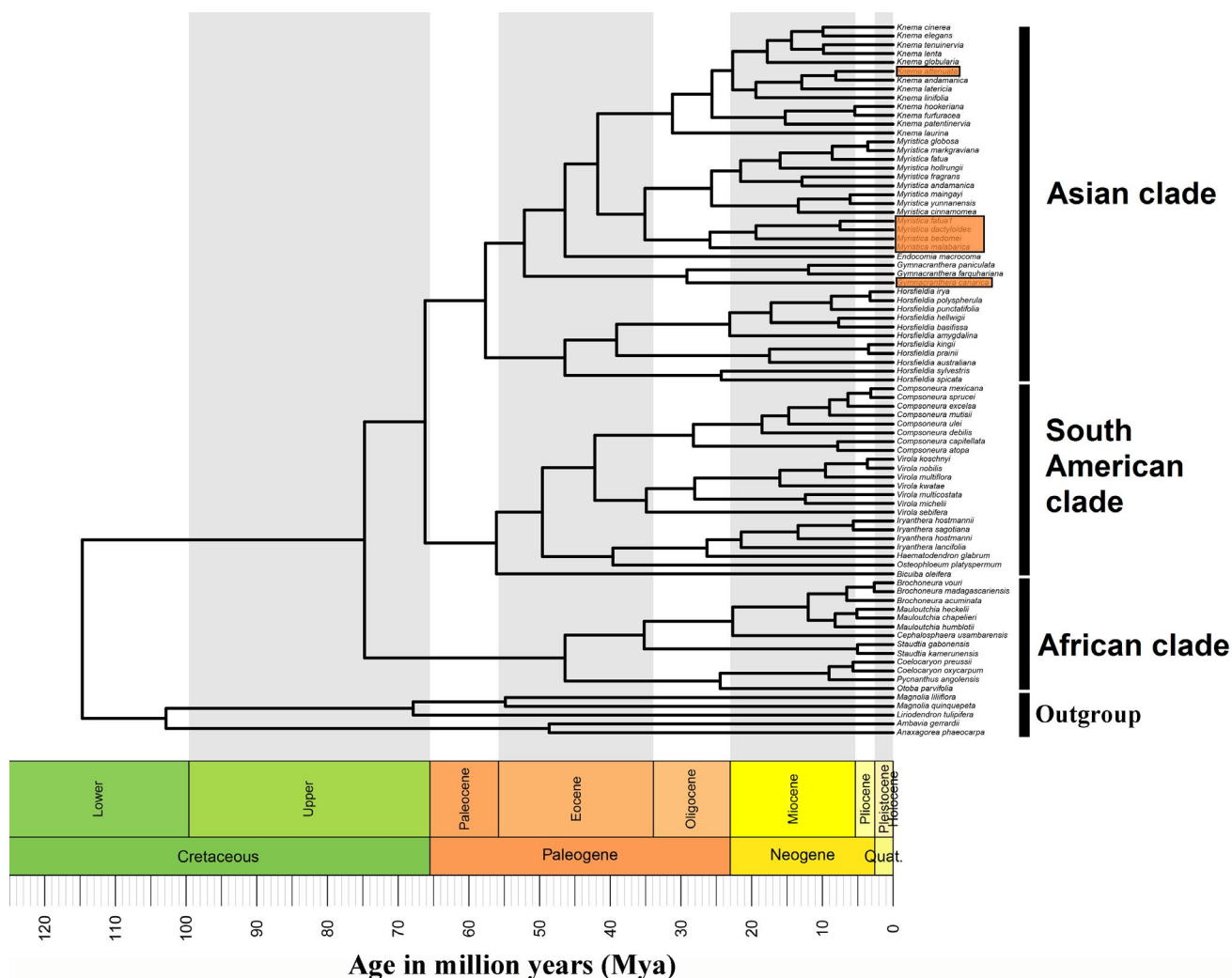


FIGURE 1 Dated phylogenetic tree of Myristicaceae. The Myristicaceae species in the Western Ghats are highlighted in orange color



### 3.3 | The niche overlap and its relationship with genetic distance

The greatest amount of niche overlap was exhibited by the non-swampy Myristicaceae members such as *M. beddomei*, *M. malabarica*, and *K. attenuata*, and the least amount of niche overlap was observed between *M. fatua* and *M. beddomei*. Overall, there was high niche overlap among species occurring in similar habitat, that is, either swampy or non-swampy habitat. Whereas the species pairs occurring in different or contrasting habitats, that is, swampy, and non-swampy exhibited least niche overlap (Table S9).

We rejected our null hypothesis that the genetic distance between two species is unrelated to niche overlap after accounting for their geographic distance. The results of the partial Mantel tests indicated that as genetic distance increases, the amount of niche overlap also increases (Mantel's  $r$ : D:  $r = 0.484$ ,  $p = 0.018$ , I:  $r = 0.812$ ,  $p < 0.001$ ) (Figure S6). MRM results also showed a significant positive relationship between phylogenetic distance and niche overlap (D:  $R^2 = 0.273$ ,  $\beta = 0.340$ ,  $p = 0.0215$ ; I:  $R^2 = 0.720$ ,  $\beta = 0.523$ ,  $p < 0.001$ ) (Figure S6).

### 3.4 | Niche conservatism and divergence among members of Myristicaceae in the Western Ghats

As compared to null models of background divergence, Myristicaceae members occurring in contrasting habitat types (flooded and non-flooded) showed strong support for niche divergence. Analysis using

ENMs showed that five of the ten pairwise comparisons among five lineages of Myristicaceae showed significant evidence for niche divergence with respect to at least one of the null distributions (Figure 4). Similarly, we found evidence for niche conservatism in all ten comparisons (Figure 4). Furthermore, Myristicaceae members in non-swampy habitats, such as *K. attenuata*, *M. malabarica* and *M. beddomei* had significantly divergent niche in comparison to Myristicaceae members in swampy habitats (*G. canarica* and *M. fatua*). The niche among Myristicaceae members occurring in similar habitats, that is, swampy, or non-swampy was highly conserved (Figure 4).

To complement the ENM approach, we also tested for niche divergence and conservatism on independent niche axes using a multivariate analysis of the raw environmental data. The first three PC factors (PC1 to 3) showed evidence for statistically significant niche divergence or conservatism in the majority of comparisons (Table 4). Other PC factors (PC4 to 7) did not show any evidence for niche divergence or conservatism in any of the comparisons. Evidence for niche divergence was detected in only 14 of 70 tests, most of these involved the comparison between swampy and non-swampy species (Table 4). Overall, the evidence for niche divergence was strong when comparisons were made between species occurring in different habitat, that is, one of the compared species occur in swampy habitat and other in non-swampy habitat. Whereas evidence for niche conservatism was strong when comparisons were made between species occurring in similar habitat, that is, compared species either occur in swampy or non-swampy habitat (Table 4).

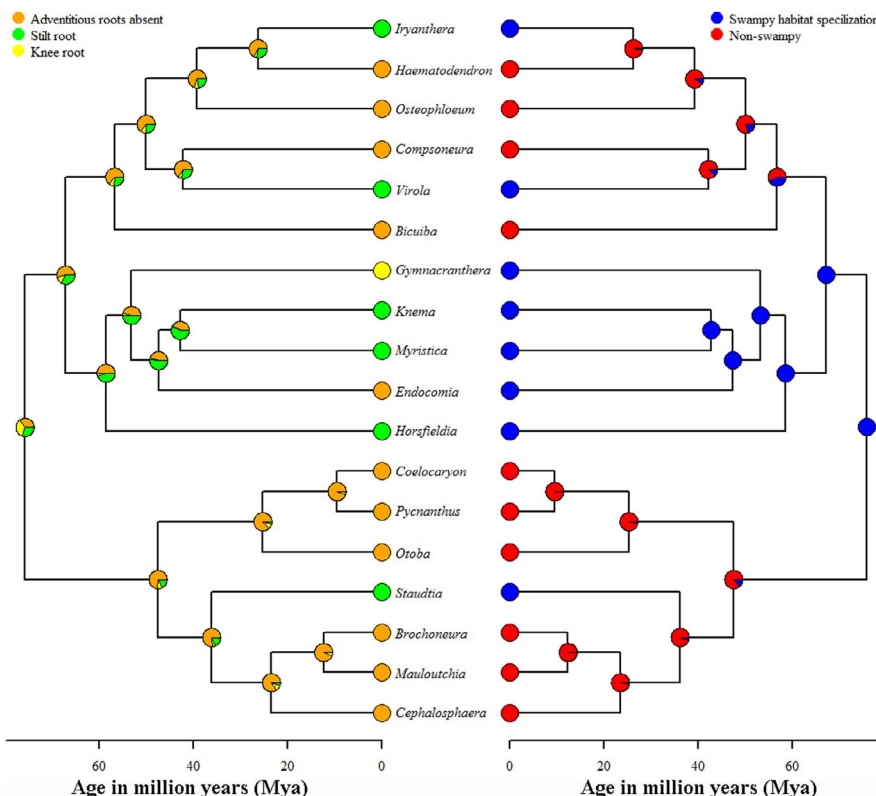


FIGURE 2 Ancestral reconstruction of habitat type and aerial roots in global Myristicaceae based on best likelihood model of stochastic mapping. The circles represent the mean posterior probability distribution of traits calculated from 1000 separate character maps

TABLE 2 Ancestral state estimates for habitat affinity and aerial root of global and Western Ghats Myristicaceae

| Trait            | States     | Parsimony |               | Maximum likelihood |               | MCMC   |               | SIMMAP |               |
|------------------|------------|-----------|---------------|--------------------|---------------|--------|---------------|--------|---------------|
|                  |            | Global    | Western Ghats | Global             | Western Ghats | Global | Western Ghats | Global | Western Ghats |
| Habitat affinity | Swampy     | 1         | 1             | 0.90               | 0.80          | 0.95   | 0.85          | 1.0    | 0.55          |
|                  | Non-swampy | 0         | 0             | 0.10               | 0.20          | 0.05   | 0.15          | 0      | 0.45          |
| Aerial roots     | Present    | 0         | 0             | 0.15               | 0.20          | 0.15   | 0.20          | 0.3    | 0.4           |
|                  | Absent     | 1         | 1             | 0.85               | 0.80          | 0.85   | 0.80          | 0.70   | 0.60          |

## 4 | DISCUSSION

### 4.1 | Habitat preferences for seasonally flooded and terra firme habitats

We found that congeneric and conspecific pairs of Myristicaceae in the Western Ghats show strong positive association with either seasonally flooded or non-flooded (terra firme) forest and the corresponding negative association with the other habitat type, indicating specialized ecological sorting of Myristicaceae in the region. If we interpret the strength of these associations as a correlate of distribution restriction to one habitat or the other, then it appears flooded habitat (swamp) specialists such as *G. canarica* and *M. fatua* are less likely to be found in terra firme forest than vice versa for their congeners (Table 1). This pattern suggests that sensitivity of swampy habitat specialist species to dryer conditions in terra firme habitat during dryer season may be a stronger constraint on distribution than limitations of flooded conditions for species associated with terra firme forest (Parolin, 2001; Parolin et al., 2010). Baraloto et al., 2007 observed similar pattern for Myristicaceae members in Amazonian flood plain forests. Their study showed that congeneric (*Virola* and *Lyranthera*) pair of Myristicaceae from the region strongly associated with either seasonally flooded forest or terra firme forest. A similar trend is reported for congeneric tree species other than Myristicaceae in lowland tropical forest habitat in neotropics and Asia (Baraloto et al., 2007; Russo et al., 2005).

### 4.2 | Evolution of flooded habitat specialization and associated morphological traits in Myristicaceae

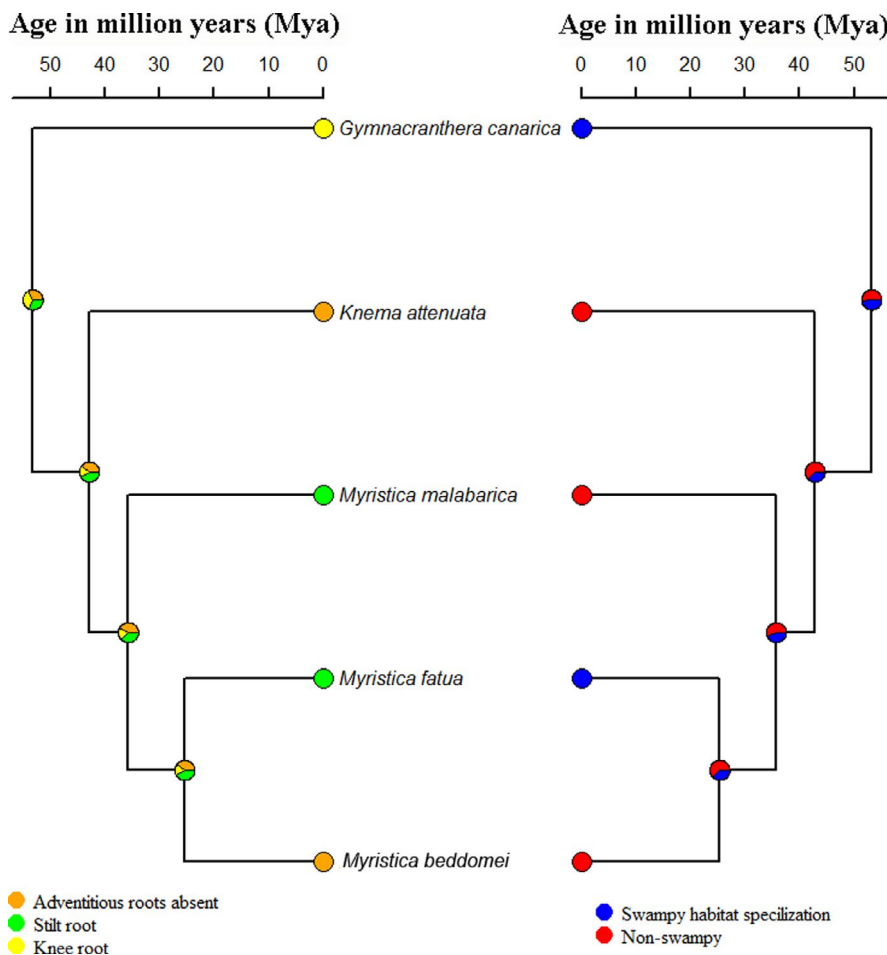
Our results are consistent with the hypothesis that flooded (swampy) habitat association was the ancestral state and evolved independently multiple times among global and Western Ghats Myristicaceae species. The morphological traits such as aerial roots (stilt root and knee root) also showed a similar trend, but the lack of aerial roots was the ancestral state. However, the fact that there are many taxa missing from our phylogenetic tree due to unavailability of DNA sequence data (at least 90% of global Myristicaceae) and therefore the ancestral state mapping of habitat association and aerial root evolution for global Myristicaceae was done using genus-level phylogenetic tree. Although the ancestral states that we have inferred could change with additional data, our results are robust given the available data and reconstruction of character states agree in many ways with deep phylogenetic history of species and traits (Figures 2-3).

If both habitat specialization and aerial roots were conservative traits in the Myristicaceae, one would expect a single shift for each habitat type and aerial root evolution, meaning that specialization towards flooded (swampy) habitat and aerial roots may have evolved only once in the group. If there is strong evidence for evolutionary lability, both flooded habitat specialization and

aerial root evolution would be involved in every single diversification event of Myristicaceae, and the number of changes would be equal to the number of species that are flooded habitat specialists with aerial roots. However, our results do not fit into these expectations despite the lack of phylogenetic signal for both habitat association and aerial roots indicating evidence for evolutionary lability (Table 3). On one hand, there are instances where putative sister taxa share a similar habitat association and either the lack or evolved the aerial roots (Figures 2-3). Contrastingly, our phylogenetic analyses indicate that association with seasonally flooded habitat and associated morphological traits such as aerial roots has evolved independently multiple times (Figures 2-3), consistent with the hypothesis that ecological speciation is driving contrasting habitat divergence. Moreover, the results from our study are likely only a conservative estimate of the amount of ecological speciation that has occurred in the Myristicaceae at the global scale, because adding additional taxa could further increase the number of habitats shifts and gain or loss of aerial roots in the clade. Overall, the data suggest that microhabitat environmental heterogeneity is involved in the diversification process for many species of Myristicaceae both globally and in Western Ghats, especially in the flooded habitat specialists.

Over the past decade, numerous studies have integrated species habitat and associated morphological trait data with species-level

phylogenies to investigate the evolution of habitat specialization in plants (Cavender-Bares et al., 2004; Emery et al., 2012; Fine et al., 2005; Patterson & Givnish, 2004; Pepper & Norwood, 2001; Rajakaruna et al., 2003). Over time, these comparative phylogenetic studies have accumulated evidence for repeated independent evolution of habitat specialization within closely related groups of species and this pattern seems to be common in plants. Recently, Emery et al., 2012 studied the vernal pool (semi-aquatic) and terrestrial habitat evolution in *Lasthenia* (Asteraceae) species and sub-species, an annual plant clade in North America. Their study estimated that *Lasthenia* lineages have undergone up to four independent transitions from strictly terrestrial habitats to a niche that incorporates semiaquatic habitats (vernal pool), and one of these transitions led to the subsequent proliferation of vernal pool species and subspecies, indicating ecological speciation in young and rapidly evolving clade. A phylogenetic study of tree species in coastal-Brazilian white sand forest indicated that closely related lineages prefer contrasting habitat types such as flooded habitat, drained habitat, and humic habitat, further strengthening the hypothesis of ecological speciation (de Oliveira et al., 2014). These examples, together with the results from our study point to an active role for semi-aquatic habitat specialization in the diversification process of closely related lineages in both tropical forest and in temperate region. See Appendix S3: supplemental discussion section in Supporting



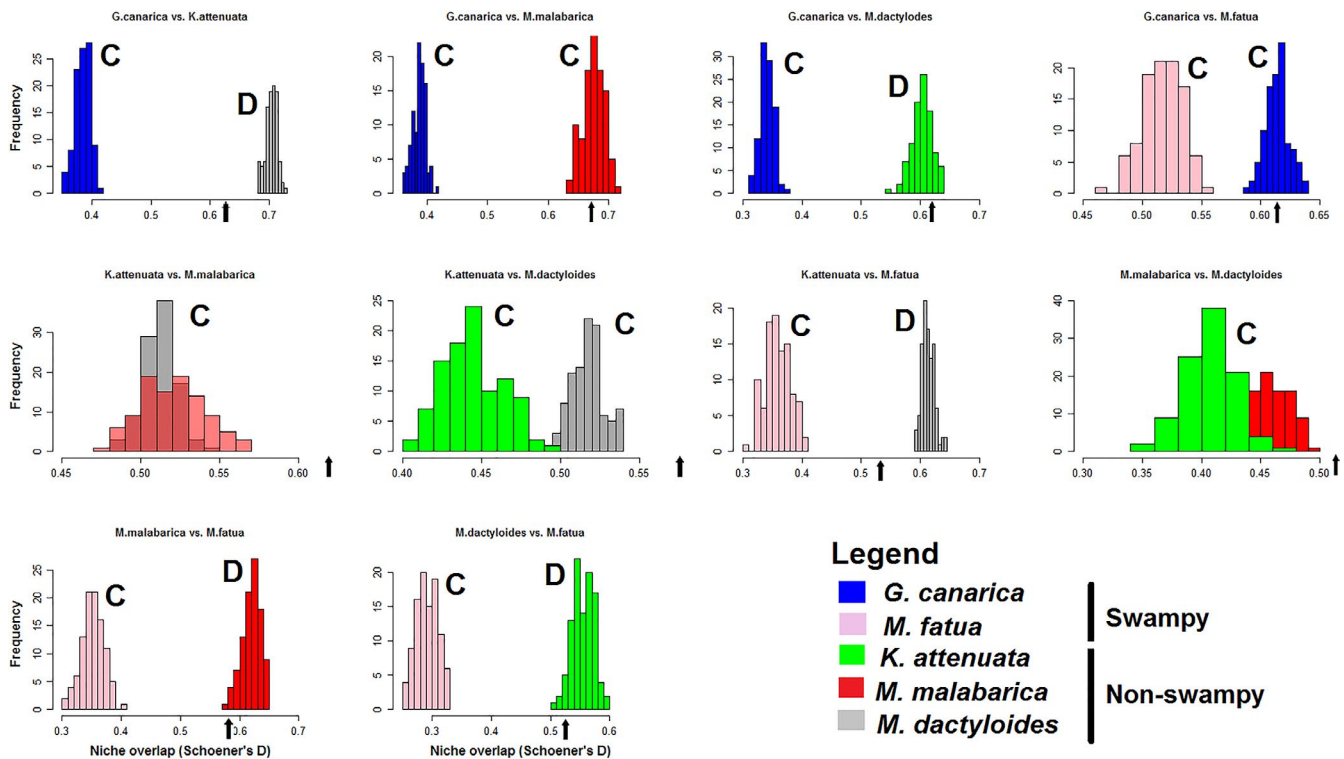
**FIGURE 3** Ancestral reconstruction of habitat type and aerial roots in Western Ghats Myristicaceae based on best likelihood model of stochastic mapping. The circles represent the mean posterior probability distribution of traits calculated from 1000 separate character maps



**TABLE 3** The phylogenetic signal statistics for swampy habitat association, and aerial roots among global and Western Ghats Myristicaceae

| Phylogenetic dispersion D | Global           |              | Western Ghats endemic |              |
|---------------------------|------------------|--------------|-----------------------|--------------|
|                           | Habitat affinity | Aerial roots | Habitat affinity      | Aerial roots |
|                           | Estimated D      | 0.631        | 0.520                 | 0.712        |
| <i>p</i> random model     | <b>0.250</b>     | <b>0.312</b> | <b>0.421</b>          | <b>0.271</b> |
| <i>p</i> Brownian model   | 0.005            | 0.023        | 0.012                 | 0.020        |
| Pagel's $\lambda$         |                  |              |                       |              |
| Lambda                    | 0.152            | 0.090        | 0.230                 | 0.121        |
| <i>p</i> -value           | 0.132            | 0.230        | 0.190                 | 0.200        |

Note: The non-significant *p* values for D statistic are in bold, which means the traits are under random evolution.



**FIGURE 4** Tests of niche divergence and conservatism for Myristicaceae native to Western Ghats. Niche overlap values (arrows) compared to a null distribution of background divergence. Each pairwise comparison produces two reciprocal analyses, one in which the niche model for species A is compared to a niche model generated from random points from the species B's geographic range and vice versa. Overlap values smaller than the null distribution support niche divergence (D), whereas larger values indicate niche conservatism (C) (see Warren et al., 2008)

Information for further discussion of ecological diversification of Myristicaceae in Western Ghats.

### 4.3 | Range-wide niche evolution in Western Ghats Myristicaceae

The greatest amount of niche overlap observed between species pairs inhabiting similar habitats such as either flooded habitat or terra firme habitat. In general, our analysis of genetic distance

versus niche overlap indicated that niche overlap increases with increasing genetic distance, that is, niche differences decrease with genetic divergence (Figure S6). This result agrees with that of Kozak and Wiens (2006), who also found positive relationship between genetic distance and environmental niche in North American salamanders. Our results, in this analysis complement result of weak phylogenetic signal found for habitat specialization and roots traits, suggesting that local habitat specialization and range-wide niche evolution among Myristicaceae lineages is not constrained by phylogenetic relationship of taxa. This pattern,

TABLE 4 Summary of niche divergence (D) and conservatism (C) using mean background differences in principal components (PC) factor scores for climate, edaphic, and hydrologic variables for Myristicaceae members from Western Ghats, India. Bold values indicate significant niche divergence (D) or conservatism (C) compared to null distribution (in parentheses) based on background divergence between their respective geographic ranges. To be divergent, niche values must also differ significantly between the two lineages

| Pairwise comparison                        | PC factor   |  |                                       |                                     |                                     |                                     |  |
|--|---|--|---------------------------------------|-------------------------------------|-------------------------------------|-------------------------------------|--|
|  | 1   | 2  | 3                                     | 4                                   | 5                                   | 6                                   | 7  |
| <i>G. canarica</i> / <i>K. attenuata</i>   | <b>9.67 ± 0.163 D</b><br>(11.16, 8.47)                        | <b>15.87 ± 0.348 C</b><br>(15.56, 15.67)       | <b>6.45 ± 0.644 (6.96, 6.75)</b>      | <b>3.40 ± 0.019</b><br>(3.34, 3.26) | <b>4.33 ± 0.025 (4.40, 4.56)</b>    | <b>3.53 ± 0.041 (3.60, 3.47)</b>    | <b>3.18 ± 0.059</b><br>(3.12, 3.21)            |
| <i>G. canarica</i> / <i>M. malabarica</i>  | <b>9.47 ± 0.041 D</b><br>(11.22, 9.14)                        | <b>15.66 ± 0.130 C</b><br>(15.58, 15.68)       | <b>6.89 ± 0.229</b><br>(6.78, 6.96)   | <b>3.39 ± 0.029</b><br>(3.40, 3.35) | <b>4.25 ± 0.100</b><br>(4.50, 4.40) | <b>3.57 ± 0.072</b><br>(3.50, 3.56) | <b>3.22 ± 0.028</b><br>(3.18, 3.12)            |
| <i>G. canarica</i> / <i>M. beddomei</i>    | <b>9.47 ± 0.037 D</b><br>(11.83, 9.14)                        | <b>16.48 ± 0.949 D</b><br>(15.61, 15.68)       | <b>6.83 ± 0.282 D</b><br>(7.16, 6.76) | <b>3.40 ± 0.018</b><br>(3.35, 3.27) | <b>4.37 ± 0.015</b><br>(4.39, 4.56) | <b>3.56 ± 0.067</b><br>(3.58, 3.47) | <b>3.09 ± 0.156</b><br>(3.10, 3.21)            |
| <i>G. canarica</i> / <i>M. fatua</i>       | <b>9.04 ± 0.463 C</b><br>(8.47, 9.14)                         | <b>15.25 ± 0.274 C</b><br>(15.37, 15.68)       | <b>8.06 ± 0.948 D</b><br>(6.42, 6.75) | <b>3.39 ± 0.021</b><br>(3.23, 3.27) | <b>4.32 ± 0.032</b><br>(4.50, 4.56) | <b>3.52 ± 0.026</b><br>(3.60, 3.46) | <b>3.32 ± 0.070</b><br>(3.04, 3.21)            |
| <i>K. attenuata</i> / <i>M. malabarica</i> | <b>9.63 ± 0.204 C</b><br>(11.23, 11.16)                       | <b>16.01 ± 0.218 D</b><br>(15.58, 15.56)       | <b>6.24 ± 0.416</b><br>(6.78, 6.96)   | <b>3.37 ± 0.010</b><br>(3.40, 3.34) | <b>4.23 ± 0.074</b><br>(4.50, 4.40) | <b>3.61 ± 0.031</b><br>(3.50, 3.56) | <b>3.16 ± 0.031</b><br>(3.18, 3.18)            |
| <i>K. attenuata</i> / <i>M. beddomei</i>   | <b>9.63 ± 0.200 C</b><br>(11.83, 11.16)                       | <b>16.83 ± 0.601 D</b><br>(15.61, 15.56)       | <b>6.19 ± 0.363 C</b><br>(7.16, 6.96) | <b>3.38 ± 0.002</b><br>(3.50, 3.46) | <b>4.34 ± 0.041</b><br>(4.40, 4.40) | <b>3.60 ± 0.026</b><br>(3.60, 3.56) | <b>3.03 ± 0.097</b><br>(3.10, 3.12)            |
| <i>K. attenuata</i> / <i>M. fatua</i>      | <b>9.21 ± 0.626 C</b><br>(8.47, 11.16)                        | <b>15.60 ± 0.623 C</b><br>(15.37, 15.56)       | <b>7.42 ± 1.592 D</b><br>(6.42, 7.0)  | <b>3.38 ± 0.002</b><br>(3.23, 3.34) | <b>4.30 ± 0.006</b><br>(4.50, 4.40) | <b>3.56 ± 0.016</b><br>(3.60, 3.56) | <b>3.26 ± 0.129</b><br>(3.05, 3.12)            |
| <i>M. malabarica</i> / <i>M. beddomei</i>  | <b>9.43 ± 0.003 C</b><br>(11.83, 11.23)                       | <b>16.61 ± 0.819 D</b><br>(15.61, 15.60)       | <b>6.60 ± 0.052 C</b><br>(7.20, 6.78) | <b>3.37 ± 0.012</b><br>(3.35, 3.40) | <b>4.27 ± 0.116</b><br>(4.40, 4.50) | <b>3.63 ± 0.005</b><br>(3.60, 3.50) | <b>3.06 ± 0.128</b><br>(3.10, 3.18)            |
| <i>M. malabarica</i> / <i>M. fatua</i>     | <b>10.33 ± 0.422 D</b><br>(8.47, 11.23)                       | <b>15.69 ± 0.405 C</b><br>(15.38, 15.6)        | <b>6.72 ± 1.177 C</b><br>(6.42, 6.80) | <b>3.38 ± 0.008</b><br>(3.23, 3.40) | <b>4.32 ± 0.068</b><br>(4.50, 4.50) | <b>3.57 ± 0.048</b><br>(3.60, 3.50) | <b>3.19 ± 0.098</b><br>(3.04, 3.18)            |
| <i>M. beddomei</i> / <i>M. fatua</i>       | <b>9.01 ± 0.426 D</b><br>(8.47, 11.83)                        | <b>16.20 ± 1.224 D</b><br>(15.37, 15.61)       | <b>7.78 ± 1.229 D</b><br>(6.42, 7.17) | <b>3.38 ± 0.003</b><br>(3.23, 3.35) | <b>4.34 ± 0.048</b><br>(4.57, 4.40) | <b>3.59 ± 0.041</b><br>(3.60, 3.60) | <b>3.16 ± 0.226</b><br>(3.05, 3.10)            |
| Variance explained (%)                     | 30.079  | 22.260   | 17.038                                | 7.657                               | 5.536                               | 5.271                               | 3.367  |
| Top four variable loadings                 | BIO7, AET, AI, BIO12  | BIO1, BIO5, DEM, PET                           | BIO15, BIO14, BIO12, BIO19            | FD, CTI, Aspect, Slope              | Slope, Aspect, CTI, FD              | Aspect, CTI, Slope, PH              | PH, BIO19, AET, BIO15                          |
| Biological interpretation                  | Precipitation or temperature or aridity or evapotranspiration | Temperature or elevation or evapotranspiration | Precipitation                         | Hydrological variables              | Hydrological variables              | Hydrological variables or soil PH   | Soil PH or precipitation or evapotranspiration |

Note: Niche values differ significantly between lineage pair (t-test: Bonferroni-corrected  $p < 0.05$ ).

See Table S5 for variable descriptions. Parentheses indicate opposite sign. Values in italics reflect variables with particularly high contributions to a given PC axis.

that is, two ecologically similar species that are parapatric across mutually habitable space and phylogenetically divergent, suggests that phylogenetically related species are prevented from invading similar niche by competitive exclusion (Graham et al., 2004; Kozak & Wiens, 2006). Because competitive interactions are likely to be strongest among close relatives (Burns & Strauss, 2011; Darwin & Mayr, 1859; Elton, 1946; Vamوسي et al., 2009) and at the most local spatial scales (Cavender-Bares et al., 2004; Weiher & Keddy, 2001). Our results in this analysis also suggest that niche conservatism is not an important feature of ecological speciation in this group, as this claim supported by evidence of weak phylogenetic signal in habitat association and associated morphological traits such as aerial roots. In other words, these results suggest that divergent evolution of range-wide environmental niche and local habitat niche plays a major role in ecological speciation of Myristicaceae in Western Ghats.

When tested against null models of background environmental differences between their geographic ranges, results from both methods showed strong support for niche divergence among the putative sister taxa of Myristicaceae occurring in contrasting habitat types. However, there was strong support for niche conservatism among taxa occurring in similar habitat such as either seasonally flooded habitat or non-flooded (terra firme) habitat. These results are compatible with a conclusion that niche divergence was likely the major driver for ecological diversification of Myristicaceae among contrasting habitat types (flooded (swampy) habitat and terra firme (non-swampy) habitat) in Western Ghats. Overall, these results suggest that local-scale habitat specialization co-evolve with a range-wide environmental niche. The study by Emery et al., (2012) also suggested similar pattern of co-evolution between range-wide climatic niche and local-scale microhabitat niche evolution among young and rapidly evolving lineages of annual plant *Lasthenia* (Asteraceae) in North America.

## 5 | CONCLUSIONS

Overall, our study represents a first attempt to gain insights into the mechanisms behind the evolution of flooded habitat specialization in lowland tropical rain forest trees by documenting the prevalence of flooded habitat specialization and associated key morphological traits (aerial roots) that confer adaptation to flooded habitat in primitive and ecologically diverse plant family Myristicaceae. Using niche evolution analysis and comparative phylogenetic approaches, our study also provides first-time evidence that range-wide environmental niche divergence and ecological sorting of closely related taxa to divergent habitats promote *in situ* radiation and diversification of tree species across flooding gradient in tropical forest of Western Ghats, India. However, further large-scale analysis of flooded habitat specialization and key morphological traits using complete species-level phylogenetic trees will likely refine our understanding of mechanisms promoting flooded habitat specialization of Myristicaceae.

However, this effort is one of the most large-scale phylogenetic studies to date for Myristicaceae and the only one to specifically focus on seasonally flooded habitats. The seasonally flooded habitat in lowland tropical rainforest of Asia including Western Ghats mainly dominated by Myristicaceae and at least 10–15% of species surveyed exclusively occur in seasonally flooded habitat and has evolved specialized morphological traits (aerial roots) to adapt in flooded condition. This is strong evidence that flooding gradient in the habitat promotes ecological diversification of species in the family. When examining the phylogenetic patterns of flooded habitat specialists and key morphological traits (aerial roots), we found that both flooded habitat associations and aerial roots have repeatedly and independently evolved and that flooding gradient in the habitat might have played a key role in the diversification of many clades within Myristicaceae at the global and local levels. The presence of multiple putative sympatric sister taxa with divergent habitat association with and without seasonal flooding is consistent with the hypothesis of ecological speciation scenario. Further, our niche evolution analysis indicated strong support for range-wide environmental niche divergence among habitat specialists (flooded (swampy) and terra firme (non-flooded)) species of Myristicaceae in Western Ghats, suggesting evidence for co-evolution of local habitat niche with range-wide environmental niche. Future work should focus on the mechanisms of how reproductive isolation may evolve among flooded (swampy) and non-flooded (terra firme or swampy) habitat specialist plants and molecular and physiological mechanisms of flooded habitat specialization in Myristicaceae family.

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## CONFLICTS OF INTEREST

The corresponding author confirms on behalf of all authors that there have been no involvements that might raise the question of bias in the work reported or in the conclusions, implications, or opinions stated.


## AUTHOR CONTRIBUTIONS

N.K.S, S.D, and R.U.S designed the study. K.N.S, J.M.R, and S.V.G. laid plots and collected species abundance data. K.N.S. undertook phylogenetic and other statistical analyses. K.N.S. wrote the paper with input from all authors.

## DATA AVAILABILITY STATEMENT

The DNA sequences of Myristicaceae from Western Ghats, India, are deposited to NCBI. Multiple sequence alignments for individual gene and combined sequence alignment of all genes and input files for ML, MrBayes, and BEAST analysis are available from the Dryad Digital Repository ([https://datadryad.org/stash/share/seOHN CW58N4u2YcP9yv1WujUodXr0B9tgaad9Ztu\\_W0](https://datadryad.org/stash/share/seOHN CW58N4u2YcP9yv1WujUodXr0B9tgaad9Ztu_W0)) along with all phylogenetic trees in nexus format.

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