Community Assembly and Habitat Specialization of Tropical Tree Species along Moisture Gradients in the Western Ghats Biodiversity Hotspot in India

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ABSTRACT

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The interactions between ecological and evolutionary processes mediated through functional traits that confer habitat specialization have been proposed to explain the spatial assembly of plant communities both across space and in different habitats. However, the scale at which these mechanisms operate and their relative importance in dominance and assembly of tree communities in different habitat types distributed across spatially-varying environmental gradients in tropical forests have been rarely tested. Here, I elucidate patterns of functional trait and phylogenetic variation and evolutionary history of key functional traits conferring habitat specialization to understand community assembly mechanisms operating within in tropical tree communities distributed across spatially varying environmental gradients and in different habitat types in Western Ghats biodiversity hotspot, India. The chapter 2 focuses on patterns of functional trait and phylogenetic co-variation among a community of tropical canopy trees distributed across spatially varying moisture gradient. I find that tree communities in plots that experience lower precipitation and longer duration of dry period show clustering of both functional traits and phylogenetic relationship suggesting environmental filtering play a key role in the assembly of tree communities in these forests. The chapter 3 explores the relationship between key functional traits, phylogenetic relationship and abundance of 210 co-occurring tree species distributed across contrasting extremes of seasonal flooding gradient i.e. flooded forest and terra-firme forest (non-flooded). I found that repeated evolution of key functional traits together with strong environmental filtering play a key role in determining the ecological success (dominance) and assembly of tree communities in flooded habitat. The chapter 4 focuses on climatic niche evolution and evolutionary history of flooded habitat specialization in global and endemic Myristicaceae members in the Western Ghats. I found that, repeated gain of swamp habitat specialization and associated morphological traits in global and Western Ghats

Myristicaceae implying seasonal flooding gradient is an important driver of ecological speciation. I also found that local habitat specialization promotes range-wide niche evolution among sister taxa. By elucidating the pattern functional traits and phylogenetic relationship across flooding and spatially varying moisture gradient and analysis of climatic niche evolution and habitat specialization among co-occurring sister taxa, this thesis contributes to our understanding of the determinants of assembly, dominance and diversification of tropical tree communities across diverse habitat types in tropical forest biomes.

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Dedication

They were always there with me in up and downs of my life. They celebrated my success and motivated me when I am failed. They made me strong to stand against all odds. They were always there with me to help. They answered my call whatever the time I call them. They taught me to listen to my heart and perceive my dreams. Wherever I go they were there with me. Without them, my life would not be so exciting. I dedicate this thesis to my family and friends.

Contributions of Authors

This thesis is the result of my own research. I am the primary author of all chapters. I collected major part of the data and analyzed it, as well as wrote the first draft of each chapter. Dr. Dayanandan helped to develop the conceptual framework and critically contributed to revision of each chapter. Chapter 2, 3 and 4 also benefited from the help of additional co-authors, which is explained in more detail below:

Chapter 2:

Authors: K.N. Shivaprakash, B.R. Ramesh, R. Umashaanker & S. Dayanandan

Shivaprakash and Dayanandan conceived the idea for this chapter. Ramesh gathered the data and Shivaprakash analyzed the data. Shivaprakash wrote the first draft of the chapter. Shivaprakash, Dayanandan and Umashaanker contributed to writing and final revisions.

Chapter 3:

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Shivaprakash and Dayanandan conceived the idea for this chapter, and the concept was further improved with inputs from Lessard. Shivaprakash collected the data with the assistance from Jagadish and Gunaga. Umashaanker and Vasudeva helped in study design. Shivaprakash analyzed the data with guidance from Dayanandan and Lessard. Shivaprakash wrote the first draft of the chapter. Shivaprakash, Dayanandan, Lessard and Umashaanker contributed to writing and revisions of the chapter.

Chapter 4:

Authors: K.N. Shivaprakash, G. Ravikanth, R. Vasudeva, R. Umashaanker & S. Dayanandan

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CHAPTER 1

1.0 General Introduction

A detailed understanding of the drivers underlying the distribution patterns of vegetation across various spatial scales and different habitat types within tropical forests is crucial for gaining insights into the evolution of biological diversity as well as formulation of sound programs for conservation and management of biodiversity in the tropics. The community assembly processes such as turnover in species composition, ecological dominance and habitat specialization of a species or clades to specific habitats can influence the composition and assembly of tropical plant communities across different habitat types and spatial scales (Cornwell & Ackerly 2009; Fine & Kembel 2011; Brown *et al*. 2013). These community assembly processes in turn results from the interaction between both ecological and evolutionary processes. Ecological processes such as dispersal, environmental heterogeneity, and interspecific competition can generate distribution patterns of biodiversity both at large and small spatial scales (Condit *et al*. 2002; Fine *et al*. 2004; Gilbert & Lechowicz 2004). The evolutionary processes such as speciation, extinction, historical biogeography of species and long-distance dispersal determine which lineage to inhabit in a region or habitat and influence the composition and assembly of species in communities of different habitat types (Ricklefs 2004; Ter Steege *et al*. 2006; Emerson and Gillespie 2008; Vamosi *et al*. 2009). In addition, the evolution of traits that confer habitat specialization over a long-time frame also play an important role in determining community composition (Chave *et al*. 2007; Hardy & Senterre 2007; Chave 2008).

Our understanding of the processes that determine composition and assembly of species along environmental gradients, especially at small spatial scales is limited due to difficulties involved in quantifying assembly processes at small spatial scales. Tree species show strong spatial association with flood and precipitation or moisture gradients at various spatial scales, sometimes at scales of as small as several meters (Pitman *et al*. 2002; Ter Steege *et al*. 2006; González-Caro *et al*. 2014). Such patterns of habitat association have been traditionally attributed to niche differentiation processes such as environmental filtering and competitive interactions that sort species from a larger pool (Weiher and Keddy 1999, Webb *et al*. 2002). This approach typically focuses on short time scales and assumes that the pool is fixed, ignoring the evolutionary processes such as speciation, extinction and biogeographical history of species. However, the lineages occupying different habitats may have different evolutionary history

(Harrison & Grace 2007) and regional environment itself may have influenced the speciation processes and evolutionary histories of species in different habitats and across environmental gradients (Forest *et al*. 2007). Thus, it is important to account for evolutionary history of a species to understand the importance of different ecological processes [deterministic (habitat filtering and competition) and stochastic (dispersal limitation)] in determining species turnover rate and composition of species in communities along environmental gradients and in different habitat types.

The recent advances in community ecology and phylogenetic analyses techniques provide an unprecedented opportunity to explore the role of different community assembly mechanisms (deterministic and stochastic) in determining species turnover, diversity and composition of species across environmental gradients and in different habitats (Kembel & Hubbel 2006; Fine & Kembel 2011). Furthermore, the integration of ecologically important traits (i.e. traits that confer fitness and adaptation to habitat) with community composition data and phylogenetic data can be used to differentiate between neutral versus niche-based community assembly processes important in shaping dominance and diversity pattern of species across environmental gradients and in different habitats (Kraft *et al*. 2008; Kraft & Ackerly 2010). In addition, ecological niche modelling tools are valuable for determining the role of different niche-based processes such as niche divergence, convergence and conservatism in assembly of species in communities across different habitat types (Warren, *et al*. 2008; McCormack *et al*. 2010). Thus, one can use approaches that integrate community phylogenetics, functional trait analysis and ecological niche modelling to test the importance of different processes (ecological and evolutionary) in driving patterns of turnover, composition and assembly of species in communities across environmental gradients and in different habitats (Kembel & Hubbel 2006; Kraft *et al*. 2008; Kraft & Ackerly 2010; McCormack *et al*. 2010; Fine & Kembel 2011).

1.1 Community assembly and underlying mechanisms

Community assembly is the processes by which species from a regional pool colonize and interact to form a local community (HilleRisLambers *et al*. 2012). Despite extensive debate about the mechanisms underlying community assembly, the processes operating at a diverse range of spatiotemporal scale are thought to be important. For example, environmental drivers generate large-scale biogeographic patterns in diversity (Wiens & Donoghue 2004), whereas competitive interactions occurring in a small neighborhood contribute to coexistence of species in local community (Chesson 2000). The composition and abundance of a species in local community is constrained by evolutionary history of regional species pool (Ricklef 2004), but also influenced on short time scale by demographic stochasticity (Tilman 2004). In short, study of community assembly unites disciplines as diverse as evolutionary biology, biogeography and community ecology (HilleRisLambers *et al*. 2012).

Central to most studies of community assembly is the concept of species pool that is larger in geographic scope than the local community under study. Species pool is defined as the set of all species available to colonize a focal site (Srivastava 1999). Assessing variation in the size and composition of regional species pools and determining their relationship to the composition of local communities is a way to include the potential influence of large-scale processes into analyses of community assembly. Development of null models with meaningful assumption of species pool are useful to understand the role of dispersal, responses to abiotic conditions, and biotic interactions in shaping local assemblages.

1.1.1 A brief history of the development of community assembly concepts

There are two persistent and central concepts in the study of community assembly. The first is the “species pool,” defined as the suite of possible colonists for a local site under study, the second is the metaphor of a “filter” or a “sieve” that represents abiotic or biotic barriers to successful establishment at a local site. These two concepts can be traced back to following distinct sources: the study of species assemblages on oceanic islands and the study of succession following disturbance.

The well known example, which laid foundation to community assembly theory, is MacArthur and Wilson’s seminal theory of island biogeography, which proposed that island species diversity depended on immigration from a mainland species pool (MacArthur & Wilson 1967). In tests of this theory (reviewed by Schoener 2010), it was shown that distance of the island from the mainland is predicted to influence the frequency with which new colonists arrive, and the size of the island influences the rate at which species go extinct on the island. Together these two properties predict the equilibrium number of species that the island will support at any point in time. Biotic interactions between species are implicit in island biogeography theory, as local extinction rates increase with species richness, though the primary focus of the theory is on the dynamics of dispersal to a community from a larger mainland species pool.

Followed by MacArthur and Wilson (1967), the next development in the evolution of community assembly theory was Jared Diamond's study of bird communities on islands near New Guinea (Diamond 1975). Diamond was the first to use the concept of "assembly" in this context. In contrast to island biogeography, Diamond primarily focused on the role of biotic interactions in shaping local communities, and in particular he proposed seven "assembly rules" that captured the competitive exclusion of species that were too ecologically similar to co-occur. Diamond's work suggested that community assembly was guided by non-random processes, such as competition, with certain rules that could be used in predictive modelling, although his work soon became a source of contention amongst community ecologists (e.g Connor & Simberloff 1979; Strong *et al*. 1979; Grant & Abbott 1980). The debate arising from Diamond's assembly rules was heated, with both strong opposition and support. Either the seven assembly rules were criticized as being tautologies, trivialities or patterns that would be expected if species were distributed randomly (Connor & Simberloff 1979). Diamond was criticized for lacking a proper null hypothesis for species differences when testing his assembly rules, as a null hypothesis is needed to permit the falsification of the hypothesis that competition shapes community assembly. If the process of competition is the only mechanism of community assembly that is considered, then there is no opportunity to allow for the role of other processes. Shortly following the publication of Diamond's work, and at least in part in response to it, null models were developed that offer a solution to this issue (Pielou & Routledge 1976; Connor and Simberloff 1979; Strong *et al*. 1979; Colwell & Winkler 1984). However, null models were criticized for several reasons, such as ignoring biological knowledge to determine which species should be incorporated into null hypothesis tests and for placing less importance on Type II errors (Grant & Abbott 1980; Diamond & Gilpin 1982).

The resurgence of interest in community assembly in the past decade, and arrival of a broader perspective, was fostered by two important developments in recent times. First, ecologists began integrating newly available phylogenetic data with community data, introducing an evolutionary perspective to community assembly (Webb 2000; Webb *et al*. 2002, Cavender-Bares *et al*. 2004). Second, Hubbell's unified neutral theory, which is a direct descendant of island biogeography theory, depicts local communities as stochastic samples from a regional pool in which the probability of dispersal to the community is related to the distance and abundance of a species in the pool rather than its identity. The pool is in turn governed by the vagaries of biogeographic history, expressed as random speciation and extinction events. In general, however, neutral theory focuses more on the absence of niche differences than on the detailed understanding of regional influences on local communities. These developments have significantly contributed to emergence of community assembly theory as more statistically rigorous science, using carefully constructed null models for hypothesis testing (Gotelli & Graves 1996).

1.1.2 Mechanisms of community assembly

To explain local community assembly, ecologists have proposed two main mechanisms a) stochastic and b) deterministic. Stochastic mechanisms mainly include "neutral theory" which suggest that stochastic processes such as dispersal limitation, random drift, ecological equivalence, demographic stochasticity, neutral speciation and extinction events mainly determine observed pattern of species assembly and abundance in local communities (Hubbell 2001; Chave 2004). Alternatively, deterministic mechanisms mainly include niche-based processes such as "habitat filtering" and "niche differentiation (competition)" and argue that these niches-based processes play a crucial role in determining the observed pattern of species assembly and abundance in local communities (MacArthur & Levene 1967; Keddy 1992; Silvertown 2004; Shipley *et al*. 2006; Kraft *et al*. 2008). However, in a community both mechanisms can operate simultaneously in assembly of species or each process can operate independently and play a dominant role (Fig. 1-1; Kraft *et al*. 2015). Therefore, in recent times the main goal of community ecology is to differentiate and understand relative importance of different community assembly mechanisms and their processes in determining the observed pattern of species composition and abundance in local and regional communities (Adler *et al*. 2007; Kraft *et al*. 2008; Maire *et al*. 2012). Moreover, each of these mechanisms and their processes have their own merits and limitations in determining composition, abundance and assembly of species in communities, which has been reviewed in recent literature (Clark 2008; Mayfield & Levine 2010; HilleRisLambers *et al*. 2012; Wennekes *et al*. 2012; Kraft *et al*. 2015; Cadotte & Tucker 2017). However, in recent times many ecologists have strived to reconcile the stochastic (neutral) and deterministic (niche-based) mechanisms in a single unified framework, rather considering them as independent and opposing mechanisms (e.g. Gravel *et al*. 2006; 2011;

Leibold & McPeek 2006; Adler *et al*. 2007; Herault 2007; Vellend 2010; Chisholm & Pacala 2010; Haegeman & Etienne 2011). For example, it is realized that both stabilizing (niche-based) forces, where a species limits itself more than it does others, and equalizing (neutral) forces that reduce fitness differences between species play a role in determining species composition and abundance in community (Chesson 2000; Adler *et al*. 2007). Nevertheless, the resistance against each of these mechanisms and processes remains strong and attempts are frequently made to falsify or reject each of these mechanisms, albeit on very different grounds (McGill 2003; Wootton 2005; Etienne & Alonso 2005; Dornelas *et al*. 2006; McGill *et al*. 2006; Etienne 2007; Clark 2008, 2010).

1.1.2.1 Fundamental processes of stochastic or neutral community assembly mechanisms

Ecologists and evolutionary biologists have long debated the role that stochastic processes play in structuring the diversity and composition of species in ecological communities (Gleason 1917; Connor & Simberloff, 1979). Chance variation among individuals in their vital rates can have important consequences for ecological communities. The stochastic variation in species abundance causes communities to randomly drift from deterministic expectations and reduces local species diversity (Chesson 2000; Hubbell 2001). Five fundamental processes underlying stochastic or neutral assembly of species in communities are: ecological drift, dispersal limitation, ecological equivalence, demographic stochasticity, and neutral speciation and extinction.

Ecological drift - random changes in local species relative abundances happens when birth and death events in a community occur at random with respect to species identity (Hubbell 2001). Thus, ecological drift is unambiguously neutrally stochastic and synonym to demographic stochasticity. Hubbell’s development of the neutral theory of biodiversity has significantly contributed to understanding the effects of ecological drift among species with identical vital rates (Hubbell 2001; Gilbert *et al*. 2006), and forms the basis of testing, and frequently rejecting, the hypothesis that communities are structured by demographic stochasticity alone (Gilbert *et al*. 2006; Wootton 2005).

Dispersal limitation – Generally, dispersal is one of the most ambiguous processes concerning inferences about stochastic versus deterministic mechanisms underpinning community assembly (Lowe & McPeek 2014). Dispersal refers to the movement of an individual organism during its lifetime, from its place of birth to the location where it produces offspring. Dispersal can be deterministic when certain species are better dispersers than others and can be stochastic, when it is occurring through passive processes like wind (Nemergut *et al*. 2013; Lowe & McPeek 2014). Low or limited dispersal can also introduce stochasticity. Dispersal limitation, which is one of the important basis of the neutral theory, represents a process in which the location of an individual is restricted by the location of its parent in some sense (Hubbell 2001; Rosindell *et al*. 2011). Earlier studies have demonstrated that the dispersal limitation was the primary mechanism that explains the tree species spatial patterns, particularly in the high-diversity tropical forests (Hubbell 1979; Condit *et al*. 2000, Seidler & Plotkin 2006).

Ecological equivalence - is the fundamental yet controversial idea behind neutral theory. It assumes that tropically similar species are demographically alike (symmetric) on a per capita basis.

Neutral speciation and extinction – It is the process that leads to a proportional relationship between the speciation and extinction rate of a species in a community and its abundance. It assumes that, all the individuals of all the species in the community have the same probability of speciation and extinction. The abundance of each species increases or decreases randomly, and the number of species in the community depends on the dynamic equilibrium between speciation (or immigration) and extinction (Hubbell 2001).

1.1.2.2 Fundamental processes of deterministic assembly mechanisms

Deterministic models of community assembly emphasize the importance of ecological and evolutionary differentiation between species and their non-random response to abiotic and biotic environment (Tilman 1982). Two main fundamental processes underlie deterministic assembly of species in communities; abiotic or environmental filtering and biotic filtering or competition.

Abiotic or environmental filtering: It is one of the most enduring concepts in the study of community assembly and dynamics. Environmental filtering or habitat filter is a process, where the environment selects against or “filters out” certain species by limiting establishment or survival at particular sites and thought to be a major mechanism structuring community. The current use of the environmental filtering concept has its roots in the study of plant community assembly and dynamics in the late 1970s and early 1980s (Nobel & Slatyer 1977; vander Valk 1981; Bazzaz 1991; Woodward & Diament 1991). These studies laid the foundation and described the environment as a metaphorical ‘sieve’ or ‘filter’ that only permits species with particular traits or phenotypes to establish and persist, excluding all others. The concept has grown in usage considerably since this time, playing an important role in many studies of community assembly, succession, invasion biology and biogeography (e.g. Weiher *et al*. 1998; Richardson *et al*. 2000; Webb 2000; Cornwell *et al*. 2006; Whitfeld *et al*. 2012).

Biotic filtering or competition: Like abiotic factors which can serve as filter to prevent establishment and persistence of species, interactions between plants and other organisms can have important consequences for community assembly. Competition and natural enemies (herbivory, predation, parasites, pathogen) can negatively impact establishment and survival of species in a given site. Whereas positive interactions can allow species to establish and persist at given sites. In many conceptual models of community assembly, biotic interactions are often considered to impact community assembly after abiotic filtering has occurred.

As stated earlier, competition has long been considered to be a central biotic factor in community assembly, dating back to Jared Diamond’s initial study of bird communities on islands (and before that back to Darwin, writing in the Origin of Species). Competition is hypothesized to impact community assembly by the failure of species to establish or persist at a location in the face of competitive interactions. Early community assembly theory focused on the competitive exclusion principle (Hardin 1960), which hypothesizes that “complete competitors cannot coexist,” meaning that species are more likely to be able to coexist if they have niche differences. Early work in this area focused on the concept of limiting similarity, which hypothesized that there was a finite limit to how similar two coexisting species could be. While theoretical work has since suggested that there is not likely to be an absolute limit to similarity, the general idea that differences between species promote coexistence by reducing competition has persisted as a central theme in many community assembly studies.

1.2 Tools to infer community assembly mechanisms

The main goal of community ecology studies is to infer the mechanisms of community assembly and diversity pattern from observed patterns of species occurrences and abundance. Over many decade, ecologists have developed many conceptual framework and tools to infer community assembly mechanisms (Diaz *et al*. 1999; Webb 2000 and Webb *et al*. 2002) and these tools have provided important insights on processes determining species assembly in communities

(Mittelbach 2012). These tools can be broadly classified into two categories: 1) functional (or trait based) and 2) phylogenetic (or the amount of evolutionary divergence). Both tools measure species differences in a community and summarize the degree to which the constituent species differ in terms of their function, niche or evolutionary history. Both tools have led to new insights in community ecology (Webb 2000), yet both are limited by some methodological issues and important assumptions.

1.2.1 Community phylogenetics and inference of community assembly mechanisms

The potential application of phylogenetics in community ecology was first discussed by Webb *et al*. 2002 and introduced field of modern community phylogenetics. The authors suggested that, phylogenetic relatedness of a co-existing species in a community (i.e. distribution of pairwise distances measured on a phylogenetic tree between species within a community) can be used as a proxy to elucidate the processes structuring community assembly. The use of phylogenetics in community ecology relies on two main assumptions 1) phylogenetic relatedness of species in community reflect species ecological or niche difference and can be used as proxy for traits that mediate fitness and persistence in a given environment, and 2) phylogenetic niche conservatism: species ecological niches and niche-related traits tend to be maintained between ancestors and descendants (e.g. Prinzing *et al*. 2001). Based on these assumptions, one can expect either of these patterns for species in community a) phylogenetic clustering, and b) phylogenetic over-dispersion. Under 'phylogenetic clustering' scenario, species that are present in a community more closely related to each other than expected by chance. Therefore, phylogenetically clustered community also expected to share similar traits among closely related species to persist in a particular environment assuming such traits are phylogenetically conserved. Thus, it is assumed that 'phylogenetically clustered' community is mainly shaped by environment or habitat filtering effect (i.e. environment or habitat select or filter species to assemble in a community, based on whether species possess suitable traits to establish and persist in a particular environment or habitat). By contrast, in a 'phylogenetically over-dispersed' community, species that are present more distantly related to each other than expected by chance. Therefore, in a 'phylogenetically over-dispersed' community distantly related species is expected to share dissimilar traits further assuming such traits phylogenetically conserved. Phylogenetic over-dispersion thought to be driven by competition for resources acting on conserved traits (i.e. the traits that mediate establishment and persistence of species to its abiotic niche are conserved on the phylogeny). This assumption is mainly stems from the idea of 'limiting similarity', where ecologically similar or closely related species would tend to competitively exclude each other (see Gause 1934; MacArthur & Levins 1967) because they exploit similar resources (Wiens & Graham 2005; Losos 2008). Thus, since co-occurring species were limited in their phylogenetic similarity because of competitive exclusion, we would predict that they would also be over-dispersed in their trait similarity (Moulton & Pimm 1987; Weiher *et al*. 1998)

There are several metrics to quantify phylogenetic diversity pattern across landscape and new methods are consistently being developed. Generally, these metrics combine species presence/absence, species richness and abundance with phylogenetic relationship of taxa. There are at least 70 phylo-diversity metrics currently available (Tucker *et al*. 2017). In order to clarify the conceptual relationship between existing metrics, to highlight their redundancies and to encourage correct usage and interpretation of metrics, recent overview have called for a unifying framework to classify these metrics (Pavoine *et al*. 2009; Tucker *et al*. 2017). Despite a vast array of phylo-diversity metrics, a natural scheme with a simple set of mathematical underpinnings were used to group the metrics into three conceptual dimensions by Pavoine *et al*. 2009 and recently updated by Tucker *et al*. 2017: richness, divergence and regularity. These dimensions capture the mathematical operation inherent to a metric, either 1) the sum of accumulated phylogenetic difference among taxa (richness); 2) the mean phylogenetic relatedness among taxa (divergence), representing the average phylogenetic difference between taxa in an assemblage; and 3) the variance in differences among taxa, representing how regular the phylogenetic differences between taxa in an assemblage are ('regularity'). The unifying framework proposed by Tucker *et al*. 2017 to classify different diversity metrics has following advantages: (i) it provides an intuitive approach based on the mathematical formulations of the metrics, (ii) it can be used to assesses both within and between assemblage diversity components, (iii) it is analogous to the functional diversity framework, thus aiding comparisons between phylo and functional diversity (Vill´eger *et al*. 2008) and (iv) it is applicable to both abundance and presence/absence formulations.

Some of these metrics used in the thesis are described below.

Phylogenetic alpha diversity metrics: measures sum of phylogenetic diversity per site or habitat e.g. Faiths's PD, alpha net relatedness index (alphaNRI), alpha nearest taxon index (alphaNTI) etc.

Phylogenetic beta diversity metrics: measures difference in phylogenetics diversity across space or between sites or habitat e.g. beta net relatedness index (betaNRI), beta nearest taxon index (betaNTI), local contribution to beta diversity (LCBD) etc. Recently, Cadotte *et al*. 2010 proposed number of abundance weighed phylogenetic metrics such as phylogenetic abundance evenness (PAE), abundance weighed evolutionary distinctiveness (AED), imbalance of abundance at clade level (IAC). The details about different phylogenetic metrics can be found elsewhere in the literature (Cadotte *et al*. 2010; Kembel *et al*. 2010).

1.2.2 Functional traits and inference of community assembly mechanisms

Among two related sets of methods or tools to infer community assembly mechanisms, I have reviewed community phylogenetic methods which exploit phylogenetic relatedness of cooccurring species to determine community assembly mechanisms (Webb 2000, Cavender-Bares *et al*. 2004, 2009; Vamosi *et al*. 2009). Similarly, another set of methods infer community assembly processes based on observational data by quantifying the ecological similarities and differences among co-occurring species using functional traits (Ricklefs & Travis 1980; Weiher *et al*. 1998; Stubbs & Wilson 2004; Cornwell *et al*. 2006, Kraft *et al*. 2008, Cornwell & Ackerly 2009). Assembly of species in communities is often results from two opposing mechanisms operating along a single niche axis: environmental filtering (stress tolerance) that increases species similarity through abiotic constraints (Weiher & Keddy 1995; Cornwell *et al*. 2006) and competitive interactions (niche partitioning, limiting similarity) that prevent coexisting species from being too similar (MacArthur & Levins 1967; Chesson 2000). Based on these assumptions, a widespread expectation for functional diversity environmental filtering (stress tolerance) that, diversity in traits that influence community structure and ecosystem function (Schleuter *et al*. 2010), is low in regions of strong abiotic stress and increases in regions where competitive interactions are relatively stronger (Weiher & Keddy 1995).

Though, many authors have tried to define functional traits (Lavorel & Garnier 2002; McGill *et al*. 2006; Violle *et al*. 2007), according to updated definition by Díaz *et al*. 2013 functional trait is a any morphological, biochemical, physiological, structural, phenological, life historical, or behavioral characteristic(s) that are expressed as measurable attributes of individual organisms, and which can be used to make comparisons across species. The proposal for using functional traits to infer community assembly mechanisms is recent (Diaz & Cabido 2001; Mason *et al*. 2005). and studies have increased since last decade (Schleuter *et al*. 2010; Cornwell *et al*. 2006, Villéger *et al*. 2008; Helmus *et al*. 2007; Cavender-Bares *et al*. 2009; Cadotte *et al*. 2011; Mouquet *et al*. 2012). However, the functional trait concept appears to have evolved within the rich history of comparative plant ecology in the last half century (Dansereau 1951). By the mid-1990s, researchers have increasingly used in understanding the relationship between plant morphological traits and ecosystem 'functions,' such as production and nutrient cycling (Hooper *et al*. 2005). Considering the suitably of functional traits in measuring species ecological difference and their role in ecosystem functioning, they have been extensively used to infer community assembly processes both in tropical forest (Hubbell 2005; Kembel & Hubbell 2006; Kraft *et al*. 2008, Swenson & Enquist 2009) and in other ecosystem (Schleuter *et al*. 2010; Cornwell *et al*. 2006, Villéger *et al*. 2008; Helmus *et al*. 2007; Cornwell & Ackerly 2009; Cornwell & Ackerly 2010; Cavender-Bares *et al*. 2009; Cadotte *et al*. 2011; Mouquet *et al*. 2012).

One advantages of using functional trait-based methods to infer community assembly mechanisms is that (Kraft & Ackerly 2010), they have more power to detect strategy-based ecological processes than analyses that simply place species into functional groups (Turner 2001) or that divide a forest or communities into conspecifics and hetero-specifics (e.g., Janzen 1970). Similar to community phylogenetic methods, functional traits also similar conceptual framework to infer community assembly mechanisms. Where observed distribution of traits within a local community is compared to a null expectation generated by drawing species at random from a regional pool of potential colonists (Cornwell *et al*. 2006). Deviations from the null expectation can be used as evidence for the influence of a number of ecological processes in the assembly of the local community (see Table 1-1). However, similar to community phylogenetic methods, functional traits also have methodological limitations and the observed results of functional trait metrics also should be interpreted with caution (Table 1-1).

Several methods have recently been proposed to help identify the necessary measures of functional diversity (reviewed in Ricotta 2005; Petchey & Gaston 2006; Podani & Schmera

2007; Ville´ger *et al*. 2008). There are two main approaches: 1) define functional groups based on on few behavioral/morphological characteristics (e.g., diet affinities, food acquisition methods, preferred habitat) and assign species to these functional groups (Bremner *et al*. 2003; Stevens *et al*. 2003; Petchey & Gaston 2006). Then use conventional species diversity indices to analyze this data (functional group richness, Shannon index, Simpson diversity index, etc. e.g., Stevens *et al*. 2003). This approach is suitable for macro-ecological studies which need low level detail in contrasting species traits, and 2) here functional diversity is calculated based on specific functional traits measured for each species. This approach provide data in finer resolution and suitable for inferring assembly mechanism in regional and local scale. These measured functional traits can be morphological traits that represent adaptations to different diets or habitats, physiological traits (e.g., temperature tolerance,), reproductive traits (e.g., number of eggs and egg diameter, seed mass, seed size), or behavioral traits (e.g., migratory behavior or parental care) (Bremner *et al*. 2003, Dumay *et al*. 2004, Lepˇs *et al*. 2006). As many of these measured traits have real value, more than one trait can be used to describe the different functions. However, commonly used species diversity measures (e.g., Simpson diversity index) cannot be applied to such traits to infer community assembly mechanisms. However, species diversity indices can be transposed to functional diversity metrics to infer such processes. Recently, several new functional diversity indices have been proposed and they describe two broad aspects of functional diversity: (1) how much of the functional niche space is filled by the existing species (functional richness) and (2) how this space is filled (functional evenness, functional divergence/variance). Therefore, Mason *et al*. 2005 identified three primary components of functional diversity – functional richness, which reflects the total variation in functional traits encapsulated by a community, functional evenness, which reflects the equity with which traits values are distributed among individuals within a community and functional divergence, which reflects the degree to which species within a community differ from each other (Mason *et al*. 2005) in functional strategy. Each component provides independent information on the distribution of species in functional trait space, and a separate index is required to quantify each component (Mouchet *et al*. 2010). Of the three components, functional richness and functional divergence (or indices that combine them) have most often been linked to community assembly processes (Mouchet *et al*. 2010; Mason *et al*. 2012; Spasojevic & Suding 2012) or ecosystem functioning (Petchey *et al*. 2004; Mouillot *et al*. 2011). There are dozens of functional diversity indices proposed to date (Rao 1982, Champely & Chessel 2002; Mason *et al*. 2005; Mouillot *et al*. 2005; Cornwell *et al*. 2006; Mouchet *et al*. 2008; Ville´ger *et al*. 2008; Cornwell & Ackerly 2010: Kraft & Ackerly 2010; Schleuter *et al*. 2010) and they have been reviewed thoroughly in recent literature (Schleuter *et al*. 2010; Cadotte *et al*. 2013; Mason *et al*. 2013). However, caution should be taken to choose appropriate functional diversity index that reflects the goals of the analysis.

Using functional trait metrics to infer assembly mechanisms, poses several methodological problems: First, the selection and the treatment of the traits, e.g., how many and which traits to use, how to weigh them, and how to combine them (Lepˇs *et al*. 2006; Petchey & Gaston 2006). Second problem is related to metrics itself i.e., do the indices measure exactly what the user wants to describe? Are the chosen indices independent from one another? Will diversity be measured for a single trait only or for a multivariate trait data set? Does the data set contain categorical and continuous variables? However, recently combining information from multiple traits into a single summary index of functional diversity is gaining more importance in the literature, particularly with the development of statistical tools that generate univariate summary statistics from multivariate trait data (Villéger *et al*. 2008). However, this approach of combining traits has received criticism recently due to following reasons: 1) multi collinearity between traits may force indices give very small values, making it difficult to identify processes and differentiate between communities (Cornwell *et al*. 2006; Lefcheck 2015; Lefcheck *et al*. 2015) and 2) Trade-offs among traits may also mask or nullify multivariate trends. Though, there are some methodical limitations, functional traits still serve as one of the important tool to infer community assembly mechanisms.

1.2.3 Caveats and assumptions of community phylogenetic and functional trait diversity metrics

Despite growing number and use of phylogenetic and functional diversity metrics for inferring mechanisms of community assembly from observed patterns of species occurrences, as those reviewed above (habitat filtering, competition), several concerns have been raised about the underlying assumptions on which they are based (Cavender-Bares *et al*. 2004; Kraft *et al*. 2007; Mayfield & Levine 2010; Gerhold *et al* 2015; Kraft *et al*. 2015; Pigot & Etienne 2015). To infer two opposing processes of community assembly such as habitat filtering (environment act as a selective force, to filter out species which are unable to persist in given environment) and competition (niche partitioning or limiting similarity) both community phylogenetics and functional trait metrics assume and expect that environmental filtering reduces both phylogenetic and functional trait diversity (increases phylogenetic and functional similarity) because closely related species would evolve similar traits which confer adaptation and persistence to given environment, contrastingly competition increases both phylogenetic and functional diversity (reduce phylogenetic and functional similarity) because closely related species will compete more strongly due to their ecological or functional similarity. Therefore, communities which experience environmental or abiotic filtering produce clustering pattern for both phylogenetic diversity and functional trait metrics. Contrastingly, communities which experience competition show over-dispersion pattern for both phylogenetic diversity and functional trait metrics. However, the over-dispersion pattern in community may also emerge as a result of abiotic filtering, where phylogenetically distantly related species have evolved similar trait to establish and persist in a given environment (Webb *et al*. 2000; Mayfield & Levene 2010). Similarly, the clustering pattern in community can also emerge from competition, if traits in question are associated with competitive dominance (Kraft *et al*. 2015). Furthermore, recent studies have suggested that multiple processes aside from abiotic filtering and competition could produce similar pattern of over-dispersion and clustering in community (reviewed in Cavender-Bares *et al*. 2009; Mayfield & Levene 2010; Kraft *et al*. 2015). For example: facilitation and mutualism (Bruno *et al*. 2003; Valiente-Banuet & Verdu 2007; Elias *et al*. 2009); stabilizing niche difference ((HilleRisLambers *et al*. 2012; Adler *et al*. 2013) and average fitness difference (Chesson 2000). Recently, several authors have questioned Webb's framework of phylogenetic community assembly by demonstrating that competition is not always strong among close relatives, and that it can also drive clustering pattern (Cahill *et al*. 2008; Mayfield & Levine 2010; Kraft *et al*. 2015). Furthermore, it has been argued that the assumption of a single stress–competition niche axis considers both below and above ground competition in community assembly is similar and overlooks large body of work differentiating their importance (Tilman 1982; Samuel *et al*. 2006). This additional niche axis associated with below-ground resources suggest that functional diversity associated with competition for below-ground resource [i.e. nitrogen (N), water] should be high when soil resources are limiting and decrease as these resources become more available.

Moreover, when inferring community assembly mechanisms, it is assumed that traits are conserved on the phylogeny. Certainly, this assumption is not true for all traits, several traits show lack of phylogenetic conservatism. In many cases, both phylogenetic and functional diversity metrics show opposing pattern of over-dispersion and clustering. This contrasting pattern mainly influenced by 1) traits show lack of conservatism among closely related taxa, and 2) distantly related species evolve similar traits or convergent evolution of traits among distantly related taxa. In addition, the processes such as dispersal limitation, speciation, extinction and predation can also influence trait evolution and misinterpret assembly processes (Crisp and Cook 2012).

Other critiques questioning assumptions behind phylogenetic and functional diversity pattern to use as a proxy to infer assembly mechanisms are related to 1) models underlying trait evolution and 2) neutral null models of community phylogenetic metrics. Models underlying trait evolution assume that, trait evolves at a constant rate over evolutionary time scale and therefore phylogenetic distance correlate linearly with time. However, such mode of trait evolution may be rare. But, most of the comparative phylogenetic analysis commonly uses Brownian model (BM) of trait evolution. If BM is a true model of trait evolution, assuming linear scaling of phylogenetic distance of taxa with evolutionary time would over-weighing of taxa with long evolutionary branches (Letten & Cornwell 2015). Therefore, in a recent article (Letten & Cornwell 2015) introduced correction to phylogenetic distance to calculate over dispersion of community to match best with BM model of trait evolution. Further, most of the null model used to infer assembly mechanisms based on community phylogenetic metrics produce communities that are random in a statistical sense and ignore the historical processes (speciation, extinction, dispersal) through which communities are assembled (Gotelli & McGill 2006; Vellend 2010). However, such null models are problematic to infer dynamics of assembly mechanisms, if community assembly is purely influenced by historical processes such as speciation, extinction and dispersal limitation or identical ecological processes operating at large temporal and spatial scale (Diamond 1975; Connor & Simberloff 1979; Bell 2001; Hubbell 2001; Warren *et al*. 2014). Recently, to account for such limitations (Pigot & Etienne 2015) developed a dynamic null model of community assembly based on the fundamental historical processes such as colonization, local extinction and speciation, or 'DAMOCLES' (Dynamic Assembly Model Of Colonisation, Local Extinction and Speciation). This null model, account for historical evolutionary processes and asses the relative importance of niche based (habitat filtering) and niche differentiation processes to community assembly. It also assesses whether historical evolutionary processes purely influence community phylogenetic structure of clustering and over-dispersion. In such cases, over-dispersion and clustering pattern should not be interpreted as competition or other ecological processes structuring community coexistence.

It has also been criticized that, using solely either of single functional trait, combing multiple traits into multivariate functional diversity (Weiher *et al*. 1998; Cornwell *et al*. 2006; Thompson *et al*. 2010) or phylogenetic diversity (Cadotte *et al*. 2009; Machac *et al*. 2011) suffer from integrating multiple niches axes into one variable to infer community assembly mechanisms. As different traits always associated with different ecological processes, they relate to different niche axis, using single trait or combining multiple traits into multivariate functional diversity or phylogenetic diversity alone can mask community assembly processes when traits are associated with opposing niche axes such as habitat filtering, competition and other processes (Violle *et al*. 2007). Therefore, integrating multiple traits separately and phylogenetic diversity in single analysis can provide better insights to community assembly processes.

The use of phylogenetic diversity and functional traits metrics as a proxy to detect general patterns and rules governing community assembly faces many challenges and attracted criticisms (Cavender-Bares *et al*. 2004, Kraft *et al*. 2007; Kraft & Ackerly 2010; Mayfield & Levine 2010; Kraft *et al*. 2015; Pigot & Etienne 2015). Despite these challenges, these approaches have provided deeper insights to evolutionary and ecological process shaping community composition and structure (Webb 2000; Cornwell & Ackerly 2010; Kraft *et al*. 2008; Kraft & Ackerly 2010; Kraft *et al*. 2015). Though, our interpretation of community phylogenetic and functional traits pattern is mostly limited to our understanding of two processes such as abiotic filtering and competition, other processes such as facilitation affect, stabilizing niche difference, average fitness difference and historical processes such as speciation, extinction and dispersal limitation also influence community assembly (Cavender-Bares *et al*. 2004; Kraft *et al*. 2007; Kraft & Ackerly 2010; Mayfield and Levine 2010; Kraft *et al*. 2015; Pigot & Etienne 2015). Therefore, the interpretation of community phylogenetic and functional traits pattern is not straightforward and integrating of phylogenetic diversity and functional traits in single analysis with robust null models accounting for historical processes can solve such limitations.

1.3 Mechanisms of tropical tree species community assembly across spatially varying environmental gradients and in different habitat types

Ecologists have utilized phylogenetic relatedness and plant functional traits that link physiological mechanisms with species persistence to detect different assembly processes operating at both large and small spatial scale environmental gradient and also in different habitat types (John *et al*. 2007; Kraft *et al*. 2008; Kraft & Ackerly 2010; De Oliveira *et al*. 2014; Liu *et al*. 2014; Fortunel *et al*. 2014). The studies determining assembly mechanisms of tropical tree species suggest that both niche based, and neutral processes contribute to assembly of tropical tree communities (Hubbell 2001; Kraft *et al*. 2008; Kraft & Ackerly 2010).

The first landmark study by Webb (2000) used community phylogenetic analysis to determine the phylogenetic structure of tropical tree communities. In his study Webb (2000) outlined the conceptual and methodological approach that could be used to utilize phylogenetic relatedness of cooccurring species as a proxy to detect assembly mechanisms, which being largely used even today in community ecology literature (Cavender-Bares *et al*. 2006; Kraft & Ackerly 2010, Pei *et al*. 2011, Oliveira *et al*. 2014; Liu *et al*. 2016). Webb (2000) study also defined the two community phylogenetic metrics net relatedness index (NRI) and nearest taxon index (NTI) to quantify whether closely or distantly related trees in Borneo tend to co-occur (Webb 2000). With slight modification to include branch length information and null models, these metrics also being largely used even today in community ecology literature (Cavender-Bares *et al*. 2006; Kraft & Ackerly 2010; Pei *et al*. 2011, Oliveira *et al*. 2014; Liu *et al*. 2016). Webb (2000) for first time showed that the species in plots were more phylogenetically related than expected by chance. Further work by Webb & Pitman (2002) analyzed the phylogenetic structure of two tropical forests accounting for relative abundance of individual species and studied the influence of neighborhood phylogenetic diversity on seedling demographic rates (Webb *et al*. 2008). Aside from Webb’s early work, many studies explored phylogenetic overdispersion and clustering pattern in tropical tree communities and concluded that biotic interactions were more important locally, giving rise to patterns of phylogenetic overdispersion, and abiotic filtering was more important at larger scales giving rise to patterns of phylogenetic clustering (Kembel & Hubbell 2006; Swenson *et al*. 2006, 2007)). Recent studies have yielded similar results for tropical tree communities both within forest plots and on regional scales (Kraft & Ackerly 2010; Pei *et al*. 2011, Oliveira *et al*. 2014; Liu *et al*. 2016).

Similar to community level phylogenetic analysis, community-level functional analyses have been commonly used to detect assembly mechanisms in tropical tree communities (Kraft *et al*. 2008; Swenson and Enquist 2009; Lebrija-Trejos *et al*. 2010, Paine *et al*. 2011, Swenson *et al*. 2011, 2012a, b, Andersen *et al*.2012, Baraloto *et al*. 2012, Ding *et al*. 2012, Katabuchi *et al*. 2012, Liu *et al*. 2012). Functional trait analyses of tropical tree communities have almost revealed the same pattern to that of community phylogenetic analysis. The first set of community level functional studies from Ecuador (Kraft *et al*. 2008) and Costa Rica (Swenson & Enquist 2009) revealed both overdispersion and clustering pattern of functional traits in tropical tree communities. Both studies found that individual traits often have opposing patterns of dispersion at the same spatial scale. These studies highlight opposing assembly mechanisms are likely operating simultaneously in shaping the assemblage of trees and that these opposing mechanisms are operating on different functional traits linked to different physiological mechanism of organism (Grime 2006, Kraft *et al*. 2008, Swenson & Enquist 2009, Paine *et al*. 2011). These studies also highlight that opposing assembly mechanisms operating on independent axes of plant function may result in a random community phylogenetic structure (Swenson & Enquist 2009, Kraft & Ackerly 2010). Prior to these studies, random community phylogenetic structure was generally inferred to support neutral processes governing community assembly. Given the evidence that, functional traits show both overdispersion and cluster pattern in the same study the inference of neutrality from random community phylogenetic structure is no longer straightforward (Swenson & Enquist 2009). This highlight an advantage of integrating functional trait analysis along with community level phylogenetic analyses. Several recent studies have specifically used functional traits to demonstrate the importance of environmental filtering in determining the assembly of species-rich tropical forests (ter Steege *et al*. 2006; Engelbrecht *et al*. 2007; Kraft *et al*. 2008; Swenson & Enquist 2009; Paine *et al*. 2011; Katabuchi *et al*. 2012). However, in general majority of studies using either functional trait or phylogenetic relatedness or both revealed environmental or abiotic filtering as the major assembly mechanism shaping structure and composition of tropical tree communities (reviewed in Kraft *et al*. 2015) and very few studies support competitions as the main assembly mechanism (Silva & Batalha 2009; Cavender-Bares 2006; Kraft *et al*. 2007).

Environmental gradient is one of the major determinants of composition and structuring of tropical tree communities. The underlying mechanisms contributing to assembly of species across environmental gradient depend on spatial scale (HilleRisLambers 2012). At larger spatial scale climate is the predominant determiner of species occurrence and distribution. While at the small spatial scale, disturbance, soil, elevation, topographic factors and plant-plant interactions are important factors (Weiher & Keddy 1995; Kubota 2016). Large spatial scale includes continental and region wide studies while small spatial scale includes local habitat types, microhabitat variability etc. Several studies have shown evidence for strong to moderate influence of environmental variables such as precipitation and temperature on species turnover and diversity patterns of tree species in tropical forests (Clinebell *et al*. 1995; Gentry & Dodson 1987; Pitman *et al*. 2002; Ter Steege *et al*. 2005). These studies highlight the role of environmental variables in determining the diversity, composition and assembly of tropical plant communities. 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 (Ricklef 2006; Fine & Kembel 2011; González-caro *et al*. 2014). It is possible that tree communities occurring along an environmental gradient may have different evolutionary history and as a result one can expect variations in species turnover across the gradient be related to the phylogeny of the species (Fine *et al*. 2005). Moreover, they may also have evolved different strategies or traits to adapt to the environmental gradient in a given location (Kraft *et al*. 2008). However, there are very few studies which used either functional traits or phylogenetic relatedness to detect assembly mechanisms shaping structure and composition of tropical tree communities along broad scale environmental gradient (Fine and Kembel 2011; Hardy *et al*. 2012; Fortunel *et al*. 2014; González-Caro *et al*. 2014). Therefore, the extent to which different assembly mechanisms contribute structure and composition of tropical tree communities along broad environmental gradients at large scales remains unclear, especially in highly diverse tropical forests (Asner *et al*. 2013). Previous studies have shown that phylogenetic and functional turnover of tropical plant communities is often related to topographic, edaphic and climatic gradients (Fine & Kembel 2011; Swenson 2011; Anacker & Harrison 2012; Hardy *et al*. 2012; Baldeck *et al*. 2013; Fortunel *et al*. 2014; González-Caro *et al*. 2014). Most of these studies reveal abiotic filtering as the main mechanism shaping structure and composition of tropical plant communities along a broad scale environmental gradient (Fine &

Kembel 2011; Swenson 2011; Anacker & Harrison 2012; Hardy et al. 2012; Baldeck *et al*. 2013; Fortunel *et al*. 2014; González-Caro *et al*. 2014).

The habitat heterogeneity or presence of different habitat types is one of the major factors thought influence species abundance and distribution in tropical forests (Phillips *et al*. 2003, Chave 2008). Tropical tree species show spatial association with particular habitat type and these habitats mostly show variation in edaphic, topographic, soil moisture and flooding gradient, sometime at the scale of only several meters (Harms *et al*. 2001; Valencia *et al*. 2004; Fine & Kembel 2011; Katabuchi *et al*. 2012; Fortunel *et al*. 2014). Such pattern of habitat association of tropical trees mostly linked to niche-based processes such as habitat filtering (Keddy 1992) and limiting ecological similarity (MacArthur & Levins 1967; Pacala & Tilman 1994). However, associations of species occurrence with particular habitat can be influenced by either of these processes (Jabot *et al*. 2008; Kraft *et al*. 2008). Both functional traits and phylogenetic diversity pattern used as proxy to detect such mechanisms influencing tree community assembly across different habitat types in tropics (Fine & Kembel 2011; Katabuchi *et al*. 2012; Fortunel *et al*. 2014), studied community phylogenetic structure of tree communities from 34 plots of Amazonia across white-sand and clay terra firme forests. They found dominant taxa in white sand forest are phylogenetically clustered and phylobetadiversity measures found significant phylogenetic clustering between terra firme communities separated by geographic distances of <200 to 300 km. They interpreted the pattern consistent with habitat filtering and recent local speciation. Further, Fortunel *et al*. 2014 sampled 15 functional traits in 800 Neotropical trees from 13 plots representing broad climatic and soil gradients encompassed by three widespread lowland forest habitats such as terra-firme, seasonally flooded and white sand forest. They found directional shift in community functional composition correlated with environmental changes across 13 plots. They concluded that environmental filtering consistently shapes the functional composition of highly diverse tropical forests at large scales across the terra firme, seasonally flooded and white-sand forests of lowland Amazonia.

1.4 Habitat specialization and its role in ecological speciation of sister taxa

The environmental heterogeneity at small spatial scale can act as local habitat filter and restrict subset of species to co-occur in limited abiotic conditions. Such niche differentiation at small spatial scale due to local habitat heterogeneity, thought to lead to habitat specialization and there by regional pattern of species diversity (MacArthur & Levins, 1964; Chase & Leibold, 2003; Kneitel & Chase, 2004; Baraloto *et al*. 2007). The plants are widely known to exhibit habitat specialization as indicated by their strong association of species turnover and abundance with abiotic conditions (e.g., altitude, soil type, rainfall gradient, seasonal flooding; Gentry 1986, 1988; Tuomisto *et al*. 1995; Ruokolainen *et al*. 1997; Davies *et al*. 1998; Clark et al. 1998, Webb & Peart 2000; Svenning, 2001; Pyke *et al*. 2001; Potts *et al*. 2002; Fine *et al*. 2005; Baraloto *et al*. 2007). Such association may lead to ecological speciation among closely related or sister taxa. The evolution of closely related lineages across different habitat types can give an insight about what are the evolutionary reasons behind the diversification of taxa are across different habitats. Thus, case studies of understanding diversification of taxa across different habitat types have a power to reveal the role of ecological selection in speciation. But, there are only few examples from literature to show that how different habitat types play a major role in speciation events. For example, there are numerous studies mostly tested for evolutionary basis of edaphic habitat specialization among tropical trees (Harms *et al*. 2001; Potts *et al*. 2002; Palmiotto *et al*. 2004; Russo *et al*. 2005; Fine *et al*. 2005), serpentine habitat (Westerbergh 1996) and heavy metal tolerance (Wu *et al* 1975; Al-Hiyaly *et al.* 1993, Schat *et al* 1996) in rapid evolutionary diversification of plant species. Seasonal flooding during heavy rains creates heterogeneous landscape of seasonally flooded and terra-firme (non-flooded) forest in lowland tropical rain forest. Despite knowing the fact that two habitats differ in micro habitat variables (flooding gradient, edaphic variables) and species composition, relatively little attention has been paid to understand how habitats with difference in seasonal water stress promote habitat specialization and ecological speciation and limit species distribution both at small and large spatial scale (Prance 1979; Lopez & Kursar, 2003; Parolin *et al*. 2004).

1.5 Ecological niche models and niche evolution analysis

Understanding the process determining niche evolution, the series of changes in niche parameters that promote taxonomic diversification within a lineage, is fundamental to understand the origin and diversification of taxa (Knouft *et al*. 2006). As a result, in recent years increased attention has been given to understand the niche evolution and its role in ecological speciation (Peterson *et al*. 1999; Weins *et al*. 2010). Such studies have tried to answer the question such as whether recently evolved organisms show evidence for niche conservation or divergence (McCormack *et al*. 2010; Weins *et al*. 2010; Wooten *et al*. 2014; Hu *et al*. 2015). There is a considerable evidence that divergent selection operating on lineages which inhabit different environmental conditions favor speciation in certain lineages especially during early stages of their genetic divergence (reviewed in Schluter 2009; Nosil *et al*. 2009). In particular, selection along sharp ecological gradients can influence lineages to diverge and adapt to such ecological gradient leading to ecological speciation (Warren *et al*. 2008). Alternatively, Niche conservatism (Wiens & Graham 2005; Crisp & Cook 2012), i.e., the tendency of lineages to retain similar niche (Wiens 2004) may also promote speciation when population are isolated in ecologically similar refugia due to environmental fluctuations (e.g. climate change) and prevent geneflow among isolated populations due to uninhabitable intervening space (Wiens 2004; Hua & Wiens 2013). The possible widespread occurrence of both niche conservatism and divergence and their consequence on emerging species, they have emerged as importance processes driving evolution and diversification of lineages (McCormack *et al*. 2010; Weins *et al*. 2010). Over few decades, number of research articles dealing with influence of these processes on ecological speciation across variety of taxa have tremendously increased (Warren *et al*. 2008; Kozak *et al*. 2008; McCormack *et al*. 2010; Weins *et al*. 2010; Sánchez-Fernández *et al*. 2011; Crisp & Cook 2012; Wooten *et al*. 2013; Jaime *et al*. 2015; Hu *et al*. 2015). This is mainly due to availability of spatially explicit ecological data with comparable geographic coverage to phenotypic and genetic data, which has proven a formidable barrier to determine the relative prevalence of these two processes in ecological speciation in nature. Such data can be used in tools such as a) Ecological niche models (ENMs) and 2) Modern comparative phylogenetic methods to assess the prevalence of niche conservatism and divergence in ecological speciation. These tools measure niche evolution in ecological and evolutionary contexts (Kozak *et al*. 2008; Peterson 2011; Wooten *et al*. 2013).

ENMs use location-specific, environmental data associated with occurrence localities of a species' geographic range (Knouft *et al*. 2006; Warren *et al*. 2008; McCormack *et al*. 2010). Then, this data is used to predict the species potential suitable habitat in a mathematical framework, the predicted suitable habitat can be used as surrogate measure of an organisms' ecological niche (Kozak *et al*. 2008). After predicting the potential suitable habitat of species, robust, and statistically reliable analyses such as niche overlap, Schoener's (1968) D, and I can be used to distinguish between biologically meaningful niche differences between species and simple environmental differences due to geography. Finally, these analyses are statistically compared with null distributions of background environmental data (McCormack *et al*. 2010). Using this procedure, one can distinguish between niche conservatism and divergence processes contributing to species diversification.

Similarly, to study the niche evolution in phylogenetic context, a number of procedures have also been developed, including restricting analyses to sister species at the tips of phylogenetic trees (e.g., Kozak & Wiens 2006) or to lineages in the process of speciation (e.g., McCormack *et al*. 2010). Several studies have also tested for phylogenetic signal or phylogenetic conservatism- the tendency of phylogenetically relatedness and trait (ecological niche) similarity to be positively correlated due to the divergence of both in a random. Brownian motion like models have been used by some (Losos 2008), though not all (Swenson *et al*. 2007; Crisp & Cook 2012) to distinguish niche conservatism from random divergence. However, recently Struwe *et al*. (2011) proposed the use of spatial evolutionary and ecological vicariance analysis (SEEVA) that statistically tests for niche separation within a phylogenetic context in a standardized way by treating both deep cladistic splits and sister species at the tips in similar manner. SEEVA tests the null hypothesis that there is no ecological vicariance associated with phylogenetic splits, which would be expected of a group experiencing niche conservatism.

1.6 Thesis outline

The tree communities distributed across moisture (precipitation and dryness) and flooding gradient in the tropical forests of Western Ghats, the mountains of Southern India, offers an excellent opportunity to investigate the role of ecological and evolutionary processes in determining turnover, composition and assembly of species across local (flooding gradient) and broad scale (precipitation and dryness gradient) environmental gradient.

The regional climate or the variation in precipitation and number of dry months is correlated with dominance and distribution patterns of evergreen and deciduous tree species in the Western Ghats, and therefore the distribution of deciduous and evergreen tropical forest habitat. Several authors have suggested that these climatic factors as the first-order predictor for the dominance and distribution of evergreen versus deciduous tree species (Chabot & Hicks 1982; Reich *et al*. 1992). However, the relative importance of deterministic (habitat filtering and competition), stochastic (dispersal limitation)] and evolutionary (evolutionary history of a species) processes in determining turnover and composition of tree communities with contrasting leaf type (deciduous and evergreen) across the climatic gradient have not been tested.

Seasonal flooding during heavy rains creates heterogeneous landscape of seasonally flooded and terra-firme (non-flooded) forest in lowland tropical rain forest of Western Ghats. Despite knowing the fact that two habitats differ in micro habitat variables (flooding gradient, edaphic variables) and species composition, relatively little attention has been paid to understand how habitats with difference in seasonal water stress promote habitat specialization and limit species distribution both at small and large spatial scale (Prance 1979; Lopez & Kursar, 2003; Parolin *et al*. 2004). Globally and in Western Ghats, the primitive and ecologically diverse pantropical plant family Myristicaceae known to dominate seasonally flooded tropical forest in lowlands and congeneric and conspecific species of the family known to exhibit divergent patterns of habitat associations in a heterogeneous landscape of seasonally flooded and terra-firme forest. Interestingly, congeneric and conspecific pair of Myristicaceae members occurring in these divergent habitats show unique morphological and physiological adaption to the respective habitat and have contrasting pattern of distribution across their geographic range. Owing to this fact, many authors have believed that, flooding gradient in the lowland tropical forest habitat might have promoted ecological speciation in the Myristicaceae family (Nair *et al*. 2007; Tambat 2003). The flooded habitats in Western Ghats are also known as freshwater swamps or Myristica swamps, and tree species in these swamps are thought to be primarily assembled from the regional species pool through the exclusionary action of permanent inundation (Chandran *et al*. 1999; Nair *et al*. 2007). Thus, features of tree species in swamps are often purported to be adaptations to life in temporary or permanently wet conditions (Chandran *et al*. 1999; Nair *et al*. 2007). However, despite a long history of ecological research, how and which traits determine the distribution and abundance of species along flooding gradients remain poorly understood. A rigorous test of the abiotic filtering hypothesis and testing whether tree species composition in swamps is similar to regional species pool are needed to shed light on community assembly along the flooding gradient.

The aim of this thesis is to investigate assembly processes of tropical tree communities distributed across broad scale (precipitation and dryness) environmental gradient and in different habitat types such as flooded and non-flooded habitat using phylogenetic comparative methods, community phylogenetic approaches, trait-based analyses and comparative niche evolution analyses. I test following general hypothesis a) tree communities in lower rainfall area with long period of dryness assembled from regional species pool by mechanism of environmental filtering that results in phylogenetic clustering and trait convergence, while in areas of high rainfall with short period of dryness interspecific competition or niche partitioning processes assemble tree communities from regional species pool that leads to phylogenetic overdispersion and functional trait divergence b) the deciduous leaf phenology is derived from evergreen leaf phenology and show convergent evolution, therefore the deciduous forest biome in Western Ghats is recently derived from evergreen forest c) tree communities in freshwater swamps primarily assembled from the regional species pool through the exclusionary action of permanent inundation that lead to convergent evolution of key functional traits conferring adaptation in flooded habitat c) deterministic (niche-based) ecological processes such as environmental filtering interact with trait evolution to influence ecological success of tree communities in freshwater swamps d) flooded habitat specialization has evolved repeatedly among global and Western Ghats endemic Myristicaceae members leading to ecological speciation in the clade and e) the Myristicaceae members distributed across flooded and non-flooded habitat show evidence for range-wide niche divergence, thus ecological speciation in Western Ghats Myristicaceae members.

In **Chapter 2**, I will use tree species abundance, stand structure, functional trait and phylogenetic data from a network of 96, one-hectare plots distributed along a gradient of moisture (precipitation and dry period) in the central Western Ghats to infer the community assembly processes of tree communities distributed along a gradient of moisture (precipitation and dry period) in the central Western Ghats, India. **Chapter 3** aims at inferring influence of different community assembly processes and key functional trait evolution on ecological success of lowland tropical tree communities in flooded habitat using community composition data, trait data and phylogenetic data of trees species from fresh water swamps across the latitudinal gradient in the Western Ghats, India. In **Chapter 4**, I will study the evolution and diversification of dominant tree species of fresh water swamps, Myristicaceae, across swamp and non-swamp habitats in the Western Ghats using molecular phylogenetic and ecological niche modelling approaches. In **Chapter 5**, I conclude by describing main community assembly processes influencing distribution and abundance of tree communities across environmental gradient and in different habitat types in tropical forest of Western Ghats. I also conclude the role of key functional trait evolution and habitat specialization in ecological success and diversification of tropical tree species in flooded habitat in Western Ghats. Finally, I discuss the future directions to understand the tropical forest evolution in Indian subcontinent by integrating phylogenetic comparative methods, community phylogenetic analyses, trait-based analyses and other approaches.

Table 1-1: Conceptual framework for interpreting patterns of trait and phylogenetic community structure for the ecological processes of interest (after Cavender-Bares *et al*. 2004, Kraft *et al*. 2007; Kraft & Ackerly 2010).

Process	**Trait pattern**	**Phylogenetic pattern**	
		Trait conserved	**Trait convergent**
Habitat filtering (community sample includes one habitat)	Resource use and/or environmental tolerance traits clustered	Clustered	Evenly dispersed
Habitat filtering (community sample includes >1 habitat)	Random or resource use and/or environmental tolerance traits evenly dispersed	Random or evenly dispersed	Random
Competitive exclusion/niche Differentiation	Resource use strategy traits evenly Dispersed	Evenly dispersed	Random
Enemy-mediated negative density Dependence	Physical and/or chemical defense traits evenly dispersed	Evenly dispersed	Random
Dispersal assembly (e.g., neutral theory, lottery models)	Random	Random	Random

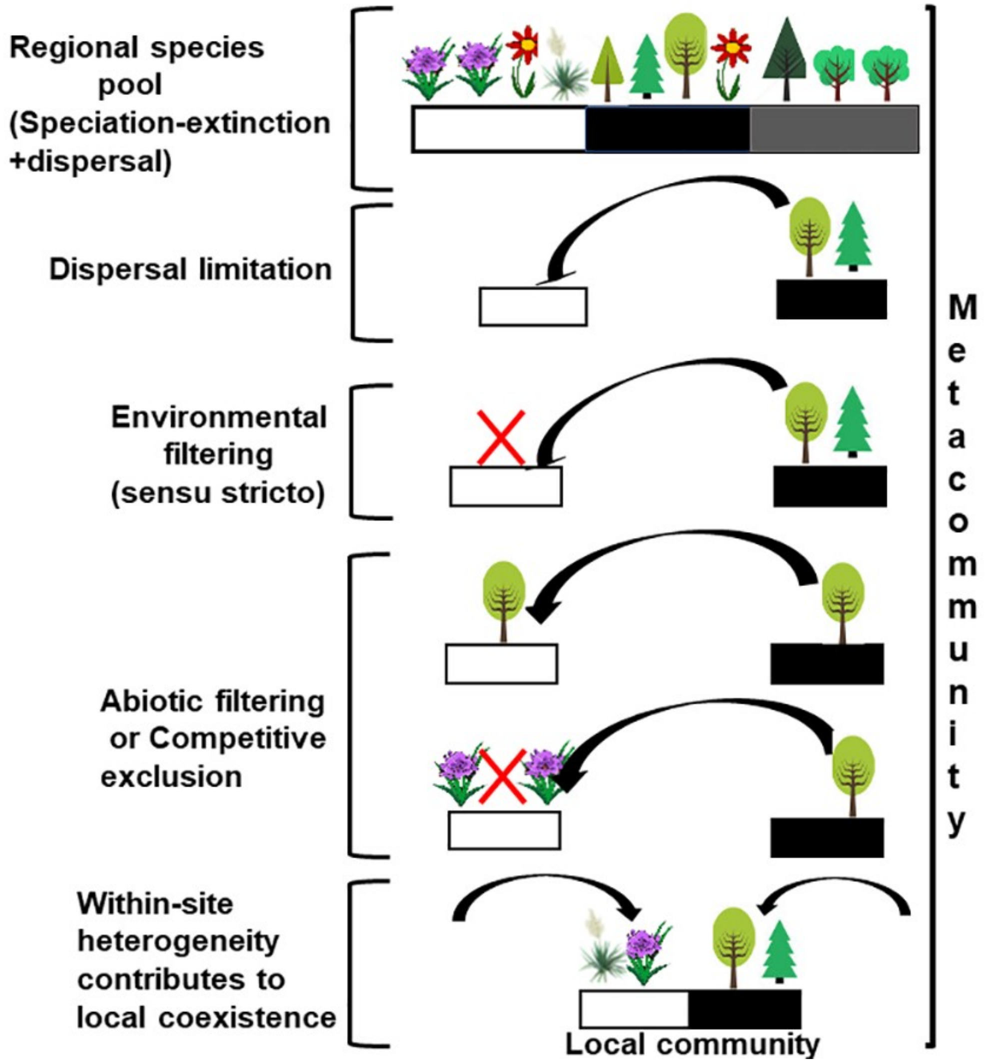

Figure 1-1: Model of community assembly (modified from Kraft *et al*. 2015): Fristly, dispersal limitation may limit the occurrence of species in focal site on the gradient. Next, environmental filtering (sensu stricto) occurs when a species arrives at a focal site but fails to establish or persist in the absence neighbours. Competitive exclusion occurs when a species arrives, and species can persist only in the absence of neighbours but not in their presence. Finally, at a different focal site, within-site abiotic heterogeneity (not typically defined as environmental filtering) can contribute to the ability of community members to persist locally. Note that in this hypothetical example, but the observed pattern of species abundance shifts across the gradient emerges from the combined action of all four processes.

CHAPTER 2

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.

2.1 Abstract

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 considered as 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 evolution of these patterns remain poorly understood. Here we perform integrated analysis of the data on tree species abundance, functional traits and community phylogeny from a network of 96 forest plots, each 1ha in size, distributed along a broad environmental gradient in central Western Ghats, India to determine the relative importance of various process in assembly and structuring of tropical forest communities with evergreen and deciduous leaf phenology. The deciduous leaf phenological trait has evolved repeatedly 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 key 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. These findings revealed that the environmental filtering plays a major role in assembly of tree communities in the biologically diverse tropical forests in the Western Ghats biodiversity hotspot.

2.2 Introduction

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 (Westoby & Wright. 2006; Woodward *et al.* 2004). In particular, the distribution and abundance patterns of tropical trees with contrasting leaf phenology such as deciduous and evergreen have attracted considerable attention from ecologists, biogeographers, and mathematical modelers for decades (Monk 1966; Givnish 2002; Lavorel & Garnier 2002; Bowman & Prior 2005; Kikuzawa *et al.* 2013). The cooccurrence and contrasting distribution and abundance pattern of evergreen and deciduous tree species across a variety of landscapes shown to be strongly influenced by environmental factors, mainly by climatic variables such as precipitation, temperature and length of the dry season (Ramesh *et al.* 2010; Ge & Xie 2017). Thus, 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 & Hicks 1982; Reich *et al.* 1992; Ramesh *et al.* 2010). In addition, the external factors such as anthropogenic disturbance may also lead to changes in 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.* 2010; González-Caro *et al.* 2014).

However, our current understanding of how the 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 as the interaction between ecological and evolutionary processes influencing these patterns are often been ignored in many studies (Ricklef 2006; Fine & Kembel 2011; González-caro *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 & Ackerly 2010) influences the spatial distribution and abundance of species across gradients at both large and small spatial scales (Harms *et al.* 2001; Fine *et al.* 2004; Gilbert & Lechowicz 2004.; Kraft *et al.* 2015; Cadotte & Tucker 2017). Species with contrasting 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-caro *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 & Schluter 1993; Ricklefs 2004; ter Steege *et al.* 2006; 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 (Hardy & 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 & Kembel 2011; González-caro *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 & Kembel 2011; González-caro *et al*. 2014) as well as in distinct habitat types (Shipley *et al.* 2006; Kraft *et al*. 2008; Cornwell & 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 & Kembel 2011; González-caro *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 key role of neutral or other random stochastic processes such as dispersal limitation and external factors in assembly of the community. Thus, integrating multiple approaches is important to gain in depth understanding of mechanisms shaping spatial and geographic distribution and abundance patterns of species in habitats across environmental gradients and assembly of communities.

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 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 contrasting leaf phenology? (ii) Does the phylogenetic structure and functional trait strategies of different 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 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?

2.3 Methods

2.3.1 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 (13º30’–15º50’ N, 74º15’–75º40 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). This covers 21,970 km^2 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, b). The diameter at breast height (dbh) of all living trees ≥10 cm in each plot along with phenological classification of each tree as evergreen or deciduous based on existing literature (Pascal 1986) and botanists' expertise have been recorded.

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.

2.3.2 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 (). 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 (Appendix A1). The details of variables and their source are given in Appendix A1. 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 >2000mm/yr), moist deciduous (rainfall 1500 to 2000mm/yr) and dry deciduous (rainfall <1500mm/yr), 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.* 2010.

2.3.3 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 (Appendix A2). The five continuous traits included maximum dbh (m), wood density (g/cm^3), leaf size (cm), seed size (mm^2) and seed mass (g), and the discrete traits were seed dormancy type (orthodox and recalcitrant) and leaf phenology (deciduous and evergreen). We calculated the maximum attainable dbh by taking average of three largest dbh values for common species (100+ individuals), the largest two for less common (50+), and the largest observation for rare species (<50 individuals). For species represented by a single individual, the maximum attainable dbh was obtained from published regional flora, online biodiversity databases and journal articles. The leaf size (cm) for entire leaves was estimated using Area= Length*Width*0.70, by following the procedure of Thomas & Ickes (1995). We obtained leaf width and leaf length data from online biodiversity databases, regional floras, journal articles and digital images of specimens. The wood density (g /cm3) data was obtained from primary literature sources and from the Global Wood Density Database (Zanne *et al*. 2009; Chave *et al*. 2009). The seed size (mm2) was estimated using the relationships of seed length and width (length*width) using standard procedure (Dias & Ganhão 2012). We obtained seed length and seed width information from published regional flora, online biodiversity database and journal articles. Finally, we obtained seed mass information from published regional flora, online biodiversity database, journal articles and KEW seed information database (http://data.kew.org/sid/). In case where trait information was not available for the species, we used trait information from closely related species or for the genus. The seed dormancy type and leaf phenology data were retrieved from multiple sources including online biodiversity databases, regional flora, journal articles and published reports. The function of each of these traits and their collection source is given in Appendix A2.

2.3.4 Phylogenetic tree reconstruction

We reconstructed the dated phylogenetic tree for all tree species (339 species) occurring in our study plots using three candidate loci that are frequently used in angiosperm phylogenetic studies (Appendix A3). All three loci were from the chloroplast genome and included ribulose-bisphosphate/carboxylase Large-subunit gene (*rbc*L), maturase-K gene (*mat*K) and *psb*A-*trn*H intergenic region. We searched and retrieved the nucleotide sequences of three selected chloroplast regions (matK, rbcL and psbA-trnH) from Genbank both manually and using the phylogenerator (Pearse & Purvis 2013). Our searches yielded nucleotide sequences for 139 species out of 339 species. For remaining species, we used sequences of related species from the region or nearby region (Appendix A4). The details of loci and missing data for each locus is given in (Appendix A5). The taxon sampling with the corresponding Genbank accession numbers and related species sequences used are given in the Appendix. The nucleotide sequence alignment, editing and assembly of concatenated aligned nucleotide sequences of all loci were performed using Geneious R9 ((http://www.geneious.com). The sequence alignments were carried out using the global alignment algorithm MUSCLE (Edgar 2004).

We inferred phylogenetic relationships of tree species using maximum likelihood (ML), and Bayesian inference (BI). Best fitting models of sequence evolution for each locus were determined using the Corrected Akaike Information Criterion (AICc) in jModeltest v.2.1.4 (Dariba *et al*. 2012) (Appendix A5). Maximum likelihood (ML) and Bayesian inference (BI) analyses were performed using the CIPRES Science Gateway v.3.3 (Miller *et al*. 2011) (www.phylo.org). ML analyses were conducted using default parameters in GARLI v.2.01 (Zwicki 2006). One thousand bootstrap (BS) replicates were conducted using the same parameters used in ML searches. BI was performed using MrBayes v.3.2.3 (Ronquist *et al*. 2011). All BI analyses were run for 30,000,000 generations with four chains in four parallel runs sampling every 1000 generations. Both ML and BI analyses were topologically constrained at the family level. A recent phylogenetic tree from the Angiosperm Phylogeny Group III was used as backbone tree (R20120829 for plants) and uploaded to the program Phylomatic (V3) (Webb & Donoghue 2005) to obtain family level constrained tree to use in ML and BI analyses. The family and genus level relationships were resolved in both ML and BI phylogenetic trees without any polychromies by comparing to previous phylogenetic analyses. Finally, the resulting best likelihood tree served as the input phylogram for the subsequent age estimation analyses.

We used a Bayesian method (Sanderson 2002) implemented in the program BEAST v.1.8.2 (Drummond & Rambaut 2007) to obtain the dated phylogenetic tree. We estimated rates and ages from our sequences, modeling fossils as lognormal priors. We partitioned the data set by the gene, estimating separate rates and rate-change parameters for each partition. We set GTR + I + Γ model of molecular evolution for each of the individual genes and uncorrelated log-normal clock (UCLN), which allows for rates of molecular evolution to be uncorrelated across the tree. We also constrained the minimum ages of several of the clades in the tree to prior probability distributions. For each analysis, we initiated two independent Markov chain Monte Carlo (MCMC) simulations from starting trees with branch lengths that satisfied the priors on divergence times. A starting tree with branch lengths satisfying all fossil prior constraints was created using the program r8s version 1.7 (Sanderson 2002) using NPRS method. For each MCMC analysis, we ran two independent chains for 600 million generations and assessed convergence and stationarity of each chain to the posterior distribution using Tracer v.1.3 (Rambaut and Drummond 2009). After stationarity was achieved, we sampled each chain every 1000 steps until an effective sample size (ESS) of more than 200 samples was obtained. If convergence between independent chains was evident, we combined the samples from each run using the program LogCombiner v.1.8.2 included in the BEAST software suite.

We treated all fossils as minimum age constraints (see Appendix A6) in dating analysis, except for the root node which we set to a uniform distribution between 132 Myr (minimum age of angiosperms) and 350 Myr to correspond to the age of the most recent common ancestor (MRCA) of extant seed plants (Rothwell & Scheckler 1988). We modeled all other fossil constraints as lognormal distribution with different means and standard deviations. In total, we further applied fossil constraints on eleven deep nodes (e.g. families) (See Appendix A6). We assigned ages of the fossils to crown groups by enforcing the monophyly of these clades. In all cases, the monophyly of these constrained clades was well supported by previous phylogenetic analyses (Bell *et al*. 2010).

2.3.5 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. 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).

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 Bayesian posterior distribution of BEAST. All the phylogenetic diversity measures were calculated using R package picante ver 1.6.2 (Kembel *et al.* 2010).

2.3.6 Functional trait metrics

We used four community level functional trait metrics following the method of Kraft & Ackerly (2010). Of these four metrics, two measures, the community trait range (RANGE) and variance (VAR) are sensitive to habitat filtering (Kraft & Ackerly 2010) and other two metrics, the standard deviation of nearest neighbor distance and the single direction normalized to range (SDNDr, referred to as even spacing) and kurtosis are sensitive to niche differentiation (competition) (Cornwell & Ackerly 2009). All functional trait metrics were calculated using the R script from Kraft & 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 & Ackerly 2009; Kraft & Ackerly 2010).

In all analyses, we used one-tailed tests based on a priori predictions of habitat filtering and niche differentiation.

2.3.7 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 & 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 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 posterior distribution of BEAST to account for phylogenetic uncertainty. The mean of posterior probability distribution for each state (deciduous and evergreen) of the trait on each node from 100 trees were mapped on each node of the phylogenetic tree.

2.3.8 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 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 modelling (GLM) (McCullagh & Nelder 1989) with log link and Poisson errors.

Since the main goal was to identify the environmental variables with a high direct influence on species richness, abundance and phylogenetic alpha diversity of tree communities with contrasting leaf phenology, we used hierarchical partitioning for the analysis (Chevan & 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 & 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 & Nelder 1989) with log link and Poisson errors. All five selected variables were included in the multi-model analyses, and the best model was selected from the 31 models representing all possible combinations of the additive variables based on the lowest AICc value. If the AICc values for multiple models were nearly equal (ΔAICc<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. All twelve environmental variables were standardized using 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). In addition, we calculated the percentage of NRI and NTI values and functional trait metrics that indicated significant clustering (values >1.96) or significant 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.

2..4 Results

2.4.1 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 (Appendix A7). The first two axes together explained 85.24% of variation after accounting for important constraining abiotic and biotic variables (Appendix A7). 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 (Appendix A7). 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 (Appendix A8 to A10).

The hierarchical partitioning analysis suggested that, the major predictors contributing to 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 (see Chevan & 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). Whereas model with Bio12 and Bio16 was retained as final best model to explain the richness pattern of evergreen and deciduous tree species (Table 2).

2.4.2 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 environment and discrete habitat variables (Appendix A11 to A13). 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 (Appendix A11 and Appendix A14). In other words, phylogenetic clustering of closely related species decreased with precipitation and aridity index and increased with temperature and evapotranspiration (Appendix A11 and Appendix A14). 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 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 (see Chevan & Sutherland 1991) and joint contribution of predictors explain more of the variation in 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 lower disturbance, indicating that human disturbance further lead to the co-occurrence of closely related species (Table 3; Fig. 3). Our results showed that NRI values were positively correlated with 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 (Appendix A15 to A16). However, none of the results were significant for nearest taxon index (NTI) (Appendix A12, A13 and A15). 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 (Appendix A17 to A18).

2.4.3 Phylogenetic signal in functional traits of wet and dry forest communities

The evaluation of phylogenetic signal in five continuous and two discrete traits (Appendix A19 to A20) 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 (Appendix A19 to A20). 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, Fig. 4 and Appendix A21). The values of RANGE and VAR for leaf size, seed size and wood density significantly differed among three forest (wet evergreen, moist deciduous and dry deciduous) types (Table 4, Fig. 4 and Appendix A21). The RANGE and VAR for leaf size and wood density 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, Fig. 4 and Appendix A21). Conversely, seed size showed contrasting 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, Fig. 4 and Appendix A21).

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 (Appendix A22 to 23). The communities dominated by deciduous species had lower negative VAR and RANGE, whereas communities dominated evergreen tree species had higher and positive VAR and RANGE (Appendix A22 to A23). 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 suggest that the distribution and dominance of tree species with contrasting leaf phenology (deciduous and evergreen) in these habitats is strongly determined by habitat filtering.

2.4.4 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 (Appendix A19 to A20). Furthermore, we found no significant difference between chronology of the evolution of deciduous and evergreen leaf phenology in tree species in the Western Ghats (Fig. 5).

2.5 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 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). In addition, this study investigated the role of human disturbance on community assembly and phylogenetic structure of tree species with contrasting leaf phenology. Although a few studies have evaluated the role of historical and environment 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*. 2010; Joseph *et al.* 2012; van Ommen Kloeke *et al.* 2012; González-Caro *et al.* 2014; Lohbeck *et al.* 2015; Krishnadas *et al.* 2016; Ge & 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 assembly of tropical tree communities. In addition, our results also highlight the role of historical factors such as human disturbance in 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 evolutionary history of ecologically important traits in assembly of tree communities along wet and dry climatic gradients.

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 (Table 1 to 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, water deficit (aridity index) associated with length of dry season and temperature (Ramesh *et al*. 2010; 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 tradeoff between water availability and competitive ability exists, and greater tolerance to limited water supply can result in reduced competitive ability for either leaf type in a given climatic regime (Chabot & Hicks 1982; Reich *et al.* 1992; van Ommen Kloeke *et al*. 2015). The tropical forests in Western Ghats occur along broad scale precipitation gradient (<1000mm to >5000mm) with varying length of dry season ranging from 3 to 7 months (Davidar *et al.* 2007; Ramesh *et al.* 2010). The evergreen broad-leaved tree species adapted to high rainfall of >5000mm with < 3 months of dry season in lower altitudes seldom thrive and fail to reproduce in low rainfall areas with 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, directional shift in abundance and contrasting 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 & 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.* 2010). In our study, the temperature related variables were less important compare to precipitation related 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) (Table 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 were 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 (Appendix A7 to A12 and A14). 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 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 regions also confirms that historical factors such as human disturbance strongly influence the taxonomic turnover and phylogenetic structure of plant assemblages (Verdu & Pausas 2007; Knapp *et al.* 2008, Norden *et al.* 2009; Helmus *et al.* 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 (Verdu & 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 random pattern of phylogenetic turnover (betaNRI and betaNTI) with both spatial and environmental distances (Appendix A17 to A18). This pattern may emerge due to mix of lineages among plots due to historical human induced disturbance. In our study region, many plots have experienced high level of human disturbance (logging) and forest degradation leading to mixing of lineages from different habitats (wet and dry).

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 *&* Hubbell 2006; Fine & 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 & 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 dry season in these environments (Kembel & Hubbell 2006).

Furthermore, the habitat specialization and environmental filtering can also lead to phylogenetic clustering when traits that provide 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 & Hubbell 2006; Cornwell & Ackerly 2010; Lohbeck 2015). In our study, dry deciduous forests were dominated by individuals with short lived leaves (deciduous leaf) and individuals were phylogenetically clustered (Fig. 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 phylogenetically convergent could interact with environmental filtering to produce these patterns (Fine & 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 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 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 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 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 Western Ghats.

Associations of divergent functional trait strategies between contrasting 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 & Reich 1999). Our phylogenetic analyses showed that most of the traits which showed shift in traits metrics also showed significant phylogenetic signal (Appendix A19 to A20), indicating 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 & Ackerly 2010; Lohbeck 2015) and directly influence species interactions and assembly across wet and dry environmental gradient (Cornwell & Ackerly 2010; Lohbeck 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 greater hydraulic safety but reduced conductive efficiency (Hacke *et al.* 2001; Pratt *et al.* 2007). This physiological trade-off apparently 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 & Ackerly 2009).

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 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) (Appendix A19 to A20). However, within lineages (family) deciduous leaf habitat is conserved. Earlier studies also suggest similar trend at family level (Pennington *et al.* 2009; Lavin 2006; Lavin *et al.* 2003; 2004). 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, high number of deciduous lineages with young age (0 to 20Ma) suggest that plant clades with adaptations to dry forest habitats are the result of recent evolutionary radiations. Pennington *et al.* (2009) also suggested similar pattern for neotropical plant clades adapted to dry forest habitat. Fossil and climate data suggest that both tropical evergreen and dry deciduous forest are old biomes and evolved around late Eocene to early Miocene around 54 to 33Mya (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 Western Ghats are geologically old lineages and both types of leaf has evolved early in the evolutionary history of angiosperms. However, deciduous habit may have evolved convergently among tree species in the Western Ghats.

2.6 Conclusions

There is a distinct compositional and evolutionary imprint in tropical tree communities distributed across broad scale environmental gradient in Western Ghats and this imprint is mainly influenced by environmental variables and historical human disturbance. These imprints can be detected through the integration of functional trait data and phylogenetic relationship of co-occurring species. The distinct phylogenetic structure and divergent 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.

Table 2-1: 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

Note: Z-scores are calculated as (observed - mean(randomizations))/sd(randomizations), and statistical significance (*) is based on upper 0.95 confidence limit (Z>=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 Table S1 for details of predictor variables abbreviation.

Table 2-2: 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

	Standard coefficient of the best mode									
Response variables	**Bio3**	**Bio4**	**Bio12**	**Bio13**	**Bio15**	**Bio16**	**Bio19**	**GAI**	**Psuedo-R^2**	**AICc**
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

Note: 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 Appendix A1 for details of predictor variables abbreviation.

Table 2-3: The results of the T-tests between NRI values and forest types and levels of disturbance. Significant results are indicated in bold.

Variable	Comparison	Mean	T	DF	P 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. Abbreviations: DF: degrees of freedom, EVG: evergreen, DEC: deciduous, MD: moist deciduous, DD: dry deciduous. The formula for t-test used is $t = \overline{x}_1 - \overline{x}_2/\surd((N_1-1)s^2_1+(N_2-1)s^2_2/N_1+N_2-2)(1/N_1+1/N_2)$, where $\overline{x}_1$ and $\overline{x}_2$ represent means of two different forest types or disturbance level; N_1 and N_2 are sample size and s^2_1 and s^2_2 are an estimator of the common variance of the two samples

Table 2-4: The results of the T-tests between functional trait metrics (Range and Variance) and forest types. Significant results are indicated in bold.

Variable	Comparison	Mean	T	P 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 Abbreviations: EVG: evergreen, DEC: deciduous, MD: moist deciduous, DD: dry deciduous. The formula for t-test used is $t = \bar{x}_1 - \bar{x}_2/\sqrt{((N_1-1)s^2{}_1+(N_2-1)s^2{}_2/N_1+N_2-2)(1/N_1+1/N_2)}$, where $\bar{x}_1$ and $\bar{x}_2$ represent means of two different forest types; N_1 and N_2 are sample size and $s^2{}_1$ and $s^2{}_2$ are an estimator of the common variance of the two samples

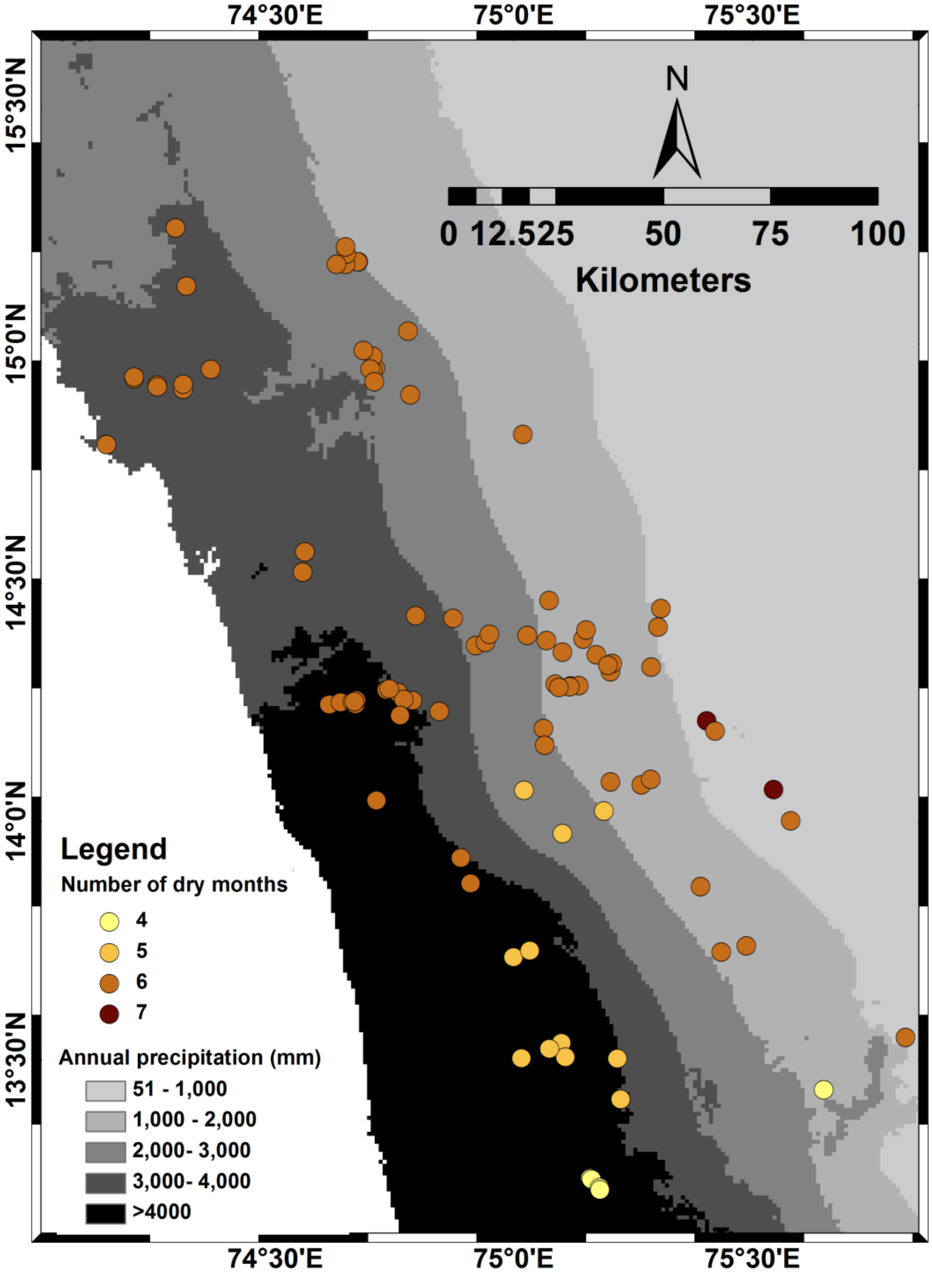

Figure 2-1: Location of sampling plots across precipitation and number of dry month's gradient in the central Western Ghats region of Karnataka, India

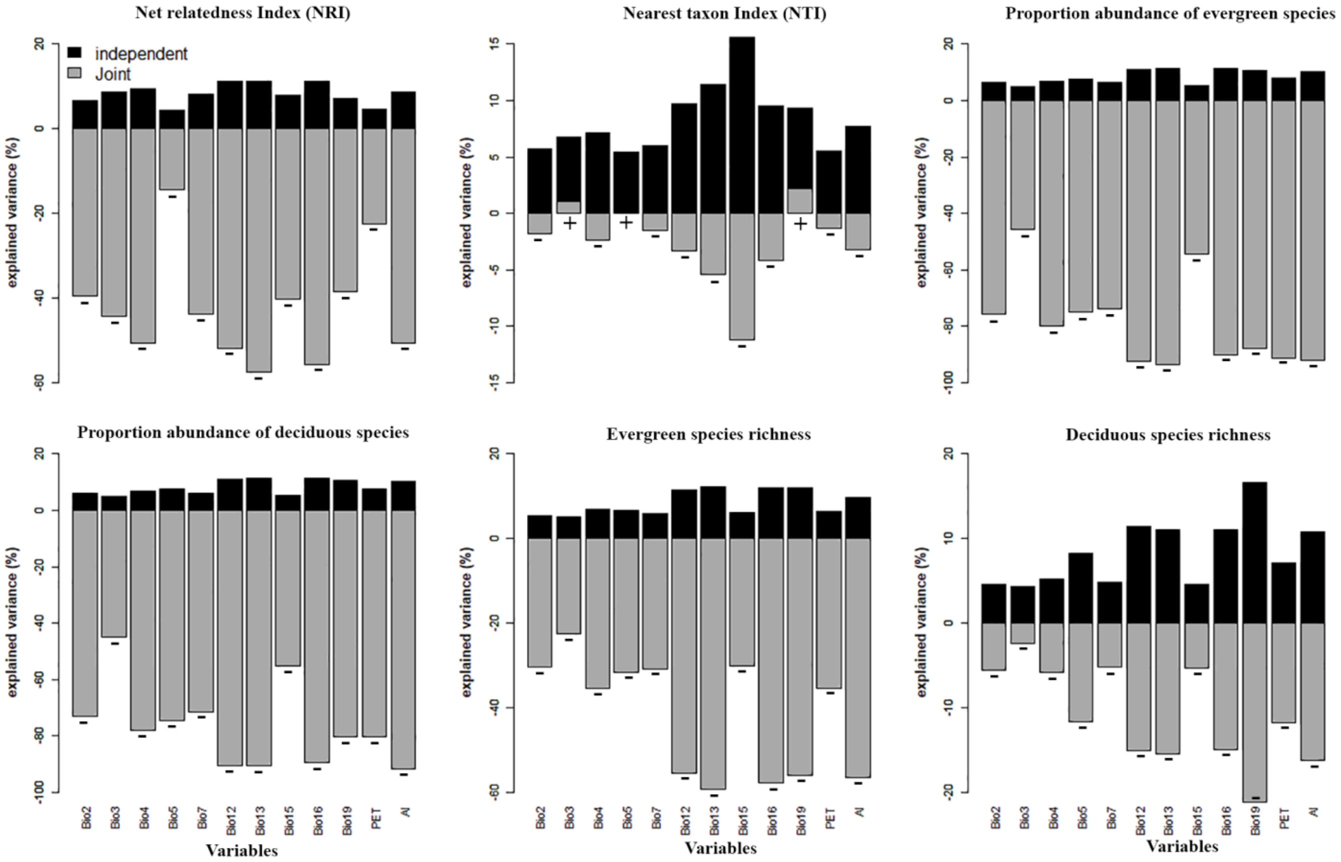

Figure 2-2: The independent and joint contributions (given as the percentage of the total explained variance) of the predictor variables for richness, abundance and phylogenetic structure of tree communities in central Western Ghats, India as estimated from hierarchical partitioning. The sign indicates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

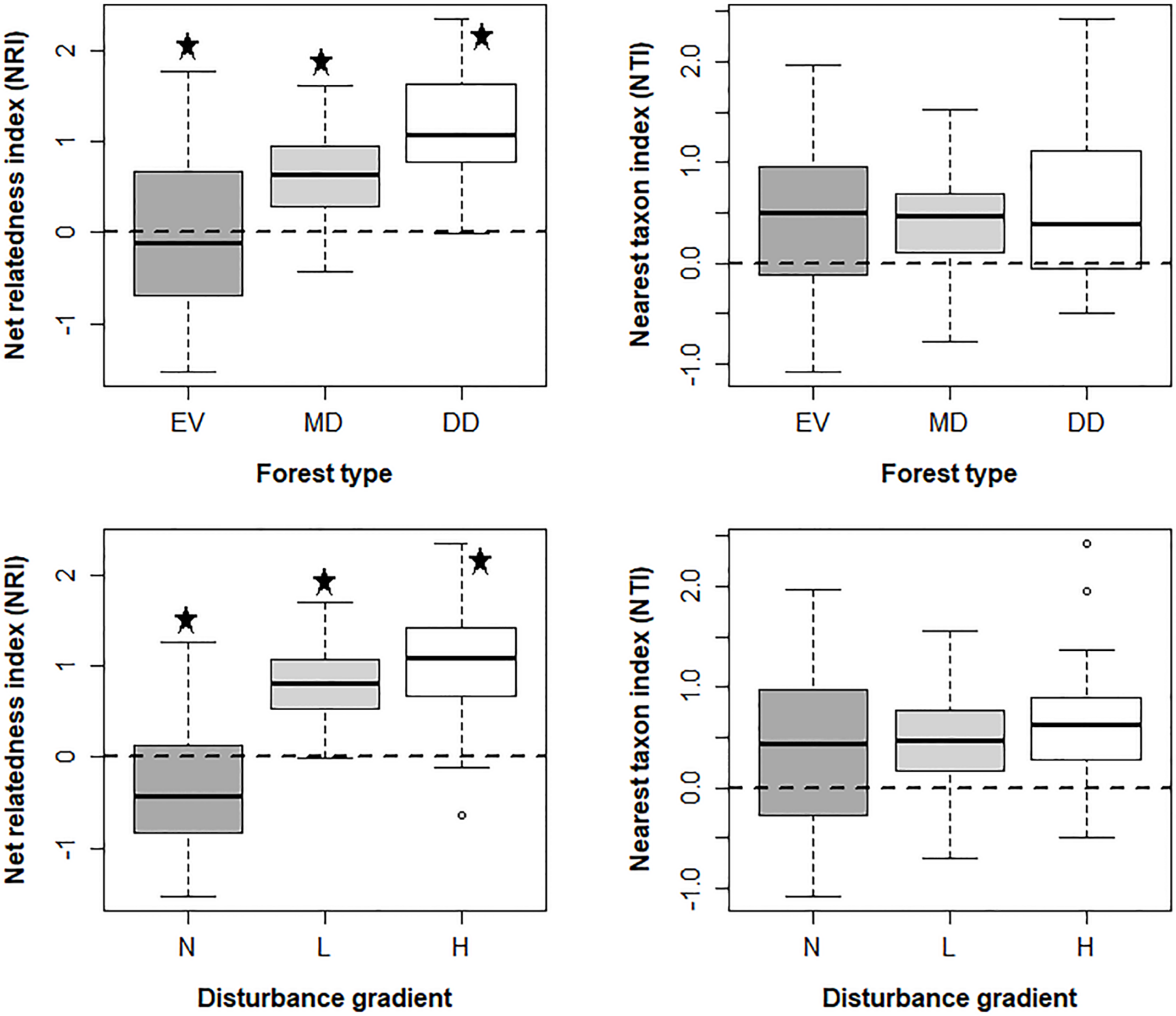

Figure 2-3: The boxplot of phylogenetic alpha diversity indexes (NRI and NTI) distributed among discrete habitat variables (forest type and human disturbance). Asterisks represent result significant among groups. Habitat variable abbreviations: EV=evergreen, MD=moist deciduous, DD= dry deciduous, H=high disturbance, L=low disturbance, N=no disturbance.

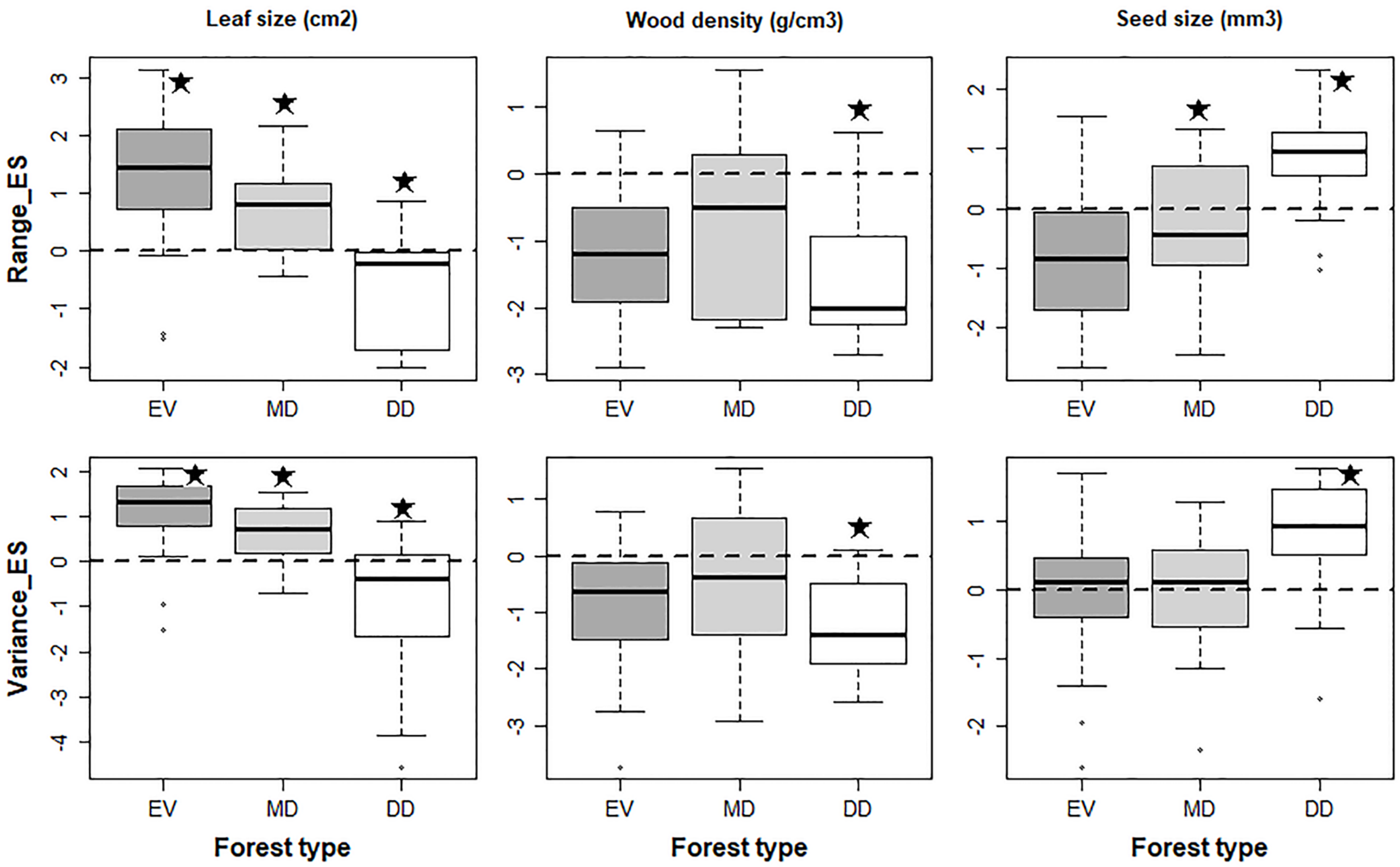

Figure 2-4: The boxplot of functional trait metrics (Range and Variance) distributed among discrete habitat variable forest type. Asterisks represent result significant among groups. Habitat variables abbreviations: EV=evergreen, MD=moist deciduous, DD= dry deciduous.

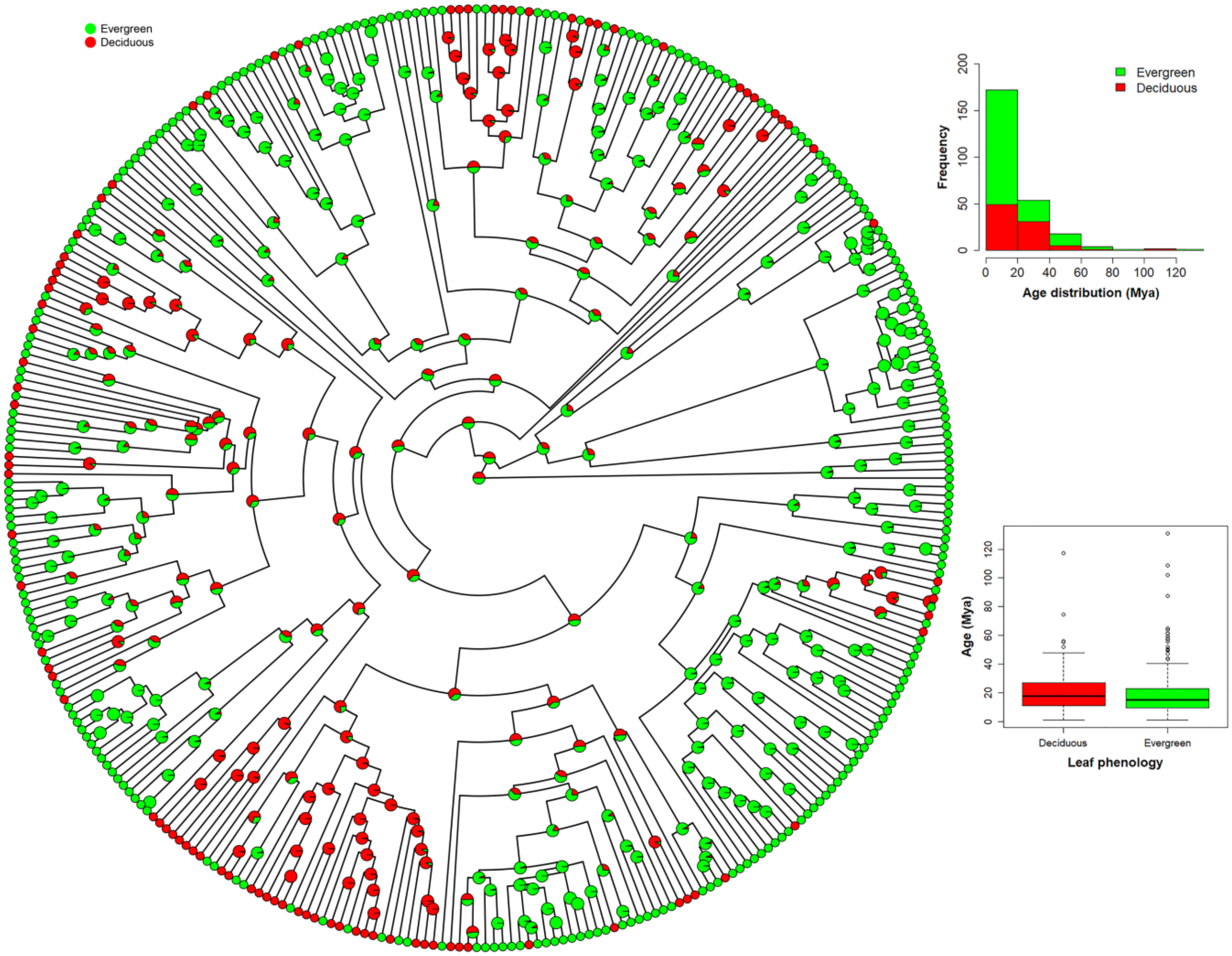

Figure 2-5: Stochastic trait mapping of leaf phenology (deciduous and evergreen) on dated phylogenetic tree of 339 tropical trees and age distribution for evergreen and deciduous species occurring in 96 sampling plots in Western Ghats, India.

CHAPTER 3

Convergent evolution of key functional traits drives ecological success in tropical forest communities

3.1 Abstract

Tropical forest communities are numerically dominated by relatively few species while a majority of species are rare. The ecological and evolutionary processes underlying the origin and maintenance of this pattern remain obscure. One critical challenge is to assess the relative influence of stochastic and deterministic processes while considering the relative contribution of evolutionary and ecological processes. While evolutionary history may dictate the diversity of lineages and functional traits in the pool, these traits may determine which species can establish in local communities as well as their relative abundances. Here, we assess whether the evolution of key functional traits predict ecological success across 42 freshwater swamp tree communities distributed over seven degrees of latitude in the Western Ghats, India. We compiled data on the evolutionary relationships, functional traits and relative abundance of 210 tree species of freshwater swamp and adjacent terra-firme (non-flooded) forest. We found that key functional traits, which evolved independently several times in the evolutionary history of lineages occuring in swamps, predict the ecological success (i.e. relative abundance) of species in these communities. In addition, using null-model analyses of community-wide functional trait structure, we detected a strong signature of habitat filtering, which indicates that species are deterministically filtered from the regional pool into freshwater swamp communities. Finally, we show convergent evolution of some key functional traits that permit establishment into swampy habitats and confer flood tolerance. Taken together, our results suggest that the repeated evolution of key functional traits together with deterministic, niche-based, ecological processes play a key role in determining the ecological success of species and their assembly in freshwater swamp tree communities.

3.2 Introduction

Ecological communities are generally made of a few common and many rare species. This pattern is even more pronounced in tropical forest communities, where the relative abundance of trees is strongly skewed towards few ‘dominant’ species (Campbell 1994, Richards 1996, Pitman et al. 2001, Hubbell 2001). There has been progress in understanding ecological processes driving the relative abundance of species in tropical forest communities over the last decades (Hubbell 2001; Pitman et al. 2001; McGill *et al*. 2005; Kraft *et al*. 2008; Morlon *et al*. 2009; Cornwell and Ackerly 2010, Jabot & Chave 2011; Maire *et al*. 2012; Seabloom *et al*. 2015), but the evolutionary processes that might be involved remain poorly understood (Maire *et al*. 2012; Seabloom *et al*. 2015). Although ecological processes can determine the relative abundance of species in communities through a suite of deterministic and stochastic processes (Cornwell and Ackerly 2010; Uriarte *et al*. 2010; Maire *et al*. 2012; Kunstler *et al*. 2012), the evolutionary processes that gave rise to key functional traits of species might impose limits on the distribution of individuals among species (Ricklefs & Renner 2012). Because some species have evolved traits that are sub-optimal in a given habitat, they may never be abundant, whereas those who did may be numerically dominant. As such, understanding how key functional traits have evolved and how these same traits affect species sorting from the regional pool into local communities is key to elucidating the drivers of ecological success (Vellend 2010). However, the fundamental question of whether traits determine the ecological success of species in a community remains largely unresolved (Shipley 2010; Cornwell & Ackerly 2010; Shipley *et al*. 2006).

Understanding how and why a particular trait has evolved in the past might be crucial for understanding community assembly and in particular, ecological dominance. As an example, the evolution of functional traits that promote habitat specialization can play a crucial role in determining the assembly ‘path’ of communities (Cornwell & Ackerly 2010; Keddy 1992). Such trait can evolve either once or multiple times in the evolutionary history of a lineage. Moreover, such trait can be either phylogenetically conserved or labile (Losos 2008). If they are conserved, closely related species share similar traits, whereas if they are labile, closely related species differ in those traits. Distinguishing between these evolutionary scenarios can provide insights on assembly mechanisms. As an example, a given trait may independently evolve multiple times during the evolutionary history leading to convergent evolution (Losos & Mehler 2010; Winemiller *et al*. 2015). If a key ecological trait has evolved several times and has led to ecological success of a species in present-day communities, this trait is highly beneficial and contributes to ecological success of the species in a given environment. Moreover, if the ecological process of environmental filtering is strong, meaning that only species possessing traits that promote persistence in local conditions can establish in a local community, then convergent evolution may lead to convergence in the functional trait structure of communities (Losos & Mehler 2010; Ricklefs & Renner 2012; Winemiller *et al*. 2015). Therefore, considering functional traits involved in ecological dominance in a phylogenetic framework can reveal the evolutionary underpinnings of ecological success of species in a present-day community.

Evolutionary history shapes the composition and diversity of functional traits in regional species pools and ecological processes might determine the relative abundance of such traits and associated species in local communities. The relative importance of neutral and niche-based processes in determining ecological success remains unclear (Morlon *et al*. 2009; Cornwell & Ackerly 2010; Maire *et al*. 2012). Neutral theory posits that stochastic processes such as dispersal limitation, ecological equivalence, and demographic stochasticity drive ecological success, which is often measured as the number of individuals of a given species (Hubbell 2001; Chave 2004). Alternatively, deterministic processes such as environmental filtering and niche differentiation may also play a crucial role in determining ecological success (MacArthur & Levene 1962; Keddy 1992; Silvertown 2004; Shipley *et al*. 2006). Although deterministic and neutral processes jointly influence the relative abundance of species, assessing their relative strength of such processes and their context-dependency may bring much insight in community ecology (Lessard *et al*. 2012, Vellend 2010).

One can infer the relative importance of neutral and niche-based processes on ecological success by examining correlations between particular functional traits and patterns of relative abundance (Kraft *et al*. 2008; Violle & Jiang 2009; Cornwell and Ackerly 2010; Kraft & Ackerly 2010; Maire *et al*. 2012; Violle *et al*. 2012; Blonder *et al*. 2014). If stochastic processes predominate, then functional trait values of species will not predict their relative abundance within a community (Cornwell & Ackerly 2010). In this scenario, the relative abundance of species in the regional species pool, as opposed to niche-based processes, dictate their relative abundances in local communities. The relative abundance of species in the regional pool may in turn result from neutral speciation and demographic processes (Hubbell 2001). Alternatively, the processes that affect ecological success could be based on functional traits associated with the niche of the species (Kraft *et al*. 2008; Cornwell & Ackerly 2010; Kraft & Ackerly 2010). In this scenario, associations between functional traits of species and the availability of the niche where such traits permit establishment, persistence and coexistence with other species influence the relative abundance of the species. If deterministic, niche-based, processes predominate, then the functional trait values of species will predict their relative abundance within a community (Grime 2006; Shipley 2006). Therefore, the relationship between trait values and relative abundance can be used to test the relative importance of stochastic and niche-based processes in determining ecological success.

A second approach to assessing the relative importance of community structuring processes on ecological success is to relate the functional trait structure of communities to the evenness of species in a community. If deterministic (niche-based) processes such as environmental filtering (EF) and niche differentiation (ND) drive ecological success of a species in community, the functional trait strategies and phylogenetic relationships between co-existing species in the community should exhibit significant non-random patterns of clustering or even dispersion. Therefore, the degree of dominance in a community (i.e. the inverse of evenness) is expected to show a strong association with patterns of phylogenetic and/or functional trait clustering or even dispersion within communities (Shipley *et al*. 2006; Cornwell & Ackerly 2010; Maire *et al*. 2012, Fine and Kembel 2010). Specifically, if environmental filtering determines ecological success, then communities where dominance is high should exhibit clustering of traits (negative or reduced variance and range) and phylogenetic clustering (positive or increased NTI or NRI) (Kraft et al. 2008; Kraft & Ackerly 2010; Cornwell & Ackerly 2010; Fine & Kembel 2010; Maire *et al*. 2012). Alternatively, if niche differentiation determines ecological success, communities where the degree of dominance is high should exhibit even dispersion of traits (negative or reduced SDNDr and kurtosis) and phylogenetic evenness (negative or reduced NTI and NRI) (Kraft et al. 2008; Kraft & Ackerly 2010; Cornwell & Ackerly 2010; Fine & Kembel 2010; Maire *et al*. 2012). An integrative approach that combines the evolutionary histories and functional traits of species can thus be useful in evaluating relative role of stochastic and deterministic processes in determining the ecological success of species within a community (Kraft *et al*. 2008; Cavender-Bares *et al*. 2009; Kraft *et al*. 2015).

Here, using data on the relative abundance, functional traits and phylogenetic relationships of 210 species of tropical trees in 71 communities distributed across a flooding gradient spanning eight degree of latitude, we assess the evolutionary and ecological processes driving ecological success in tropical forest communities in Western Ghats, India. We specifically address the following questions: 1) Does the evolution of key ecological traits drive ecological success, 2) do deterministic (niche-based) ecological processes such as environmental filtering interact with trait evolution to influence ecological success? 3) is there any evidence of convergent evolution leading convergence in the functional trait structure of tree communities in flooded habitat?

3.3 Methods

3.3.1 Community composition data and measuring species abundance

Freshwater swamps and adjacent terra firme forests were sampled from 42 locations distributed across latitudinal gradient (8°S to 15°S) in Western Ghats, India (Appendix B1 to B2). We extracted data for 19 swamps and 14 adjacent terra firme forest from project report published by Kerala Forest Research Institute (Nair *et al*. 2007). These plots are 0.1 ha tree inventories including all trees > 10 cm d.b.h (diameter at breast height). Further, we collected data from 23 more swamps and 15 adjacent terra firme forest from our own field survey conducted during 2013 and 2014, we followed the same sampling method to avoid the sampling error across the plots. However, few swamps were smaller than 0.1 ha, in that case we sampled entire swamp. In total we collected tree community data from seventy-one plots, of which 42 were swamps and 29 were terra firme forest. In each plot all stems were identified to species and each individual's d.b.h (diameter at breast height) and height was recorded. Terra firme plots contained 2634 individuals belonging to 174 species and range of 12 to 60 species per plot. Alternatively, freshwater swamp plots contained 4782 individuals belonging to 149 species and range of 5 to 47 species per plot. In total there were 210 tree species representing both swamp and terra firme forest.

The difference in number of plots sampled between swamp forest and terra firme forest did not have a large effect on the community level analysis of trait metrics and diversity measures such as abundance and evenness. Though number of plots differed among habitat types, the sampling scheme followed exhaustively sampled all adult trees in plot of each habitat type and almost all samples recorded same number of individuals, except in few plots where sampled area was smaller than 0.1 ha. The difference in community composition, species diversity and dominance of common species between habitat types is a strong pattern, not an artifact introduced by sampling difference, as illustrated by high-diversity per number of individuals sampled and no dominant species in terra firme forest (Fig. 3-1 and Appendix B3) versus low-diversity per number of individuals sampled and dominated by few tree species in freshwater swamp forest (Fig. 3-1 and Appendix B3). However, the difference in species richness and diversity within habitat type could be due to spatial and regional environmental difference, as the sampling was done across latitudinal gradient (8°S to 15°S) in Western Ghats. However, we have controlled for these differences in further community level analysis. Moreover, in the present study our main aim is to understand the community level processes between habitat types and these differences are of minor importance.

Abundance can be measured as number of individuals, biomass or resource use[3]. In this analysis, we measure abundance as number of individuals per unit area, as it provides a common metric to relate ecological dominance and rarity of tropical trees with that of trait metrics in the present study.

3.3.2 Functional trait data

Selection of traits plays an important role in determining assembly processes in communities of interest. Our selection of traits (Appendix B4) connected to the leaves, seeds, wood, root type and overall life form of each species covers a range of traits frequently mentioned essential to woody plant strategy in flooding environment[16] and also in other environmental conditions. In total, we collected data on 11 traits reflecting morphology, physiology, growth and reproduction, which includes 6 continuous traits and 5 categorical traits (Appendix B4).

The six continuous traits included maximum attainable height (m), maximum DBH (m), wood density (g/cm^3), leaf size (cm), seed size (mm^2) and seed mass (g). In each of the plot for all trees >10 cm diameter at breast height (dbh), we measured dbh and total height. For those trees with buttresses that precluded measurement of dbh at the usual height (1.37 m), the diameter was measured outside bark immediately above the buttresses. Then we calculated maximum attainable height by taking average of three tallest values for common species (100+ individuals), the tallest two for less common (50+), and the tallest observation for rare species (<50 individuals). We followed the same procedure for obtaining the maximum DBH by taking average of largest dbh values. In case of species, which are represented by single individual, we obtained maximum attainable height and maximum DBH from published regional flora, online biodiversity database and journal articles. Leaf size (cm) for entire leaves was estimated using Area= Length*Width*0.70, by following the procedure of Thomas & Ickes (1995). We obtained leaf width and leaf length data from direct measurements, as well as from online biodiversity database, regional floras, journal articles and digital images of specimens. Wood density (g /cm^3) data was obtained from primary literature sources and from the Global Wood Density Database (Chave *et al.*2009; Zanne *et al.*2009). Seed size (mm^2) was estimated using relationships with seed length and width (length*width) using standard procedure (Dias & Ganhão 2012), we obtained seed length and seed width information from direct measurement, as well as from published regional flora, online biodiversity database and journal articles. Finally, we obtained seed mass information from direct measurement following standard procedure (Pérez-Harguindeguy *et al*. 2013), as well as from published regional flora, online biodiversity database, journal articles and KEW seed information database (http://data.kew.org/sid/). In case where trait information was not available for the species, we used trait information from closely related species or for genus. See Appendix B4 for strategy correlation and function of each of these traits and their collection source.

We collected five categorical trait data which included root type, flooding tolerance or Inundation tolerance, seed dormancy type (Orthodox or recalcitrant), germination type (epigeal or hypogeal) and habitat preference (swampy, non-swampy and riparian). All categorical trait data was collected from multiple sources including direct field observations, online biodiversity database, regional floras, and journal articles and published reports. The function of each of these traits and their collection source is give in Appendix B4.

Trait coverage is shown in Appendix B4, and trait correlations are shown in Appendix B5. As suggested for community level trait analysis, we log transformed continuous traits prior the analysis when necessary.

3.3.3 Phylogenetic tree construction

To construct a dated phylogenetic hypothesis for tree species from fresh water swamps and terra firme habitat, we first identified candidate loci that have been frequently and successfully used in angiosperm phylogeny in the region. Based on this information we selected 3 candidate loci derived from chloroplast genome, which included ribulose-bisphosphate/carboxylase Large-subunit gene (rbcL), maturase-K gene (matK) and psbA-trnH intergenic spacer. For these selected loci, we conducted GeneBank searches for DNA sequences both manually and using phylogenerator (Pearse & Purvis 2013). A using species list of tree species occurring in both swampy and terra firme habitat. Our searches yielded sequences for 90 species out of 200 species. For remaining species, we used sequences of related species from the region or nearby region and 10 tree species were sequenced as a part of this project used in the analysis. In total we collected sequences for 210 tree species. Not all the species had sequences for all loci, the details of loci and missing data for each locus is given in Appendix B6. The taxon sampling with the corresponding Genbank accession numbers and related species sequences used are provided in Appendix B7.

The sequence alignment for each locus and editing and assembly of concatenated alignment of all loci was done using Geneious R9 ((http://www.geneious.com). Sequence alignments were done using the global alignment algorithm MUSCLE (Edgar 2004).

We inferred phylogenetic relationship for tree species occurring in swampy and terra firme forest from DNA sequence data using maximum likelihood (ML), and Bayesian inference (BI). Best fitting models of sequence evolution for each locus were determined using the Corrected Akaike Information Criterion (AICc) in jModeltest v.2.1.4 (Dariba *et al*. 2012). The AICc was used for model selection based on its ability to outperform other model-selection criteria. The details of model selected for each locus are given in Appendix B6. Maximum likelihood (ML) and Bayesian inference (BI) analyses were performed using the CIPRES Science Gateway v.3.3 (Miller *et al*. 2011) (www.phylo.org). ML analyses were conducted using default parameters in GARLI v.2.01 (Zwickl 2006). One thousand bootstrap (BS) replicates were conducted using the same parameters applied for ML searches. BI was performed using MrBayes v.3.2.3 (Ronquist *et al*. 2011). All BI analyses were run for 20,000,000 generations with four chains in four parallel runs sampling every 1000 generations. Both ML and BI analyses were topologically constrained at family level. A recent phylogenetic hypothesis of the Angiosperm Phylogeny Group 111 was used as backbone tree (R20120829 for plants) and uploaded to program Phylomatic (V3) (Webb & Donoghue 2005) to obtain family level constrained starting and constraining tree to use in ML and BI analyses. We made sure that, family and genus level relationships was resolved in both

ML and BI phylogenetic tree without any polychromies by comparing it to previous phylogenetic analyses. Finally, the resulting best likelihood tree served as input phylogram for the subsequent age estimation analyses.

We used a Bayesian method[31] implemented in the program BEAST v.1.8.2 (Drummond & Rambaut 2007) to estimate the phylogeny and divergence times simultaneously. We estimated rates and ages from our sequences, modeling fossils as lognormal priors. We partitioned the data set by gene, estimating separate rates and rate-change parameters for each partition.

We set the underlying model of molecular evolution to be GTR + I + Γ, for each of the individual genes. We also used the UCLN model, which allows for rates of molecular evolution to be uncorrelated across the tree. BEAST also allows for uncertainty in the age of calibrations to be represented as prior distributions rather than as strict/fixed calibration points. We therefore constrained the minimum ages of several of the clades in the tree to prior probability distributions (see supplementary information for fossil constraints). For each analysis, we initiated two independent Markov chain Monte Carlo (MCMC) analyses from starting trees with branch lengths that satisfied the priors on divergence times. A starting tree with branch lengths satisfying all fossil prior constraints was created using the program r8s version 1.7 (Sanderson 2002) using NPRS. For each MCMC analysis, we ran two independent chains for 500 million generations and assessed convergence and stationarity of each chain to the posterior distribution using Tracer v.1.3 (Rambaut & Drummond 2009). After stationarity was achieved, we sampled each chain every 1000 steps until an effective sample size (ESS) of more than 200 samples was obtained. If convergence between the independent chains was evident, we combined the samples from each run using the program LogCombiner v.1.8.2 (part of the BEAST distribution).

We treated all fossils as minimum age constraints (Appendix B8) in dating analysis, with the exception of the root node which we set to a uniform distribution between 132 Myr (minimum age of angiosperms) and 350 Myr to correspond to the age of the most recent common ancestor (MRCA) of extant seed plants (Rothwell & Scheckler 1988). We modeled all other fossil constraints as lognormal distribution with different means and standard deviations. In total, we further applied fossil constraints on eight deep nodes (e.g. families) (Appendix B8). We assigned the ages of the fossils to crown groups by enforcing the monophyly of these clades. In all cases, the monophyly of these constrained clades was well supported by previous phylogenetic analyses

(Bell *et al*. 2010). The dated phylogenetic hypothesis for 210 tree species documented from swamp and terra-firme habitat is given in Appendix B9.

3.3.4 Defining the species pools

We used hierarchically nested species pools to explore ecological dominance of tree communities at two different spatial scales: regional and local.

Regional pool: The regional pool consists of all species from both swamp and adjacent terra firme forest across all sites.

Local pool: The local pool consists of the species on a swamp and adjacent terra firme vegetation; we thus defined twenty nine local pools, one each for each location from where both swamp and adjacent terra firme vegetation was sampled.

Our regional pool is a collection of the local pools from all forty two sites from which 42 swamp and 29 adjacent terra firme vegetation was sampled. An alternative would be to use a regional species list from the area; however, it is difficult to define the extent of such a pool as the topography and environment of the region are highly variable. Therefore, we decided to limit our regional pool to the relevant subset of species closer to, and more likely to establish on, the freshwater swamp forest.

3.3.5 Landscape and plot scale abundance of tree species in freshwater swamps

To estimate abundance at the landscape scale, first we summed the abundance values for each species in all plots to produce a measure of the abundance of each of 149 species occurring in swamp at the scale of 93.02 ha swamp forest surveyed across Western Ghats. Then we calculated abundance of each species per m^2 of swamp by using summed values of abundance across all plots. Finally, we compared these values to the trait mean values of the 149 species.

We followed the method of Cornwell & Ackerly (2010) to test for non-random associations at the plot scale abundance with traits, we separately correlated absolute abundance values with trait values in each plot for each trait. This process was repeated for each plot in the study, generating 42 r-values, one for each plot, for each trait. We were then able to test whether the mean of the distribution of r-values was statistically different than zero. If the null hypothesis is correct, and there is no relationship between the trait value of a species and abundance, then the mean of this distribution is statistically indistinguishable from zero. A repeated and consistent within-plot relationship between the traits and abundance leads to, on average, a non-zero median value of within-plot r. We performed separate significance tests for each of the 6 continuous traits and first PCA axis for categorical traits.

3.3.6 Null models and significance testing

Different null models depend on different assumptions, as there is no single null model which can be seen as correct (Gotelli & Graves 1996). Here, we present four different null model methods that allow for significance testing. First, we used nonparametric statistics with each plot as a replicate, testing whether the mean of the 42 r-values collectively differs from zero. We tested the null hypothesis that the traits and abundance are uncorrelated.

We also used three null-model approaches: first, a null model in which for each plot we randomize abundances relative to species (‘abundance shuffle’). This approach maintained the observed distribution of abundance and trait values within each plot. This null model does not include any trait-based process affecting within-plot abundance. Secondly, for an alternate null model, we randomized the species’ trait vector, while maintaining the species-plot and species–abundance relationships (‘trait shuffle’). In each randomization, each species’ abundance distribution is maintained, both within plots and on the landscape scale, but is assigned a random trait value. Finally, we used non-swamp null model, this null model contains observed abundance and trait distribution for species occurring in adjacent terra firme forest. We expect that abundance-trait relationship is neutral or non-significant in non-swamp null model. Null models were run 9999 times. For first two approaches, we calculated the mean plot trait–abundance relationship for the 42 plots within a given randomization and compared the observed value to the distribution of null-model trials.

3.3.7 Statistical analysis

All analyses were conducted using R version 3.0.2 (R Foundation for Statistical Computing, Vienna, Austria, 2013). The details of all statistical analysis used in the present study is described in detail below.

Assessing dominance pattern: We tested the prediction of unequal distribution of abundance among swampy and adjacent terra firme forest using species abundance distributions (SADs). Although fitting of SADs remain controversial in community ecology (Adler & Hillerislambers 2007), their power to predict dominance and rarity in a particular system have been realized and they are being extensively used to understand the underlying mechanisms of community organization (Magurran & McGill 2011; Mathews *et al*. 2014; Simons *et al*. 2014) We plotted SADs using Whittaker's plot. We first fit our data to several SAD models (brokenstick, pre-emption, log-normal, Zipf and Zipf-Mandelbrot) using Vegan (Oksanen 2016), and compared the fitness based on the Akaike Information Criterion (AIC). As a result, we employed the log-normal model for our data.

PCoA for categorical traits: As we were not able to establish trait-abundance relationship for categorical traits, we transformed categorical traits to continuous variables using principal coordinate analysis (PCoA) as recommended by Ville´ger *et al* (2008). First, we calculated Gower's distance (it accommodates nominal, binary and categorical variables in a single measure) between all categorical traits across all species to measure the differences in trait variation across species. Then we subjected resulted distance matrix to PCoA. Finally, we extracted the first PCoA axis which explained maximum variation and converted it to absolute values and then we used this PCoA axis to establish trait-abundance relationship and in further community level trait analysis.

Trait spacing analysis and null models: To test whether habitat filtering (HF) and niche differentiation (ND) processes predict community assembly and uneven distribution (dominance) of species among swampy and adjacent terra firme forest habitat, we used community level trait metric analysis following the method of Kraft & Ackerly (2010). We used community trait range (RANGE) and variance (VAR) as measures sensitive to habitat filtering (Kraft & Ackerly (2010) and the standard deviation of nearest neighbor distance along a single direction normalized to range (SDNDr, referred to as even spacing) and kurtosis as measures sensitive to niche differentiation (Cornwell & Ackerly 2009). Negative effect size values for RANGE and VAR indicate environmental filtering, and negative effect sizes for SDNDr and kurtosis are consistent with limiting similarity and even spacing of traits, respectively, which are indicative of competition. If HF shaping dominance pattern among habitat types, we expect reduced RANGE and VAR of traits as evenness index (we use Hulbert's pie evenness index as a measure of dominance) of communities decreases. Alternatively, if ND (competition) shaping dominance pattern among habitat types, we expect decreased SDNDr and smaller kurtosis (fat tailed distribution) of traits as evenness index of communities decreases. Moreover, we expect that, the communities dominated by few species such as swamps should have negative effect size values for both HF (RANGE and VAR) and ND (SDNDr and kurtosis) measures, whereas communities with no dominant species such as non-swamp (terra-firme) forests should have positive effect size values for measures. The six continuous traits and first PCoA axis of categorical traits was considered independently for the analysis. Species without a given trait value were excluded from that particular analysis.

We tested for nonrandom patterns of community assembly and ecological dominance among habitat types by creating 999 null communities of equal richness to the sample plot by drawing species at random from two different species pools mentioned above, weighted by plot-wide species abundance. Finally, to calculate the effect size of an observed metric for each swamp and terra-firme (non-swamp) communities, we subtracted the mean metric of the simulated null communities from the observed value and divided by the standard deviation of the simulated null communities. In this analysis, we used the individual plots from both swamp and terra firme forest as our definition of a community. The calculation of trait spacing metrics and trait spacing analysis were done using the R script from Kraft & Ackerly (2010).

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& Ackerly 2009; Kraft & Ackerly 2010). In all analyses, two-tailed tests were used for trait means, while one-tailed tests were used for all other metrics based on a priori predictions of habitat filtering and niche differentiation.

We also conducted Pearson's correlation analyses between community level trait spacing metrics and Hulbert's pie evenness index (used as measure of dominance). These analyses allowed us to determine the relative role of habitat filtering and niche differentiation processes to predict the dominance of tree communities in freshwater swamps.

Phylogenetic signal of traits and PGLS: To quantify the degree to which phylogenetic relatedness predicts the similarity of species in functional traits, we calculated separately phylogenetic signal for both continuous and categorical traits. We quantified phylogenetic signal 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 & Purvis (2010) for categorical 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)

We used the subroutine PGLS in the R-package Caper ((Orme *et al*. 2012) to examine associations between plot-wide abundance of species and functional trait independent of similarity due to phylogeny. This method implements Generalized Least Squares models which account for phylogeny by incorporating estimates of relatedness between taxa into comparisons that determine whether an independent trait (here functional trait) predicts values of another dependent trait (here abundance). It provides a more general and flexible approach to the widely-used independent contrasts methods pioneered by Felsenstein (1995) for assessing correlations between traits independent of phylogenetic divergence. In our analyses we assessed whether a measure of six continuous trait (individually and combined) and categorical trait (first PCoA axis) was significantly associated with the plot wide abundance of species occurring in swamp. Significance of the association was assessed using a t-test to evaluate whether the slope was significantly different from zero.

Mapping correlation and ancestral reconstruction of root traits: We used Pagel's (Pagel 1994) method to test for correlated evolution of adventitious roots (present or absent) and habitat preference (swampy and non-swampy) by using ARD (all rate different) model of transition rates among traits (Appendix B10). The function for the method is available in the R package phytools[47]. Using likelihood, the Pagel (Pagel 1994) method fits two models for character transition in the two traits under a continuous time Markov chain: one in which the two characters evolve independently, and a second, more parameter rich model in which the rate of change in evolution of adventitious roots is influenced by the state of habitat type (swampy or non-swampy), or vice versa. We used a likelihood ratio test to ask whether a model of correlated evolution between presence or absence of adventitious roots and habitat preference significantly better explained our data than the simpler model of independent evolution of the two traits.

We used stochastic character mapping (Huelsenbeck *et al*. 2003) to reconstruct the evolution of adventitious root types and habitat preference in tree communities occurring in freshwater swamps and adjacent terra firme forest. We used the package phytools (Revell 2012) to reconstruct the trait evolution. Phytools uses a Markov chain Monte Carlo (MCMC) approach to model the evolution of a categorical trait on a phylogenetic tree (Huelsenbeck *et al*. 2003). Out of the three transition models (ER = equal rates model, SYM = symmetrical model, and ARD = all-rates-different model), we used ARD following model selection via the corrected Akaike Information Criterion (Appendix B11). We mapped two states of habitat preference (swampy and non-swampy) and two states (presence and absence) of adventitious root types (floating water roots and serpentine roots, Knee roots, stilt roots and rhizome) on phylogenetic tree. Most of the species show a clear preference for a specific habitat type. In case species had been assigned to several habitat types, we identified the most common habitat by referring to the locality and habitat information of the species provided in literature, and to our field observations.

3.4 Results

3.4.1 Abundance pattern of tree communities in swampy and terra-firme (non-swampy) habitat

To determine whether tree community in swamp and adjacent terra-firme (non-swampy) habitat differ in dominance and rarity, we plotted abundance of each tree species occurring in each habitat with log-normal SAD in a Whitakers's plot. Our observational abundance data from 42 swamps and 29 adjacent terra-firme (non-swampy) forest revealed that, abundance distribution was left skewed with a few dominant species and many rare species in swampy habitat (Fig. 3-1) as oppose to even distribution of tree species in adjacent terra-firme forest (Fig. 3-1). Notably, species belonging to family Myristicaceae and Anacardiaceae consistently dominated all 42 swamps surveyed in the present study. However, there were no dominant species observed in adjacent terra-firme (non-swampy) habitat. We observed that, species which evolved traits to adapt in swampy condition were more likely to dominate the swampy habitat and those species which lacked these traits were occurred in very low frequency (Fig, 3-2). Moreover, these dominant species were found to be either exclusive to swampy habitat or occurring very frequently in other similar habitats such as riparian forest (Fig. 3-2).

3.4.2 Phylogenetic signal of traits and trait-abundance correlations

As phylogenetic non-independence can inflate measures of correlation among traits, we first evaluated the degree of phylogenetic signal in six continuous and five categorical traits (Appendix B12). Among continuous traits, except maximum DBH all other traits showed significant phylogenetic signal (Appendix B12) and only germination type and seed dormancy type showed significant phylogenetic signal in case of categorical traits (Appendix B12). We reduced continuous and categorical traits separately into one single axis using PCoA. The first PCA axis of categorical traits explained 72% of total variance followed by PCA2 (23.15%) (Fig 3-3a). In case of continuous traits, the first PCA axis explained 65% of total variance followed by PCA2 (28.75%). Almost similar results were recovered in combined analysis of continuous and categorical traits (Fig 3-3c). Further, the redundancy analysis showed that, traits such as presence of adventitious roots, inundance tolerance and seed germination strategy significantly contributed to total variance explained by first and second PCA axis in case of categorical traits (Appendix B13) and maximum DBH and seed size explained total variance in first and second PCA axis of continuous traits (Appendix B13).

We subjected first PCA axis of categorical and continuous traits and individual continuous traits to test whether functional traits predict the dominance pattern of tree community in swampy habitat after accounting for traits similarity due to phylogenetic relationship of species using PGLS analysis. Our results suggest that, there was significant positive relationship between functional traits and dominance of species as measured by density/m^2 of swamp (Fig 3-3d to 3-3f and Table 3-1). Interestingly, categorical traits ($R^2 = 0.262$, $p < 0.0001$) (Fig 3-2, Fig 3-3d, and Table 3-1) predicted the dominance pattern better than continuous traits ($R^2 = 0.0001$, $p = 0.886$) (Fig 3-3e and Table 3-1). However, few continuous traits such as maximum DBH ($R^2 = 0.073$, $p= 0.0007$) and maximum attainable height ($R^2 = 0.051$, 0.006) showed significant relationship, but the relationship was very weak compare to categorical traits (Table 3-1). Though many of the traits showed significant phylogenetic signal, the trait-abundance relationship was independent of traits similarity due to phylogenetic relationship of species, indicating dominance pattern predicted by functional traits was not significantly influenced by evolutionary history of a species as suggested by non-significant slope difference before and after accounting for phylogenetic relationship (Table 3-1). Trait-abundance pattern of categorical traits and phylogenetic relationship of species is shown in Fig. 3-2.

We further tested whether trait-abundance relationship of tree community in swamp is due to random stochastic processes or due to non-random association using different null models both at landscape and plot-scale level. We found significant trait-abundance relationship, both at landscape and plot scale and the relationship was significantly different from random expectation

(Table 3-2, Appendix B14 to B16). At landscape level except wood density and seed mass, all other trait showed significant relationship (Table 3-2, Appendix B14 to B16) and at plot level except wood density the relationship was significant for all other traits (Table 3-2, Appendix B16). However, the results were strong at plot level than at landscape level as evidenced by higher r values for each trait at plot level than at landscape level (Table 3-2, Appendix B15 to B16) and categorical traits predicted the relationship stronger than continuous traits (Table 3-2, Appendix B14). Moreover, the results were not sensitive to the choice of null model as both trait shuffle and abundance shuffle null modes had almost similar r-values both at landscape and plot level analysis (Appendix B15 to B16). Further, we found that abundant or dominant species had different trait values than rare or less abundant species, averaged over all sites. Mainly we observed that, dominant species had relatively taller stature, larger leaf size, bigger seeds, larger seed mass and lower wood density than the less abundant species. Moreover, abundant or dominant species also had categorical traits important to adapt in flooded condition in swamp, mainly adventitious roots (knee roots, stilt roots), buttress, recalcitrant seeds with hypogeal germination and they were reported to be flood or inundance tolerant, whereas less dominant or rare species mostly lacked these categorical traits (Fig. 3-2).

3.4.3 Trait-abundance relationship and community level trait spacing metrics among habitats

As expected, the trait-abundance relationship was significant only for tree communities in freshwater swampy habitat which is dominated by few species, whereas trait-abundance relationship did not deviate significantly from random expectation for tree communities in terra-firme forest (non-swamp) which is characterized by even distribution of species (no dominant species). Moreover, the trait-abundance relationship for tree communities in freshwater swamp significantly deviated from terra-firme forest tree communities except for the trait maximum attainable height (Table 3-2).

We determined the importance of habitat filtering and niche differentiation processes such as competition on assembly and dominance of species in freshwater swamp tree communities using trait-spacing analysis. Here we only present trait spacing analysis results obtained using null models of local species pool (Figs. 3-4 to 3-5, and Appendix B17 to B19), for which the results were highly significant and consistent with prediction compared to results obtained using regional species pool null model (Appendix B20). We found that community level trait means for tree assemblages in swamp and terra-firme-forest (non-swamp) were significantly different (, Fig. 3-4a to 3-4d and Appendix B18a to B18c). Mainly, tree communities in freshwater swamps had significantly taller stature (Appendix B18a), higher maximum DBH (Fig. 3-4a), larger leaf size (Fig. 3-4b), lower wood density (Fig. 3-4c) and higher PCA values of categorical traits (Fig. 3-4d) compared to tree communities in terra-firme forest (Fig. 3-4a to 3-4d and Appendix B18a). Similarly, the community level trait means were significantly correlated with Hulberts's pie evenness index (measured of dominance) (Appendix B22), interestingly the communities with un-even distribution of species (lower Hulbert's pie values) colonized by tree species with relatively taller stature (Appendix B18d), larger maxim DBH (Fig. 3-4e), lower wood density (Fig. 3-4g), bigger leaf (Fig. 3-4f) and higher PCA values for categorical trait (Fig. 3-4h) than communities with even distribution of species (Fig. 3-4e to 3-4h and Appendix B18d). Our trait spacing analysis found evidence for niche based processes (habitat filtering and completion) in determining assembly and dominance of tree communities in freshwater swamps (Fig. 3-5 and Appendix B17 and B19). As expected, the variance (VAR) and range (RANGE) was significantly lower and negative as compared to expectations from our null model in flooded habitat (freshwater swamp) where tree communities experience water-logged stress, whereas VAR and RANGE was higher and positive as compared to expectations from our null model for adjacent non-swampy habitat (terra-firme forest) where tree communities were not exposed to flooding and water-logged stress (Appendix B17). Except seed size, all other traits showed the similar pattern of reduced and negative effect size of VAR and RANGE for tree communities in freshwater swamps, which is consistent with our prediction of habitat filtering (Appendix B17). We also predicted that if niche differentiation processes such as competition determine the assembly of species in freshwater swamp tree communities, the traits should be more evenly distributed and should have smaller kurtosis values than null model expectation. This prediction was not strongly supported (Appendix B20), as measured either by SDNDr or by kurtosis (Appendix B17). Only few traits such as maximum DBH, leaf size and wood density showed significantly lower and negative effect size either for SDNDr or kurtosis (Appendix B17), which indicates that competition plays weak role in determining assembly of species in freshwater swamp tree communities. Finally, the effect size of both VAR (Fig. 3-5b, 3-5f, 3-5j and 3-5n, Appendix B22) and RANGE (Fig. 3-5a, 3-5e, 3-5i, and 3-5m, Appendix B22) for many of the traits (maximum DBH, leaf size, wood density and categorical traits) were significantly correlated with Hulbert's pie evenness index (measure of dominance). The communities with un-even distribution (dominated by few species) of species had lower and negative VAR (Fig. 3-5b, 3-5f, 3-5n) and RANGE (Fig. 3-5a, 3-5e, 3-5m), whereas communities with even distribution of species (no dominant species) had higher and positive VAR (Fig. 3-5b, 3-5f, 3-5n) and RANGE (Fig. 3-5a, 3-5e, 3-5m). The lower and negative values of VAR and RANGE in tree communities in freshwater swampy habitat which is dominated by few species suggest that, the dominance of species in tree communities in these habitat is determined by habitat filtering and as dominance reduced the role of habitat filtering weakened (Fig. 3-5a to 3-5b, Fig. 3-5e to 3-5f and Fig. 3-5m to 3-5n). Moreover, the relationship between Hulbert's pie evenness index and effect size of SDNDr (Fig. 3-5c, 3-5g, 3-5k, 3-5o; Appendix B19 and B22) and kurtosis (Fig. 3-5d, 3-5h, 3-5l, 3-5p; Appendix B19 and B22) were non-significant indicating niche differentiation (competition) processes are not important in determining dominance of species in tree communities of freshwater swamps.

3.4.4 Ancestral history and evolutionary pattern of ecologically important traits

We reconstructed ancestral history of adventitious roots (Appendix B23a), which are important to adapt in waterlogged condition in freshwater swamps and habitat specialization (Appendix B23b) (swampy and non-swampy) across 210 tree species found in freshwater swamps and adjacent terra-firme forest using stochastic mapping. We found species which lacked adventitious roots and adapted to non-swampy habitat to be the most probable ancestors of species with adventitious roots (Appendix B23a) and specialized to colonize swampy habitat (Appendix B23b). Interestingly, we also noted that both adventitious roots and habitat specialization towards swampy habitat has evolved repeatedly across multiple lineages, indicating convergent and non-conservative evolution of root trait and habitat specialization in freshwater swamp tree communities (Appendix B12 and Appendix 23).

We further tested whether colonization and adaptation of lineages to swampy or flooded habitat depend on whether lineages evolved traits (adventitious roots) that confer tolerance to flooding or lineages colonize the habitat independent of trait evolution. The more parameter rich dependent evolution model showed a better fit than the simpler independent evolution model (LR= 63.64, P= 4.995e-13). This suggest that evolution of ecologically important traits such as adventitious roots mainly influenced by whether lineages colonize swampy or flooded habitat or vice-versa. In particular, we found higher transition rate to swampy habitat occurred only in lineages which had adventitious roots (1.620) than those lineages which lacked adventitious roots (0.070) (Appendix B24). Though, lineages in non-swampy habitat also had higher transition rate to evolve adventitious roots (0.913), it was two times lesser compare to swampy lineages (1.620) (Appendix B24). Moreover, we observed, transition to colonize non-swampy habitat was higher in lineages which lacked adventitious roots (1.296) than in lineages which had adventitious roots (0.0071). Finally, the lineages specialized to colonize swampy habitat had higher transition rate to evolve adventitious roots (0.488) than lacking the adventitious roots (where the rate was estimated to be zero in Appendix B24). Overall, these biases in transition rates for evolving adventitious roots only in lineages that are specialized to colonize swampy habitat and loss of adventitious roots in lineages adapted to non-swampy habitat, strongly suggest the possibility of tight correlated evolution between ecologically important traits and swampy habitat specialization in freshwater swamp tree communities.

3.5 Discussion

If dominance and rarity of species in freshwater swamp tree communities affected by random (stochastic) or neutral processes, then there should not be any significant correlation between observed abundance and functional traits of a species. In contrary to this expectation, our analysis found strong correlation between abundance and functional traits of species within tree communities of freshwater swamp in Western Ghats, suggesting that local scale non-neutral processes affecting dominance and rarity of species in this habitat. The relative importance of neutral versus deterministic (ecological (niche based) and evolutionary (phylogenetic)) processes in determining dominance and rarity of species among suite of co-occurring species in ecological communities have been extensively debated in literature (Hubbell, 2001; Morlon *et al*., 2009; Cornwell & Ackerly 2010; Maire *et al*. 2012; McGill *et al*. 2005; Pitman *et al*. 2001; Seabloom *et al*. 2015). In the last decade neutral theory (Hubbel 2001) was believed to be the dominant mechanism to explain abundance pattern of species in ecological communities and it successfully predicted species abundance and rarity in some cases (Chave 2004), suggesting that species functional differences may not be very important to generate the observed patterns of abundance distribution of species in ecological communities. However, recent studies using trait based approach have shown that, the processes affecting dominance and rarity of a species in community is non-neutral and mainly determined by niche based processes such as habitat filtering and competition (Cornwell & Ackerly 2010; Maire *et al*. 2012) and thus species functional differences are very important for generating observed pattern of diversity in nature. Surprisingly, multiple line of evidence from our study also support the later evidence of non-neutral local scale processes affecting abundance and rarity of species. Moreover, our study by accounting for traits evolutionary relationship among co-occurring species much more realistically determine the factors affecting abundance and rarity of species, as earlier empirical studies on abundance and rarity of species using trait based approach ignored this relationship (Cornwell & Ackerly 2010; Maire *et al*. 2012). By selecting traits that were strongly linked to individual species survival and performance in the habitat (Parolin 2012; Violle *et al*. 2007) and determining the evolutionary relationship of these traits among co-occurring species in the habitat, our study provides a general framework to untangle the relative role of neutral versus non-neutral processes affecting one of the important community assembly process dominance and abundance distribution of species in tropical tree communities.

We found strong correlation between species abundance and functional traits even after controlling for traits evolutionary relationship among co-occurring species (Table 3-1 and Fig. 3-3). These results suggest that, trait-abundance relationship observed in tree communities of freshwater swamp is independent of traits evolutionary relationship. Though many of the traits showed significant phylogenetic signal (Appendix B12) indicating closely related taxa tend to show similar traits, however this conserved nature of traits among co-occurring species did not significantly influenced the trait-abundance relationship. This pattern of dominance independent of traits evolutionary relationship observed in the study might be due to phylogenetic over-dispersion of dominant taxa, we found most of the woody taxa dominated the swampy habitat were phylogenetically distant and randomly distributed across phylogenetic tree (Fig. 3-2). Similar pattern of phylogenetic independence of traits affecting community level processes is also reported in other studies (Maire *et al*. 2012; Barlato *et al*. 2012; Lemoine *et al*. 2015). Moreover, the trait-abundance relationship was not influenced by random stochastic processes both at landscape and local scale, as our observed trait-abundance relationship significantly deviated from random expectation of trait-abundance relationship observed under null models of random trait evolution (trait shuffle) and random species abundance (abundance shuffle) (Table 3-2, Appendix B15 to B16). The existence of significant within-community correlation between functional traits and abundance is strong evidence that there are non-neutral local and landscape scale processes affecting dominance and rarity of species in tree communities of freshwater swamps in Western Ghats. The similar processes have been reported to be important for abundance and rarity pattern of woody plant species in coastal California (Cornwell & Ackerly 2010). Further the abundance of woody plant species in tree communities of freshwater swamp was strongly influenced by categorical traits, though significant the trait-abundance relationship was weaker for continuous traits (Table 3-1 to 3-2, Fig. 3-2). This pattern is expected because the categorical traits chosen in the study (Appendix B4) has been mentioned to be very important for plant species to survive under submerged and water-logged condition in swamp (Parolin & Wittmann 2010; Parolin 2012), for example the traits such as adventitious roots and buttress provide support to woody plants to stand erect in well drained alluvial soil and soft tissue inside adventitious roots and lenti cells on the surface helps for plants to breath in submerged soil condition (Appendix B4, Parolin & Wittmann 2010; Parolin 2012). Interestingly, the presence of adventitious root was one of important variable majorly contributed to abundance pattern of woody plant species observed in the present study (Appendix B13). Though chosen continuous traits are important for many life history and physiological processes (Appendix B4), they may not be as important as chosen categorical traits for plants to survive in flooded habitat. However, the chosen continuous traits such as leaf area, wood density and maximum attainable DBH may be important to exploit resource from poor nutrient soil condition in freshwater swamp (Vijaykumar & Vasudeva 2011).

We also observed that, similar species (*Semecarpus kathalekanensis, Myristica faruva var. Magnifica, Gymnocrathaera canarica*) belonging to suite of families (Myristicaceae, Anacardiaceae) dominated the swamp tree community irrespective of geographic area from where they were sampled (Fig. 3-2) and correlation between abundance and traits of species remained consistent both at landscape and local plot scale (Table 3-1 to 3-2 and Appendix B15 to B16). Similar to the observation found here, the paleontological study in mammal (McGill *et al.* 2005) found that rare species stay rare and common species remain common much longer than expected based on a model of purely stochastic processes. Further, study of Amazonian trees has also shown that patterns of abundance are consistent across vast spatial scales (Pitman *et al.* 2001). Overall these observations suggest that the ecological processes affecting abundance and rarity remain relatively constant through time and space (Cornwell & Ackerly 2010). One possibility that can explain this pattern as suggested by Cornwell and Ackerly 2010, is the three-way relationship between physiological and morphological traits of individual species that strongly linked to habitat (McGill *et al*. 2006), the relative abundance of different resource and micro-habitat variation (Grime 2006) and abiotic conditions that allow species with specific traits to become consistently dominant at a given site. In fact, dominant woody species in freshwater swamp has evolved specialized morphological (adventitious roots, hypogeal germination etc.) and physiological traits (flood or inundance tolerance) important to adapt in submerged waterlogged condition in swamp where as rare species lack these traits (Fig. 3-2). Moreover, limited availability of soil nutrient in freshwater swamps may lead to abundance of only those species which evolved trait strategies that can exploit these limited resources in the habitat (Vijaykumar & Vasudeva 2011).

We further found strong evidence for niche based processes affecting assembly and dominance of woody species in tree communities distributed across flooding gradient in Western Ghats (Fig. 3-4 to 3-5, and Appendix B17 to B20). Despite the close physical proximity, the tree communities in flooded (freshwater swamp) habitat had significantly different trait strategies than non-flooded habitat (terra-firme forest) tree communities (Fig. 3-4; Appendix B18 and B21). These results highlight the fact that, the flooding gradient in tropical forest habitats support communities with divergent trait strategies irrespective of geographical proximity of habitat and contrasting species identity. Similar pattern of divergent trait strategies has been shown for woody species occurring across gradient of topography and moisture (Kraft *et al*. 2008; Cornwell & Ackerly 2010) and also in tropical forest occurring across seasonal flooding gradient in Amazon (Fortunel *et al*. 2014). Interestingly, the trait strategies such as lighter wood, bigger leaf, maximum DBH, taller stature and number of categorical traits (adventitious roots, hypogeal germination, flood and abundance tolerance) seen in freshwater swamp tree communities are mentioned important to survive in flooded habitat (Parolin & Wittmann 2010; Parolin 2012; Fortunel *et al*. 2014) as these trait strategies promote rapid growth under poor soil nutrient availability under submerged condition (Vijaykumar & Vasudeva 2011). Whereas woody species inhabiting non-flooded and dryer habitats reported to have heavier wood, smaller leaf and lacks many of categorical traits used in the present study (Cornwell & Ackerly 2010; Parolin &Wittmann 2010; Parolin 2012) and the same was also observed in our study (Fig. 3-4, Appendix B18). Further, the community weighed range and variance for key community wood, leaf, seed (e.g. maximum DBH, wood density, leaf size and seed mass) and categorical traits varied among habitats and were significantly smaller compared to expectations from our null model (Table S9 and S10). These results are consistent with a role of habitat filtering. However, the habitat filtering effect was stronger in flooded habitat compare to non-flooded habitat, because almost all the traits showed reduced variance and range compare to null model expectation for tree communities of freshwater swamp, whereas only few traits showed the pattern for tree communities of terra-firme forest (Appendix B17 and B20). This is expected because the flooded condition in freshwater swamps act as strong ecological filter, whereas terra-firme habitat lacks such micro environment variation. It is also important to note that, the effect of habitat filtering was strong at local plot scale (Appendix B17) than in landscape scale (Appendix B20) and null models restricted either to freshwater swamp tree communities or terra-firme tree communities did not affected the habitat filtering effects (Appendix B20). These results suggest that, the strength of habitat filtering vary across local and landscape scale and two habitats (freshwater swamp and terra-firme forest) distributed across flooding gradient explain most of the habitat filtering effect observed in the present study. In contrast to results of habitat filtering, we found weak evidence for niche differentiation processes such as competition as measured either by SDNDr or kurtosis (Appendix B17 and B20). Except categorical trait, wood density and leaf size, the results were not significant for other traits (Appendix B17 and B20). The similar pattern of weak evidence for niche differentiation processes and stronger evidence for habitat filtering in assembly of species is observed in tree communities of flooded habitat in Amazonian forest and other tropical forest habitat (Engelbrecht *et al*. 2007; Kraft *et al*. 2008; Paine *et al*. 2011; Katabuchi *et al*. 2012; Fortunel *et al*. 2014). Thus, our results further confirm and extends on previous research showing the importance of habitat filtering in tropical forest habitats and demonstrate that, the micro-environmental gradient in the habitat not only assemble species with divergent strategies but also shift the community functional composition across the gradient.

Similar to species assembly, we also found strong evidence for habitat filtering determining dominance or abundance distribution of species in tree communities distributed across flooding gradient (Fig. 3-4 to 3-5; Appendix B18 and B19). As expected, the community level trait mean and effect size of range and variance were significantly correlated with Hulbert’s pie, which is a measure of dominance (Fig. 3-4 to 3-5; Appendix B18 and B19, Appendix B22). We observed that, the communities with lower Hulbert's pie (higher dominance) had significantly lower effect size values of trait range and variance compared to communities with higher Hulbert's pie (lower dominance or no dominance) (Fig. 3-4 to 3-5; Appendix B18 and B19). The results were consistent across all traits except for traits related to regeneration strategy (seed mass and seed size) and maximum attainable height (Fig. 3-4 to 3-5; Appendix B18 and B19). The consistently reduced range and variance of functional traits in tree communities dominated by few species and consistently increased range and variance in tree communities without dominant species clearly suggest that environmental filtering not only determine the species assembly, but also strongly determine relative abundance and dominance pattern in tree communities distributed across flooding gradient in Western Ghats. Moreover, the effect size values of SDNDr and kurtosis were not significantly correlated with Hulbert's pie except for maximum DBH and we did not observe either increased or decreased effect size values of SDNDr and kurtosis in tree communities distributed across flooding gradient (Appendix B18 and B19, Appendix B22) again suggesting the weak role of niche differentiation processes such as competition in determining abundance distribution of species in tree communities of freshwater swamp. The similar pattern of weak evidence for niche differentiation processes and stronger evidence for habitat filtering in determining abundance distribution of species is shown by Maire *et al*. (2012) in grassland communities. Further study by Fortunel *et al*. (2014) also confirmed the similar results in tree communities of flooded and terra-firme forest in Amazon. All these results further confirm that, the abundance distribution and dominance pattern of species in communities is not generated by neutral or stochastic processes, but these community level processes are strongly affected by non-neutral (deterministic) niche based processes such as habitat filtering. Overall our results and findings from earlier studies ((Cornwell & Ackerly 2010, Maire *et al*. 2012, Fortunel *et al*. 2014) should increase our understanding of the mechanisms that promote the rarity and abundance of species in communities.

Finally, we found that adventitious roots and habitat specialization towards swampy habitat has evolved independently across multiple distantly related lineages in tree communities distributed across flooding gradient in Western Ghats (Appendix B23), confirming the key ecological trait that confer adaptation to flooded habitat (freshwater swamp) and swampy habitat specialization in tree communities of freshwater swamp is result of convergent evolution. Moreover, the evolution of adventitious roots and swampy habitat specialization in tree communities of freshwater swamps is tightly correlated (Appendix 24), indicating that adventitious roots consistently evolved only in those lineages which are either exclusive to swampy or riparian habitat in tree communities distributed across flooding gradient. Overall these results highlight that, the key ecological traits that determine community level processes such as assembly and abundance distribution of species in a specialized habitat such as freshwater swamps have a different evolutionary history and evolve in response to environmental gradient in the habitat.

3.6 Conclusion

By adapting a framework that integrates analyses of functional traits with that of community level phylogenetic comparative analyses, we first quantified the species functional difference after accounting for traits evolutionary relationship among co-occurring species and tested their ability to determine the relative importance of neutral (stochastic) versus non-neutral (niche based) mechanisms in assembly and dominance pattern of species in tree communities distributed across flooding gradient. Our result suggest that species functional difference alone predict the relative abundance of species independent of traits evolutionary relationship among co-occurring species in a community and non-neutral niche based processes such as habitat filtering strongly affect the dominance and rarity of species in flooded forest (freshwater swamp) tree community. For the first time in this study, we have documented the strong connection between species functional difference (functional traits) and abundance of species after accounting for traits evolutionary relationship among co-occurring species in tree communities of tropical forest both at local plot and landscape scale and as well as shifts in the trait–abundance relationship across an ecological gradient (flooding gradient). Interestingly, earlier studies ignored the evolutionary relationship of traits when determining relationship between species functional difference and abundance (Cornwell & Ackerly 2010; Maire *et al*. 2012). Our study also showed that, ecologically important traits determining the assembly and abundance pattern of species in flooded forest (freshwater swamp) tree communities have a convergent evolutionary history and they have mainly evolved in lineages specialized to adapt in flooded or waterlogged condition in habitat. Overall, the findings from the present study strongly support the idea that non-neutral, niche based processes play an important role in determining abundance distribution of species within communities both at local and landscape scale and challenge the ongoing debate about whether dominance and rarity of species in communities are exclusively structured by stochastic processes (McGill *et al*. 2006, 2007; Shipley *et al*. 2006). The promising successes of trait-based approach integrated with community level comparative phylogenetic analyses to explain the patterns of species abundance offers a promising opportunity and may encourage future biodiversity research in diverse tropical forest habitats to explain the mechanisms underlying the diversity and distribution pattern of species.

Table 3-1. Results of phylogenetic regression analyses (PGLS) with functional traits (continuous and categorical) and density/m^2 as predictors of dominance. Degrees of freedom = 41. Trait data was log transformed before the analysis.

Trait	**λ**	**R^2**	**Adj R^2**	**F**	**P value**	**t-test (slope of OLS v/s PGLS)**
Maximum attainable height (m)	0.162	0.051	0.044	7.882	0.006	NS
Maximum DBH (cm)	0.182	0.073	0.068	11.87	**0.0007**	NS
Leaf size (mm^2)	0.161	0.031	0.024	4.704	0.032	NS
Seed size (mm^2)	0.139	0.027	0.021	4.125	0.044	NS
Wood density (g/cm^3)	0.169	0.005	-0.002	0.790	0.376	NS
Seed mass (g)	0.131	0.033	0.027	5.065	0.026	NS
Continuous (PCA1)	0.176	0.0	-0.006	0.0206	0.886	NS
Categorical (PCA1)	0.192	0.262	0.257	52.28	**<0.0001**	NS
Combined (PCA1)	0.187	0.312	0.307	66.76	**<0.0001**	NS

Table 3-2: The linear relationship between functional traits and abundance on landscape and plot scale. The significant relationships that were robust relative to the choice of null models are in bold. r is the Pearson product–moment correlation coefficient.

	Landscape scale			**Plot scale**			
Trait	**Mean r**	**Wilcoxon**		**Mean r**	**Wilcoxon**		
		Abundance shuffle null	**Trait shuffle null**		**Abundance shuffle null**	**Trait shuffle null**	**Non-swamp null**
Height (m)	0.118	**<0.0001**	**<0.0001**	0.349	**0.003**	**0.004**	NS
DBH (cm)	0.074	**<0.0001**	**<0.0001**	0.383	**0.002**	**0.001**	**0.00132**
Leaf size (mm2)	0.104	**<0.0001**	**<0.0001**	0.234	**<0.0001**	**<0.0001**	**<0.0001**
Seed size (mm2)	0.046	**0.0021**	**0.0032**	0.332	**0.007**	**0.008**	**0.002**
Wood density (g/cm3)	0.059	NS	NS	0.247	NS	NS	**0.00252**
Seed mass (g)	0.067	NS	NS	0.403	**<0.0001**	**<0.0001**	**<0.0001**
Categorical (PCA1)	0.300	**<0.0001**	**<0.0001**	0.624	**<0.0001**	**<0.0001**	**<0.0001**

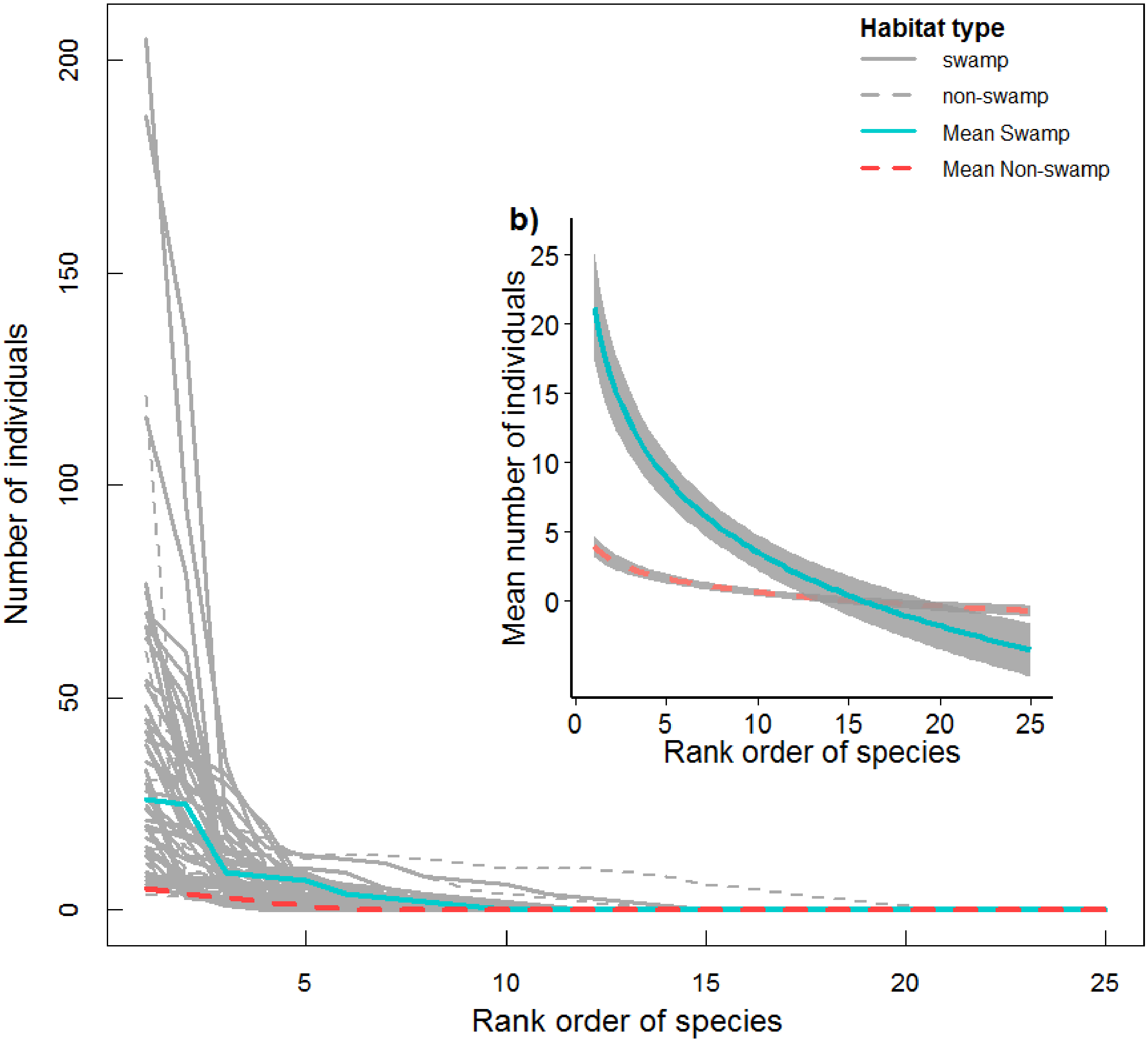

Figure 3-1: Species abundance distribution (SAD) curve for tree species in swamp and non-swampy habitat. The SADs are plotted with a log-normal model for data. a) abundance distribution for 42 swamps (thick lines) and 29 non-swamps (dashed lines) b) mean abundance distribution for swamp (blue line) and non-swamp (red line).

Note: Shaded area of curve in Figure b represent 95% confidence limit.

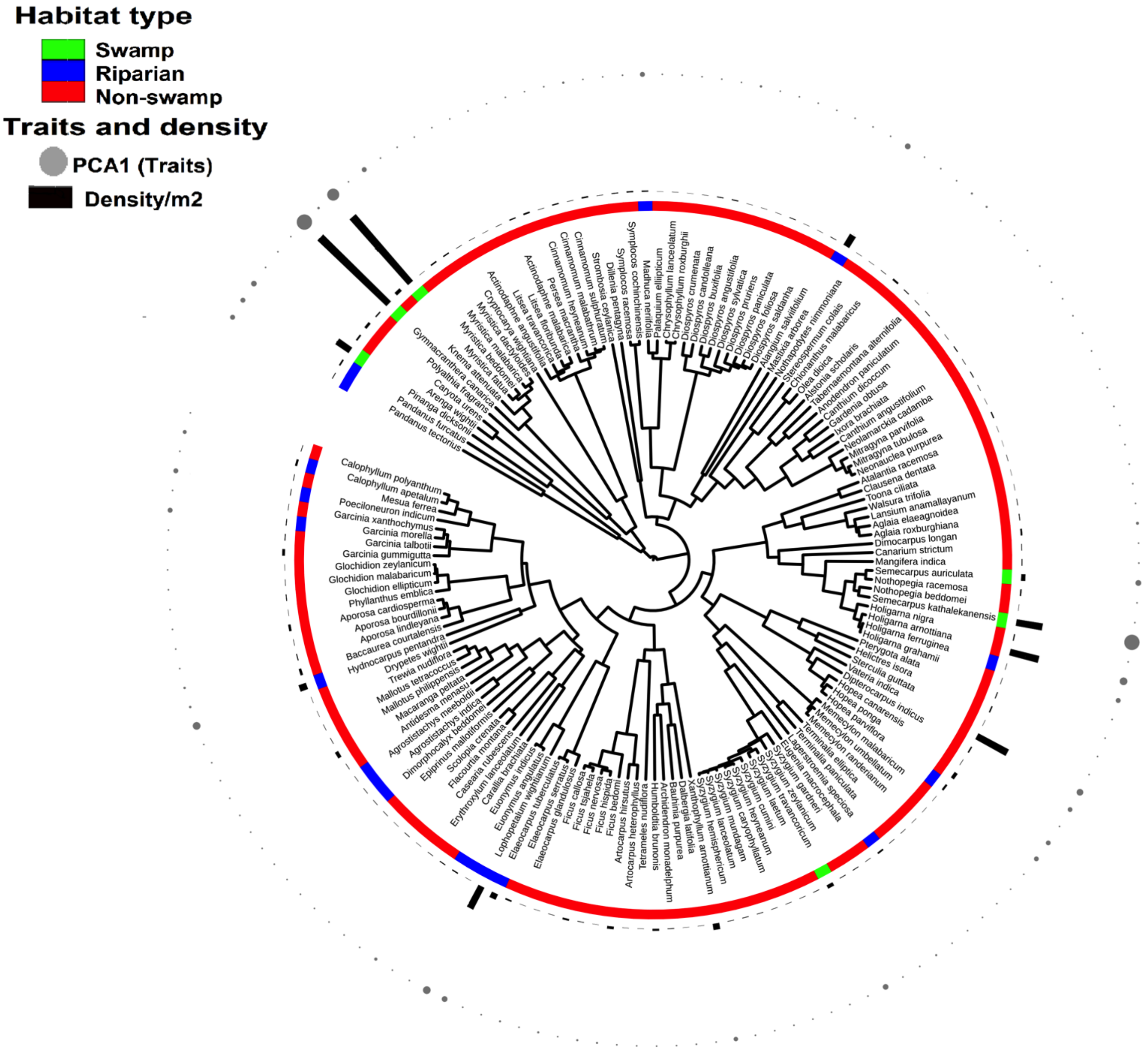

Figure 3-2: The density of individuals/m^2 (black bars) and first PCA axis (grey circles) of ecologically important categorical traits mapped on dated phylogenetic tree of 149 tree species occurring in swamps.

Note: Habitat specialization for each species marked in different colors: species restricted only to swampy habitat (green), species present in swampy habitat, but also occur frequently in other flooded habitat such as riparian forest (blue) and species very rarely occur in swampy habitat, but most frequent in non-swampy habitat (red). Presence/absence of circle indicates, whether species possess trait important to adapt in swampy condition and size of the circle represent Eigen values, bigger the circle higher Eigen values and smaller the circle lower Eigen values. Higher Eigen values means species with all categorical traits and lower Eigen values means species with only few traits.

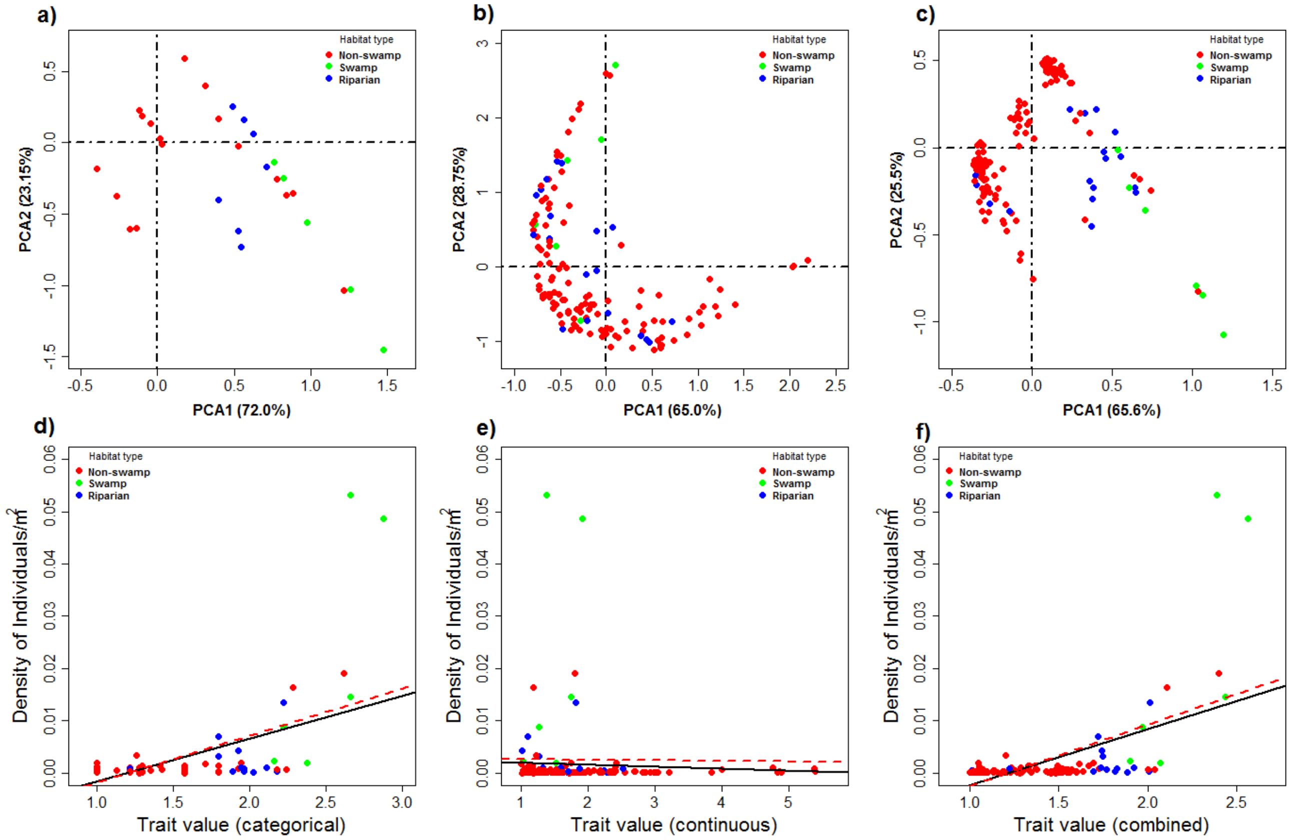

Figure 3-3: Trait-abundance relationship of tree species occurring in swampy habitat after accounting for their phylogenetic relationship. First panel, principal component analysis of five categorical and six continuous traits a) PCA for five categorical traits b) PCA for six continuous traits c) PCA for continuous and categorical traits combined. Second panel, phylogenetic generalized least square regression (PGLS) for traits and density of individuals/m2 d) first PCA axis of categorical trait e) first PCA axis of continuous trait and f) first PCA axis of combined trait.

Note: ordinary least squares (OLS; black line) and phylogenetic generalized least squares (PGLS; red line). Colored dots indicate habitat specialization of species.

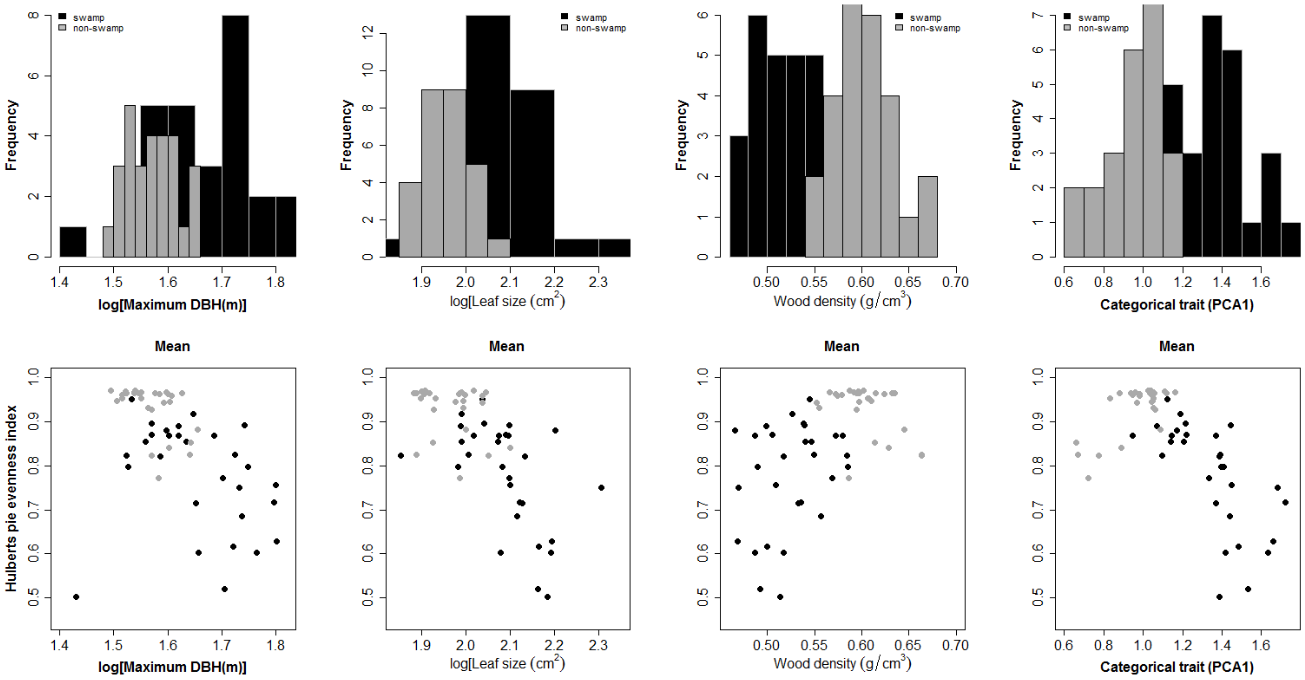

Figure 3-4: Community level trait pattern for tree communities in swampy and non-swampy habitat as a function of dominance (Hurlbert's pie) using local species pool null model. a) to d) observed distribution of traits among tree communities in swampy and non-swampy habitat. e) to f) trait mean plotted against Hulbert's pie (measure of dominance) respectively for maximum DBH, leaf size, wood density and first PCA axis of categorical traits. See results for other traits in Table S8 and Fig. S8.

Note: Colored dots indicates habitat from which plots were sampled, swamp (black) and non-swamp (grey).

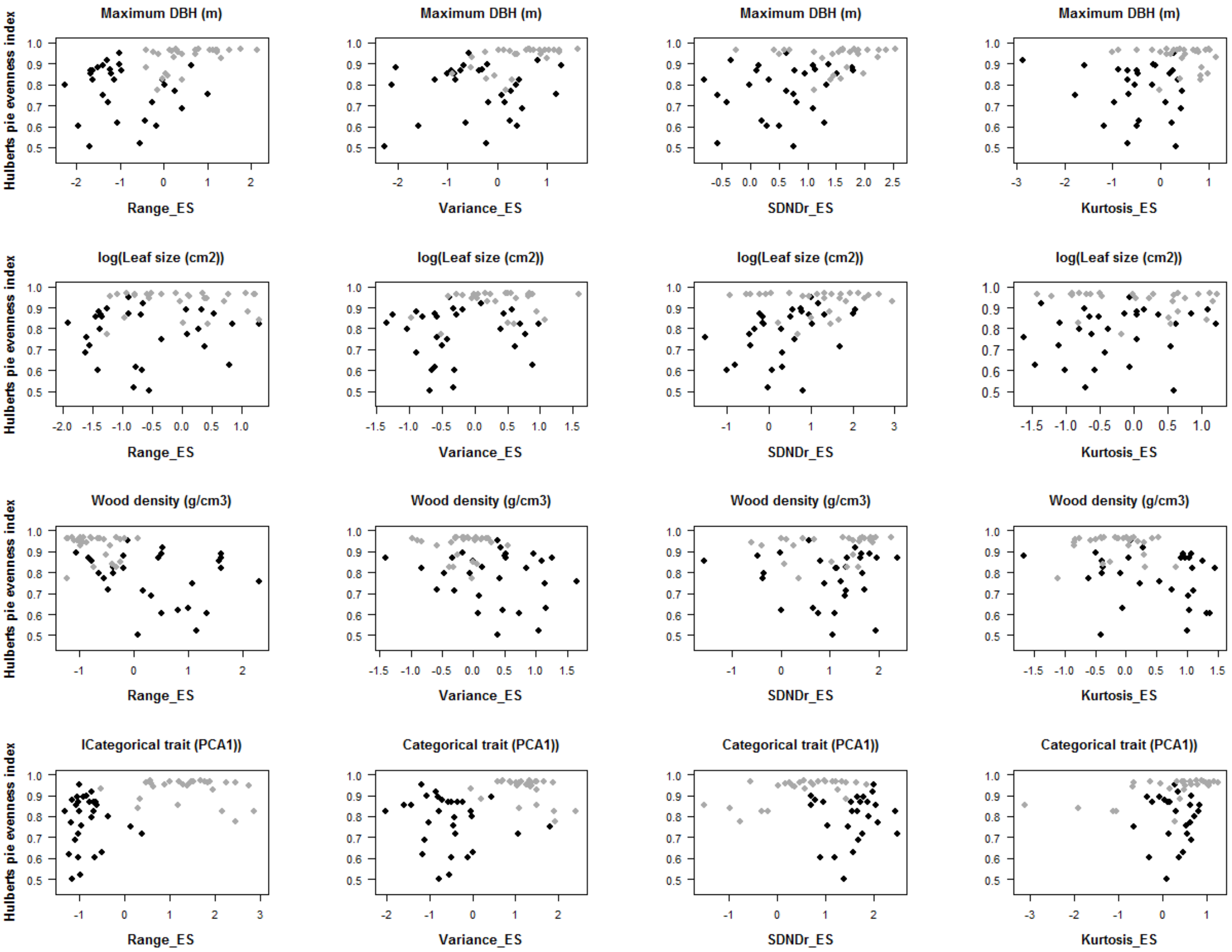

Figure 3-5: Correlation between community level trait spacing metrics and Hulbert's pie (measure of dominance). Effect size of trait spacing metrics: first row (a) to d)) maximum DBH, second row (e) to h)) leaf size, third row (i) to l)) wood density and fourth row (m) to p)) first PCA axis of categorical traits. The communities with lower values of Hulbert's pie (higher the dominance) show negative or reduced values of the metrics (Range and Variance) sensitive to habitat filtering for all traits except wood density (where relationship is reversed) compare to communities with higher values of Hulbert's pie. Whereas metrics (SDNDr and kurtosis) sensitive to niche differentiation processes such as completion show no correlations except for the trait (leaf size) metric (SDNDr). See results for other traits in Table S8 and Fig. S9.

Note: Colored dots indicates habitat from which plots were sampled, swamp (black) and non-swamp (grey).

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CHAPTER 4

Repeated evolution of swampy habitat specialization and associated morphological traits promote ecological speciation in primitive plant family Myristicaceae

4..1 Abstract

The seasonal flooding in lowland tropical rain forest thought to lead to specialization to flooded habitat and thereby contribute to ecological speciation in many tropical plants. Further, the degree to which specialization towards different habitats promote range-wide climatic niche differences among closely related lineages of plants is unclear. To address above questions, we conducted niche evolution and comparative phylogenetic analysis of key morphological traits (adventitious roots), swampy habitat association, distribution and environmental data obtained for global and endemic Myristicaceae members of Western Ghats, India. Comparative phylogenetic analysis revealed that swampy habitat association and adventitious roots were not phylogenetically clustered, suggesting repeated independent evolution of swampy habitat specialization in Myristicaceae. Habitat association mapped onto the phylogenetic tree shows association with swampy habitat to be the probable ancestral state in the group, with subsequent speciation events on non-swampy habitat. Further we found Asian Myristicaceae members have gained swamp habitat specialization more frequently than African and South American clades. Finally, our results suggest that range wide climatic niche significantly differ among swamp and non-swamp habitat specialists in Western Ghats. The repeated gain of swamp habitat specialization and associated morphological traits in parapatrically distributed sister taxa, suggest that seasonal flooding gradient was an important driver of ecological speciation in global and Western Ghats Myristicaceae. Our study also highlights the importance of local habitat specialization in promoting range-wide niche evolution and thereby species distribution pattern in sister lineages of tropical plants.

4..2 Introduction

The environmental heterogeneity at small spatial scales can act as local habitat filter and restrict subset of species to co-occur in limited abiotic conditions. Such niche differentiation at a small spatial scale due to local habitat heterogeneity is thought to lead to habitat specialization and thereby development of regional patterns of species diversity (MacArthur *et al.* 1964; Chase & Leibold 2003; Keitel & Chase 2004; Baraloto *et al.* 2007). The plants are widely known to exhibit habitat specialization as indicated by their strong association of species turnover and abundance with abiotic conditions (e.g., altitude, soil type, rainfall gradient, seasonal flooding; Gentry 1986, 1988; Tuomisto *et al.* 1995; Ruokolainen *et al.* 1997; Clark *et al.* 1998; Davies *et al.* 1998; Webb & Peart 2000; Pyke *et al.* 2001; Svenning 2001; Potts *et al.* 2002; Fine *et al.* 2005; Baraloto *et al.* 2007). The hypothesis that local environmental heterogeneity leads to habitat specialization and thereby ecological speciation in tropical plants is not been rigorously tested. Further, it is thought that niche specialization at local scale can also influence niche specialization across species range and as a result local habitat specialization co-evolves with range-wide climatic niche evolution. To date only few studies have tested this hypothesis (Emery *et al.* 2012). Finally, inferring evolutionary history of traits by explicitly incorporating phylogenetic relationships among species can provide considerable insight into adaptive evolution and niche assembly (Webb *et al.* 2002, Ackerly 2003). Thus, studies integrating analysis of climatic data, habitat association data and key morphological traits conferring specialization towards habitat in a phylogenetic context could be a useful approach to rigorously test above hypotheses. Such an approach is not only important to establish strong connection between local habitat specialization and range-wide niche evolution among sister lineages (Fine *et al.* 2005; Emery *et al.* 2012), but it is also invaluable for revealing the role of ecological selection in speciation and evolutionary basis of habitat specialization (Ricklefs *et al.* 1993).

Many earlier studies mostly tested for evolutionary basis of edaphic habitat specialization among tropical trees (Harms *et al.* 2001; Potts *et al.* 2002.; Palmitto *et al.* 2004; Fine *et al.* 2005; Russo *et al.* 2005). Seasonal flooding during heavy rains creates heterogeneous landscape of seasonally flooded and terra-firme (non-flooded) forest in lowland tropical rain forests. Despite knowing the fact that two habitats differ in micro habitat variables (flooding gradient, edaphic variables) and species composition, relatively little attention has been paid to understand how habitats with difference in seasonal water stress promote habitat specialization and limit species distribution both at small and large spatial scale (Prance 1979; Lopez & Kursar 2003; Parolin *et al.* 2004). Globally, the primitive and ecologically diverse pantropical plant family Myristicaceae known to dominate seasonally flooded tropical forests in lowlands and congeneric and conspecific species of the family known to exhibit divergent patterns of habitat associations in a heterogeneous landscape of seasonally flooded and terra-firme forest. Interestingly, congeneric and conspecific pair of Myristicaceae members occurring in these divergent habitats show unique morphological and physiological adaption to the respective habitat and have contrasting pattern of distribution across their geographic range. We therefore choose this plant group to investigate the role of flooded habitat specialization in ecological speciation and range-wide niche evolution.

Here, first we map habitat association (flooded (swamp) or non-flooded (terra-firme)) on dated phylogenetic trees of Myristicaceae 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 swamp habitat specialization i.e. swamp habitat specialists would be closely related to each other than they are to the non-swamp habitat specialists. This evidence supports the idea that evolution of swamp habitat specialization is limited by strong phylogenetic constraint and lineages are exhibiting phylogenetic niche conservatism. Alternatively, if we find that swamp habitat specialists are not clustered, or it is randomly distributed on phylogeny i.e swamp habitat specialists closely related to each other than to non-swamp habitat specialists. This evidence supports the idea that swamp 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. Second, we used recently proposed comparative niche evolution analysis to test the hypothesis that local habitat specialization co-evolves with range-wide climatic niche evolution. We specifically tested the prediction that parapatrically distributed swampy and non-swampy Myristicaceae members in Western Ghats have significantly diverged in their range-wide climatic niche and the niche divergence is not constrained by their phylogenetic relationship. We did this in two ways 1) Because these species are parapatrically distributed and recently diverged sister lineages, 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.* 2009). 2) To test niche comparison in phylogenetic context, we first compared niche divergence to genetic distance between species.

We then used comparative phylogenetic analysis to test for phylogenetic niche conservatism in range-wide climatic niche within a determined phylogeny of the study species.

4..3 Methods

4.3.1 Study system

Myristicaceae is a medium size family of angiosperm trees and shrubs with a wide pan-tropical distribution consisting of 21 genera and over 500 species (Christenhusz & Byng 2016). They are largely confined to lowland rainforest and occur in ecologically diverse habitats such as fresh water swamps, tidal forests, evergreen and semi evergreen forests. Along with Annonaceae, Magnoliaceae and three other monogeneric families, Myristicaceae belong to Magnoliales, one of the oldest angiosperm orders. Both molecular and morphological systematic studies support the monophyly of the genera in the group (Sauquet *et al.* 2003; Doyle *et al.* 2004). Although Myristicaceae has been considered as one of the primitive plant families, molecular dating evidence suggests that their evolution is very recent (about 21 Myr) (Doyle *et al.* 2004). Many of the genera in Myristicaceae are endemic to continents and South America and South-east Asia represent highest species diversity (Appendix C1 to C2). In Western Ghats, India there are six recognized species and they occur in wide range of habitats such as fresh water swamps, riparian habitat and upland terra-firme forest (Chetana & Ganesh 2013; Barik *et al*. 2017).

4.3.2 Demographic inventories and habitat association test for Myristicaceae taxa endemic to Western Ghats

All inventories were carried out in lowland tropical rain forest of Western Ghats, India spanning 8°S to 15°S latitudinal gradient. The rainfall in the study region ranges from 1200 to 4000mm and temperature ranges from 20ºC to 24ºC. The elevation of the study region ranges from 20 to 650 m. The topography within study sites ranges from 0 to 45m above sea level, and soil physical and chemical characteristics differ markedly between the resulting topographic classes of study site such as upland and lowland (Nair *et al.* 2007; Vijaykumar & Vasudeva 2011). Based on the depth of water availability in wet and dry season, the study site can be divided into two types of habitat such as seasonally flooded (swamp) forest and terra firme (non-swamp) forest. Seasonally flooded forest is defined as an area where periodic inundation at least to the soil surface occurs during the rainy season, and where a permanent water table supplied by the streams persists during the dry season, almost never receding below 1 m in depth (Nair *et al.*

2007). We define all other habitat as terra firme forest, with less severe flooding periods in the rainy season and without any access to the riparian water table during the dry season. In the present study, we surveyed these two habitat types for demographic inventory of five endemic Myristicaceae (Appendix C3) in 42 locations of Western Ghats.

In these 42 locations, we laid 42 and 29 plots respectively in seasonally flooded and terra firme forest habitat. These plots are 0.1 ha tree inventories including all trees > 10 cm d.b.h (diameter at breast height) inventoried during 2013 and 2014. In each of these plots, we enumerated all stems >10 cm dbh and seedlings belonging to Myristicaceae.

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 (Harms *et al.* 2001) by Baraloto *et al.* 2007. 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.

4.3.3 Habitat association and key morphological trait data

We determined the "habitat specificity" of both global and Western Ghats endemic Myristicaceae members from species description (http://ab.pensoft.net/articles.php?id=1141; (Verdcourt 1997; Sauquet 2004), literature (Yamuda 1997, Nair *et al.* 2007; Theilade *et al.* 2011; Rao *et al.* 2014) and our own field survey in Western Ghats, India. All species were assigned to one of the three categories: swampy, riparian and non-swampy (Yamuda 1997; Wittmann & Parolin 2005; Rao *et al.* 2014). In this classification system, "swampy" refers to those species restricted to freshwater swamps and not known from other habitats, "riparian" are species that regularly occur in freshwater swamps as well as other similar wetland habitats such as riverain habitat and "non-swampy" are species that are occasionally found near swamps but frequently occupy a variety of other non-flooded habitat types. Finally, Myristicaceae species were not listed and described as occupying other non-flooded and upland habitat types such as terra-firme forest, evergreen and semi-evergreen forest by taxonomic experts were classified as having a "non-swampy" habitat specificity. Myristicaceae species described as either ''swampy habitat specialist'' or "riparian habitat associate'', by taxonomic experts were classified as having "swampy" habitat specificity.

We also collected data on presence of adventitious or aerial roots (roots above the ground or above the anoxic zone or above the level of the water) for both global and Western Ghats endemic Myristicaceae members from taxonomic description, literature and our own field survey in Western Ghats, India. The aerial roots such as stilt root, knee root, floating water roots etc. confer flooding tolerance and there by adaptation of plants to flooding environment (Kozlowski 1984; Schlüter & Furch 1992; Parolin *et al.* 2004). In total, we collected habitat and trait data for 452 species, covering 67.2% of species in the family (Appendix C4).

4.3.4 Distribution and environmental data

Occurrence information of two swampy and three non-swampy Myristicaceae members from Western Ghats were collected in the form of latitude and longitude combination gathered from our own fieldwork (2013 and 2014), herbaria and literature. In case where no coordinates are given, the point localities were geo-referenced using the global gazzeter version 2.1 available on www.fallingrain.com/world. We excluded occurrence points that were within 1 km of an existing point (i.e., the resolution of our environmental data, see below). The details of total number of occurrence records obtained for each species is given in Appendix C3.

Environmental data included 6 hydrologic, 2 edaphic, 3 layers related to aridity and evapo-transpiration and 9 climate variables at 1 km resolution (Appendix C5). The 9 climate variables were obtained from the WorldClim ((http://www.worldclim.org) database and describe surface means of temperature and precipitation, seasonality, and potentially biologically limiting extremes generated from 50 years (1950–2000) of climate data (Hijmans *et al.* 2005). Ten of the 19 original climate variables were removed due to high correlations (R>0.80) with other climate variables. This was done mainly to improve interpretability of niche axes in the multivariate analysis (see below). The details of variables and their source are given in Appendix C5.

4.3.5 Construction of range-wide climatic niche using Ecological Niche Models (ENMs)

Occurrence data and 20 environmental variables were used to generate ENMs for five Western Ghats endemic Myristicaceae using the program Maxent version 3.2 (Phillips *et al.* 2006) (Table S3). We used 75% of randomly selected occurrence records as training data and rest as test data. Maxent is a machine learning method and needs training and test data for model comparison and to assess model performance (Phillips *et al.* 2006). We used default settings to generate ENM maps in MaxEnt except for following changes: Random test percentage was set to 30%.

Regularization multiplier was set to 1 and maximum number of background points for sampling was kept at 10,000. We ran 50 replicates for each of five species and averaged the results. Maximum iterations were set to 5000, with $1*10^6$ convergence threshold. Auto feature of environmental variables was selected. A 50-fold subsampling was used to test model performance of species. Jackknife procedure and percent variable contributions was used to estimate the environmental variable influence on each species.

An important step in evaluating the model performance is to verify that the data used to train and test the model, performed significantly better than random. The model performance was evaluated using two commonly used method Area Under Curve (AUC) (Mason & Graham, 2002) and true skill statistic (TSS) (Allouche *et al.* 2006; Liu *et al.* 2011). However, given the problem of interpreting AUC scores as a means of model accuracy without absence data (Lobo *et al.* 2008; Peterson *et al.* 2008), and because range limits of the species in our study are well described, we also assessed model performance by visualizing projected distributions using the value of minimum training presence calculated by Maxent (Pearson *et al*. 2007). The TSS statistic ranges from −1 to +1 and tests the agreement between the expected and observed distribution, and whether that outcome would be predicted under chance alone (Allouche *et al.* 2006; Liu *et al*. 2009). A TSS value of +1 is considered perfect agreement between the observed and expected distributions, whereas a value <0 defines a model which has a predictive performance no better than random (Allouche *et al.* 2006). TSS was shown to produce the most accurate predictions (Jiménez-Valverde *et al.* 2007). We used minimum training presence value from maximum training sensitivity plus specificity to evaluate the model performance, because this threshold value is considered as one of the promising approaches for predicting species distributions (Liu *et al.* 2005). All predictions of probability of presence that were less than or equal to the minimum training presence value were then removed from further analyses. The predicted ENM of each species was displayed in a single category in ArcGIS version 10.0.

4.3.6 Reconstruction of dated phylogenetic hypothesis

To build a phylogeny for the global and endemic Myristicaceae members from Western Ghats, we first searched and downloaded sequences for 10 genes which included both nuclear and chloroplast gene fragments from GenBank (for accession numbers see Appendix C6). We further sequenced two chloroplast genes (matK and psbA-trnH) for Western Ghats Myristicaceae. Our searches in GenBank yielded sequences for 70 species distributed across 18 genera of Myristicaceae. Many species had missing sequences for few loci, the details of loci and missing data for each locus is given in Appendix C7.

We aligned and edited sequences of each locus and concatenated alignment using Geneious R9 ((http://www.geneious.com). Sequence alignment was done using the global alignment algorithm MUSCLE (Edgar 2004).

We inferred phylogenetic relationship of global and endemic Myristicaceae of Western Ghats from concatenated alignment using two methods; maximum likelihood (ML), and Bayesian inference (BI). For each locus, best fitting models of sequence evolution was chosen according to the AIC implemented in jModelTest 2.1.1 (Darriba *et al.* 2012) (Appendix C7). Maximum likelihood (ML) and Bayesian inference (BI) analyses were performed using the CIPRES Science Gateway v.3.325 (www.phylo.org). ML analyses were conducted using default parameters in GARLI v.2.0 (Zwickl 2006). One thousand bootstrap (BS) replicates were conducted using the same parameters applied for ML searches. BI was performed using MrBayes v.3.2.3 (Ronquist *et al.* 2012). All BI analyses were run for 30,000,000 generations with four chains in four parallel runs sampling every 1000 generations. We made sure that, family and genus level relationships was resolved in both ML and BI phylogenetic tree without any polytomies by comparing it to previous phylogenetic analyses of Myristicaceae by (Sauquet 2004).

We estimated divergence time of Myristicaceae using an uncorrelated, lognormal relaxed clock (UCLN) model in BEAST 1.8.3 (Drummond *et al.* 2006; Drummond & Rambaut 2007). We implemented a yule speciation processes tree prior with unlinked clock models between partitions and employed the best model of DNA evolution scheme identified by jModelTest 2.1.1 (Darriba *et al.* 2012). We ran two independent MCMC analysis for 30,000,000 generations each from starting trees with branch lengths that satisfied the priors on divergence times. A starting tree with branch lengths satisfying all fossil prior constraints was created using the program r8s version 1.7 using NPRS (Sanderson 2002). For each MCMC analysis we sampled parameters after every 1000 generations. Log files were combined using the application LogCombiner 1.8.2 (part of the BEAST distribution), and the posterior distribution and estimated sample size (ESS) of all parameters were examined using the program Tracer 1.6 (Drummond & Rambaut 2007).

Because we had no reliable fossils for Myristicaceae, we employed fossils of Magnoliaceae and Annonaceae as minimum age constraints. The fossils of *Archaeanthus* (98 Ma) (Dilcher & Crane 1984) and *Lethomasites* (120 Ma) (Ward *et al.* 1989) were used as minimum and maximum age constraints for MRCA of Magnoliaceae and Annonaceae. Fossils of *Futabanthus* (89 Ma) used as minimum age constrain for crown age of Annonaceae. We modeled all fossils constraints as lognormal distribution with different means and standard deviations. Finally, we used dated tree of global Myristicaceae and tree pruned to endemic Myristicaceae members of Western Ghats for further comparative phylogenetic analysis.

4.3.7 Comparative phylogenetic analysis of habitat association and associated morphological traits

To examine the evolution of swampy habitat specialization and aerial roots in global and endemic Myristicaceae members of Western Ghats, we mapped swampy and non-swampy 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; http://www.evolution.rgd.ac.uk/BayesTraitsV3.0.1/BayesTraitsV3.0.1.html), 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 2×10^6 iterations with the first 1×10^5 iterations discarded as a burn-in, and a reversible-jump hyperprior with an exponential distribution (Pagel & Meade 2006). For SIMMAP analyses, we ran 10000 simulations.

The ancestral state reconstruction results are sensitive to root state and can potentially bias the results depending on root state. To account for this bias and to test whether changing the root state can potentially influence the ancestral state reconstruction results, we tested alternative hypotheses with ML and MCMC models by fixing the root state of both habitat affinity and presence of aerial roots following states: swampy, non-swampy, aerial root present and aerial root absent. We then compared harmonic mean log-likelihood scores across the constrained models to determine which constrained model better explained the ancestral state of habitat affinity and aerial root evolution and best model was chosen using Akaike Information Criterion (AIC) statistics. The function to run the ancestral reconstruction of traits using ML and

RJMCMC methods is available in R package phytools (Revell 2012) and BayesTraits v3.0 (Pagel & Meade 2006).

Finally, to determine the influence of phylogenetic constraint on evolution of flooded habitat specialization and associated morphological traits in Myristicaceae, we tested for phylogenetic signal in habitat affinity and aerial roots using two alternative methods such as D statistic (phylogenetic dispersion) of (Fritz & Purvis 2010) and Pagel's lambda (λ). These methods are appropriate for characters or traits considered as binary or discrete. Both D and λ varies from 0 to 1. In case of D statistic, value of 0 indicates that the trait evolves on a tree following the Brownian model (strong phylogenetic signal), whereas value of 0 in case of Pagel's λ indicates no phylogenetic signal is present and that traits have evolved in response to selective processes. Conversely, value of 1 for D statistic indicates that the trait evolves following a random model (no phylogenetic signal) and whereas λ value of 1 indicates that traits gradually accumulate changes over time in a Brownian motion process (i.e. random change in any direction). D can be negative, which means that the trait evolves in a conserved manner: more conserved than predicted by the Brownian model. Additionally, we conducted a simulation (1000 permutations) to test whether an estimated D was significantly different from the predictions of a random or a Brownian motion pattern of evolution. We also tested for significance in the phylogenetic signal assessed by Pagel's λ (null hypothesis of $\lambda = 0$) by 1,000 randomizations of species names in phylogeny under ARD (variable transition rate) transition model (Appendix C8). The significance of λ was assessed with a likelihood ratio test (Pagel 1999). The likelihood ratio test compares the likelihood of λ calculated from the true tree to the likelihood of 0.

4.3.8 Measures of niche overlap and relationships with genetic distance

We used ENMTools (Warren *et al.* 2008) to test for niche overlap among all pairwise combinations of Western Ghats endemic Myristicaceae species using two test statistics Schoener's D (Schoener 1968) and I statistic (Warren *et al.* 2008). Both measures assign a numerical value from zero to one, indicating no niche overlap to identical niches (Warrenet *et al.* 2008).

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.

4.3.9 Tests for niche conservatism versus divergence

Our main aim was to compare the patterns of niche conservatism or divergence between the parapatrically distributed swampy and non-swampy Myristicaceae members in Western Ghats. To determine if two species were more (conservatism) or less (divergence) similar than expected from differences in environmental background data, we tested the null hypothesis that a species' niche does not differ from randomly selected background points. We used two approaches to test the above hypothesis, the first through ENMtools (Warren *et al.* 2010) and second through multivariate methods. Both methods use data from species occurrence points and background points.

Following Warren et al. (2008), we first calculated niche overlap values from ENMs for each separate pairwise tests with the Schoener's D metric (Schoener 1968) implemented in ENMtools (Warren *et al.* 2008). To test the null hypothesis that niches are similarly divergent or conserved compared to background environments, we used the background test of niche similarity in ENMtools. The background similarity test compares the observed niche overlap (using Schoener's D) of two taxa (A and B) to a null distribution of 100 overlap values generated by comparing the ENM of one taxon (e.g. taxon A) to an ENM created from n random points drawn from the geographic range of the other taxon (i.e. the background of B), where n equals the number of occurrences of taxon B. This process is then repeated for both taxa in the comparison, so two null distributions are generated per analysis (A vs. background B and B vs. background A). The Hawth's Tools application in ArcMap version 10.0 was used to obtain random points, which were drawn from within a polygon generated from occurrence points of taxa.

The null hypothesis of the background similarity test states that observed niche overlap between taxa is explained by regional similarities in available background environments. This hypothesis can be statistically evaluated by two-tailed test, the hypothesis is rejected when observed D between two taxa falls outside the 95% confidence limits of the null distribution. Niche conservatism is supported when the observed value of D is larger than the upper 95% confidence limit of the null distribution, suggesting that niches are more similar than expected based on their background environments (i.e. species are occupying niches that are as similar as possible given their available habitat). Niche divergence is supported when the observed value of D is smaller than the lower 95% confidence limit of the null distribution, suggesting that niches are more divergent than expected based on background environments.

Further, we followed McCormack et al., 2010 multivariate method to determine if two species were more (conservatism) or less (divergence) similar than expected from differences in environmental background data. We first extracted 20 environmental variable data for both occurrence points and 1000 background points from within the geographic range of each taxon using ArcMap 10.0. We standardized 20 variables and were reduced with PCA of the correlation matrix. For our dataset, this consistently returned seven principal components (PCs) that explained at least a modest portion of the overall variance (>3%) and had a clear biological interpretation based on loading scores. On each of the seven axes, niche divergence and conservatism were tested against a null model of background divergence by comparing the observed difference in mean niche values on a given PC to the difference in mean background values. Significance was assessed with 1000 jackknife replicates of the mean background values. The jackknife test to assess the significance was done using open source codes generated in open source software R version 3.3.2. Further, niche conservatism or divergence was assessed by comparing the level of difference between the mean observed scores (i.e., observed niche values) and 95% confidence intervals (CI) for distribution based on background PCA factor scores. Following McCormack *et al.* 2010, divergent (D) or conserved (C) values were considered statistically significant when the mean observed PC factor score was outside the 95% CI of the null distribution. If the niche (observed) distribution was greater than the background (null), then the niche was considered diverged. Alternatively, niche distributions less than respective background distributions indicated niche conservatism. Statistical significance was then determined using Student's t tests.

4.4 Results

4.4.1 Habitat preferences of Myristicaceae among seasonally flooded (swamp) and terra firme (non-swamp) habitat

We found strong evidence for contrasting association with seasonally flooded forest and/or terra firme forest in both congeneric (*Gymnacranthera*, *Knema* and *Myristica*) and conspecific (*M. fatua*, *M. malabarica* and *M. dactyloides*) pair of endemic Myristicaceae in Western Ghats, India. The strength of association was strong both in adult and seedling stage (Table 4-1). The two species such as *G. canarica* and *M. fatua* positively associated with seasonally flooded forest and all have both absolute density (Appendix C9a) and density ratios (Appendix C9b) greater than the community average at the tree stage, and their association with seasonally flooded forest strengthened for both seedling and tree stages (Table 4-1). Conversely, the other three species such as *K. attenuata*, *M. malabarica* and *M. dactyloides* negatively associated with seasonally flooded forest and all have both absolute density (Appendix C9a) and density ratios (Appendix C9b) less than the community average at both tree and seedling stages and further this association was strengthened for both seedling and tree stages (Table 4-1)

Finally, out of 42 seasonally flooded (swamp) habitats surveyed, *G. canarica* and *M. fatua* were present in 41 (98%) and 27 (64%) of plots respectively and *K. attenuata*, *M. malabarica* and *M. dactyloides* were present in 9 (21%), 7 (17%) and 6 (14%) of plots respectively (Appendix C10). Similarly, out of 29 terra firme (non-swamp) habitat surveyed *G. canarica* and *M. fatua* were completely absent from all the plots and *K. attenuata*, *M. malabarica* and *M. dactyloides* were present in 22 (72%), 15 (56%) and 14 (48%) of plots respectively (Appendix C10).

4.4.2 Phylogenetic relationship

The dated phylogenetic trees supported the monophyletic relationship among global Myristicaceae genera restricted to South America, Africa and Asian continents (Appendix C11). These analyses support the results of the previous molecular studies of Sauquet *et al.* 2003 and Doyle *et al.* 2004. Further, the phylogenetic relationship among Western Ghats endemics were well resolved both in Bayesian and maximum likelihood analysis with strong Bayesian and bootstrap support (Appendix C12 to C13). Interestingly, the *Myristica* clade from Western Ghats was closely related to *Myristica* species from other parts of south Asia and formed a separate cluster within Asian clade (Appendix C11). The independent grouping of Western Ghats *Myristica* supports in-situ speciation and endemic radiation of Myristicaceae in the region.

4.4.3 Ancestral state of habitat affinity and associated morphological traits

The mapping of habitat affinity on dated phylogenetic hypothesis of Myristicaceae revealed that, swampy habitat affinity originated early in the evolution of Myristicaceae (Fig. 4-1). We found swampy habitat association to be the most probable ancestral state in the group, based on all ancestral state estimates analyzed (Table 4-2). The pattern was similar for Western Ghats endemics. Furthermore, comparison of MCMC and ML models with different states of habitat affinity (swampy and non-swampy) fixed as the most basal found swampy habitat association as the best-fit model of ancestral state (Appendix C14) both in global and Western Ghats

Myristicaceae. Our results further suggest that swampy habitat association has evolved more frequently and exclusively in Asian Myristicaceae (Fig. 4-1).

We found similar pattern for aerial root evolution (Table 4-2 and Fig. 4-1). Mainly we found that 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 (Table 4-2 and Fig. 1). Further we found weak phylogenetic signal in both swampy habitat association and aerial root traits (Table 3). Ancestral state analysis also suggested that both global and Western Ghats Myristicaceae has evolved swampy habitat specialization and aerial roots repeatedly and independently multiple times (Fig. 4-1 to 4-2, Table 4-2, and Appendix C14). Finally, our results suggest that aerial roots have evolved more frequently in lineages associated with swampy habitat than in lineages associated with terrestrial or non-swampy habitat (Figs. 4-1 to 4-2). 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 endemic Myristicaceae is shown in Appendix C15. The general trend shows that, there is repeated loss of non-swampy habitat association and gain of swampy habitat association. Similarly, there is repeated evolution of aerial roots. The trend is similar in both global and Western Ghats endemic Myristicaceae (Appendix C15).

4.4.4 Accuracy of predicted habitat suitability models using ENM

We obtained a total of 855 occurrence records for all five species of Myristicaceae from Western Ghats, India (Appendix C3). The predicted distribution of each species using joint information from all environmental variables (Appendix C5) simultaneously are in close agreement with the broad outlines of the current known geographic distributions of species. The predicted distribution of each species based on our analysis of environmental data are shown in Fig. 4-3. In all cases the average values of AUC and TSS obtained from 50 replicated models of Maxent analysis were very high (AUC_{TRAIN}= 0.983 to 0.986, AUC_{TEST}=0.979 to 0.995; TSS=0.942 to 0.975) (Table 4-4), indicating high accuracy of habitat suitability models generated for Western Ghats Myristicaceae species.

To determine the most important variables responsible for predicting habitat suitability, we used the relative contributions of each environmental variables to the ENM predictions generated by

Maxent (Table 4-5). It appears that temperature and annual evapo-transpiration (AET) are the most important drivers of the ENM predictions for all the species (Table 4-5).

4.4.5 Measures of niche overlap and relationships with genetic distance

Values for measures of niche overlap (Schoener's D and Warren et al.'s I) are shown in Table S9. The greatest amount of niche overlap was exhibited by the non-swampy Myristicaceae members such as *M. dactyloides*, *M. malabarica* and *K. attenuate*, and the least amount of niche overlap was observed between *M. fatua* and *M. dactyloides*. Overall, there was high niche overlap among species occurring in similar habitat i.e. either swampy or non-swampy habitat. Whereas, the species pairs occurring in different or contrasting habitats i.e. swampy and non-swampy exhibited least niche overlap (Appendix C16).

In the PCA of selected environmental variables (Table 4-6), we found that the first five PCs explained 82.6% of the variance, with 30.1%, 22.3%, 17.1%, 7.7%, and 5.4% for factors 1–5, respectively. Temperature and precipitation explained most of the variation (i.e., PC 1 and PC 2), the most important being temperature annual range (BIO7), annual evapo transpiration (AET), annual precipitation (BIO12), annual mean temperature (BIO1), maximum temperature of warmest month (BIO5) and minimum temperature of coldest month (BIO6). However, aridity index (AI), precipitation of warmest quarter (BIO18), soil PH, elevation (DEM), potential evapo transpiration (PET) and hydrological variables (PC 4 and 5) were also important in explaining the variance of the model (Table 4-6). The MANOVA of PCA factor scores yielded an overall significant difference among species ($F_{(1,35)}= 187.30$, $P < 0.0001$).

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: $r = 0.293$, $P=0.208$) (Appendix C17).

4.4.6 Test for niche conservatism and divergence among Western Ghats endemic Myristicaceae

Compared to null models of background divergence, Myristicaceae members occurring among contrasting habitat types (swampy and non-swampy) showed strong support for niche divergence. Analysis using ENMs showed that five of the ten pairwise comparisons among the five parapatric lineages of Myristicaceae showed significant evidence for niche divergence with respect to at least one of the null distributions (Fig. 4-4). Similarly, we also found evidence for niche conservatism in all ten comparisons (Fig. 4-4). We found that non-swampy Myristicaceae members such as *K. attenuata*, *M. malabarica* and *M. dactyloides* had significantly divergent niche in comparison to swampy Myristicaceae members (*G. canarica* and *M. fatua*) (Fig. 4-4). Whereas niche among Myristicaceae members occurring in similar habitat i.e. swampy or non-swampy was highly conserved (Fig. 4-4).

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. Seven niche axes were identified that explained 87.4% of the total variation and had meaningful biological interpretation (Table 4-6). Niche axes associated with climate, aridity and evapotranspiration (AET and PET) explained most of the variation (e.g., PC 1-3) (Table 4-6). Niche axes associated with edaphic and hydrologic variables (e.g., PC 4–7) explained smaller proportions of the variation (see Table 4-6).

The first three PC factors (PC1 to 3) showed evidence for statistically significant niche divergence or conservatism in the majority of comparisons (Table 4-6). Other PC factors (PC4 to 7) did not show any evidence either for niche divergence or conservatism in any of the comparison. Evidence for niche divergence was detected in only 14 of 70 tests, most of these involving the comparison between swampy and non-swampy lineages (Table 4-6). Of the ten pairwise lineage comparisons, *G. canarica*/*K. attenuate*, *G. canarica*/*M. malabarica*, *G. canarica*/*M. dactyloides*, *M. fatua*/*K. attenuata*, *M. fatua*/*M. malabarica*, *M. fatua*/*M. dactyloides* showed significant evidence for niche divergence in three PC axes (PC1 to 3) (Table 4-6). Whereas other comparisons showed evidence for niche conservatism (Table 4-6). Overall, the evidence for niche divergence was strong when comparisons were made between lineages occurring in different habitat i.e. one of the compared lineage occur in swampy habitat and other in non-swampy habitat. Whereas evidence for niche conservatism was strong when comparisons were made between lineages occurring in similar habitat i.e. compared lineages are either occur in swampy or non-swampy habitat (Table 4-6).

4.5 Discussion

In our study, demographic inventory of Myristicaceae in Western Ghats showed evidence for significant and differential pattern of distribution and abundance in contrasting habitat types (Table 4-1, Appendix C9 to C10). We mainly found that congeneric (*Gymnacranthera, Knema* and *Myristica*) and conspecific (*M. fatua, M. malabarica* and *M. dactyloides*) pair of endemic Myristicaceae in Western Ghats show strong positive association with either seasonally flooded forest or terra firme forest (Table 4-1 and Appendix C9) 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 4-1). This pattern suggests that sensitivity of swampy habitat specialist species to dryer condition 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.* 2009).

Consistent strong habitat discrimination was found in all five species of Myristicaceae in Western Ghats both for stems >10 cm dbh and at seedling stage (Table 4-1, Appendix C9). The species such as *G. canarica* and *M. fatua* had higher density and density ratio for stems and higher regeneration in seasonally flooded habitat and were completely absent from adjacent terra firme (non-swampy) habitat, indicating strong association with flooded (swampy) habitat. Conversely, the species such as *K. attenuata*, *M. malabarica* and *M. dactyloides* were rarely found in flooded habitat, but frequently distributed and represented in high density in terra firme forest (Appendix C9 to C10). This contrasting habitat preference among parapatrically distributed sister taxa both at early (seedling) and later (adult) stage of their life cycle is a convincing evidence for ecological sorting or habitat filtering of species (Table 4-1). Baraloto *et al.* 2007 observed similar pattern for Myristicaceae members in Amazonian flood plain forest. Their study showed that congeneric pair of Myristicaceae from the region *Virola* and *Lyranthera* strongly associated with either seasonally flooded forest or terra firme forest. Mainly, the species such as *V. surinamensis* and *L. hostmanii* had significantly high density ratio in seasonally flooded forest, indicating their strong association with flooded habitat. Whereas other two species *V. michelii* and *I. sagotiana* had lower density ratio in seasonally flooded forest but represent in significantly high density in terra firme forest indicating their strong association with terra firme or non-flooded forest. However, the strength of association between adult and sapling stage significantly differed among species. The similar trend is reported for congeneric tree species other than Myristicaceae in lowland tropical forest habitat in neotropics and Asia (Russo *et al.* 2005; Baraloto *et al.* 2007).

The limited distribution of sister species in contrasting habitat types may require alternative explanation involving few ecological processes, that we have not tested explicitly in the present study. First, seed dispersal of Western Ghats Myristicaceae can be constrained by behavior of dispersal agents or limited availability of colonization sites. Though, all five species of Myristicaceae in Western Ghats dispersed either by primates or birds, these dispersal agents respond differently to seeds of these species. The flooded habitat specialist such as *M. fatua* produces exceptionally heavy seeds compare to their sister taxa and are therefore transported by frugivores only over small spatial scales (Krishna & Somanathan 2016). This might limit seeds to habitat where adults are found.

The second explanation is that germination may be limited or inhibited by conditions in seasonally flooded or terra firme forest. All Western Ghats Myristicaceae produce recalcitrant seeds and need more moisture to germinate (Kumar *et al.* 2002; Tambat *et al.* 2006; Keshavachandra & Krishnakumar 2016). However, the species such as *G. canarica* and *M. fatua* lose their viability much faster than other three species in dryer condition. Moreover, these two species also shown to be viable under prolonged submerged condition in seasonally flooded habitat. Whereas other three species lose their viability under prolonged submerged condition in seasonally flooded habitat. Therefore *G. canarica* and *M. fatua* have higher germination percentage in seasonally flooded habitat than terra firme habitat (Table 4-1). This adaptation at seed stage might be responsible for different germination rate of Myristicaceae species in seasonally flooded and terra firme habitat in Western Ghats. Moreover, selective filtering during germination may contribute to the observed habitat associations of Myristicaceae members both at adult and seedling stage. Many authors have reported similar trend in germination for Myristicaceae species among seasonally flooded and terra firme forest habitat in Amazonian river floodplains and Guiana Shield forests (ter Steege 1994; Parolin *et al.* 2004).

Third and final alternative explanation is that species distributions in contrasting habitat types are constrained by herbivore or pathogen pressure (Gilbert *et al.* 1994; Fine *et al.* 2004). However, this process may not be important for distribution of Western Ghats Myristicaceae in contrasting habitat types. Because, study by Krishna & Somanathan 2016 have shown that the strong association of *M. fatua* both at adult and seedling stage in seasonally flooded (swampy) habitat is not influenced by prediction of Janzen-Connell model (enemy driven density dependence), but significantly influenced by abiotic factors.

Parsimony-based, stochastic mapping, maximum likelihood and Bayesian character optimizations are all consistent with the hypothesis that flooded (swampy) habitat association was the ancestral state in the global and Western Ghats endemic Myristicaceae (Figs. 4-1 to 4-2, Table 4-2). In addition, parsimony results suggest that flooded habitat association was lost only one times and gained two to three times in global Myristicaceae (Fig. 4-1, Appendix C15). Similarly, flooded habitat association was gained one to two times in Western Ghats Myristicaceae (Fig. 4-2, Appendix C15). Further, the morphological traits such aerial roots (stilt root and knee root) have evolved independently in global and Western Ghats endemic Myristicaceae. Our results suggest that ancestors of Myristicaceae lacked aerial roots (Fig. 4-1 and Table 4-2). Moreover, parsimony results suggest that the aerial roots were gained independently at least four times in global Myristicaceae (Fig. 4-2, Appendix C15) and at least two times in Western Ghats Myristicaceae (Fig. 4-2, Appendix C15). However, the fact that there are many taxa missing from our phylogenetic tree due to unavailability of DNA sequence data (at least 80% 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. This means that the ancestral states that we have inferred could change with additional data. However, our results are robust given the available data and reconstruction of character states in many ways agrees with deep phylogenetic history of species and traits (Figs. 4-1 to 4-2).

If both habitat specialization and aerial roots were a conservative trait in the Myristicaceae, one would expect single shift for each habitat type and aerial root evolution, meaning that specialization towards flooded (swampy) and terra firme (non-swampy) habitat and aerial roots had evolved only once in the group. In case 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 equal the number of species that are flooded habitat specialist and had evolved aerial roots. However, our results fit into these expectations. On one hand, there are instances where putative sister taxa share the similar habitat association and either lack or evolved the aerial roots (Figs. 4-1 to 4-2). In case both flooded habitat specialization and aerial root evolution showed an evidence for tendency to remain phylogenetically conserved among putative sister taxa, it can actually promote allopatric speciation, if adaptation to novel habitat type and morphological traits facilitating adaptation to the habitat constrained and prevents the evolution of generalist species that can cross habitat boundaries (Wiens 2004). Contrastingly, our phylogenetic analyses indicate that association with seasonally flooded habitat and associated morphological traits such as aerial roots has evolved independently multiple times (Figs. 4-1 to 4-2), consistent with the hypothesis that ecological speciation is driving contrasting habitat divergence (Figs. 4-1 to 4-2). Moreover, the results from our study are likely only a conservative estimate of the amount of ecological speciation that has occurred in the global Myristicaceae because adding additional taxa could only increase the minimum number of habitat shifts and gain or loss of aerial roots in the clade. Overall, the data suggest that micro habitat environmental heterogeneity is involved in the diversification process for many species of Myristicaceae both globally and in Western Ghats, especially for 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 (Pepper & Norwood 2001; Rajakaruna et al., 2003; Patterson & Givnish 2003; Cavender-Bares *et al.* 2004; Fine *et al.* 2005; Emery *et al.* 2012). Over a 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. However, such studies are widely conducted to understand the edaphic habitat specialization (Pepper & Norwood 2001; Rajakaruna et al., 2003; Patterson & Givnish 2003; Cavender-Bares *et al.* 2004; Fine *et al.* 2005) and there are hardly any studies which attempted to understand the habitat specialization of plants either across moisture gradient or flooding gradient among sister lineages in the phylogenetic context. 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. In 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). However, due to incomplete phylogenetic hypothesis the study was not able to estimate the ancestral habitat (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 in tropical forest and in temperate region.

Our comparative phylogenetic approach of studying ecological diversification of Myristicaceae among flooded and non-flooded habitat in Western Ghats suggests several potential hypotheses regarding the evolutionary history of this clade in the region. It is argued that flooding gradient with specialized edaphic condition in lowland tropical rain forest play an equal or larger role in explaining diversification of Myristicaceae among flooded (swampy) and non-flooded (terra firme) habitat. While flooded habitat lineages are obviously adapted to tolerate flooding stress, many of the non-swampy (non-flooded) Myristicaceae species are also restricted to flooding free habitats (Rajakaruna, 2003; Baraloto *et al.* 2007), ranging from lowland terra firme forest, upland evergreen forest to semi evergreen forest (Gamble & Fischer,1915-1935; Nair *et al.* 2007; Krishnamurthy, 1960; Tambat 2007). Thus, the hydrological history of Western Ghats may have played a particularly important role in the diversification of this clade. The paleobotanical and palynological data indicate that larger part of Western Ghats was periodically inundated and covered by wetland flood plains with wet tropical evergreen forest during the Late Pleistocene (~53,000 yrs BP) due to extended period of rainfall (Kumaran *et al.* 2013, 2014). Thus, the current island-like distribution of freshwater swamp (seasonally flooded) habitat in Western Ghats is markedly different from the ecological context in which much of the diversification of Myristicaceae likely might have occurred. Our results for Myristicaceae indicate that, within this historical context, the diversification of lineages restricted to flooded habitat likely followed a single transition from non-flooded habitat into swampy habitats (Fig. 4-2, Table 4-2). These patterns are consistent with the hypothesis that the initial invasion into the ‘‘non-swampy habitat’’ may have taken place when wetlands were much more widespread throughout Western Ghats (Kumaran *et al.* 2013, 2014). As these larger, more contiguous wetlands receded into smaller, relatively isolated and fragmented patches, conservatism in morphological and physiological traits associated with flooding tolerances may have facilitated the early stages of divergence by restricting populations to increasingly isolated habitats and limiting gene flow among previously connected subpopulations. Thus, niche conservatism in traits associated with adaptations to microhabitat variation in flooding stress may have facilitated sympatry, genetic divergence, and ultimately speciation among Myristicaceae lineages in Western Ghats (Wiens 2004). If the contemporary climatic associations of these species reflect different climatic adaptations, niche conservatism and specialization along local axes (e.g., specialization to seasonally habitats) may have limited the ability of species to track shifts in climate and promoted in situ adaptation to climate (Ackerly 2003). However, the lack of proper fossil calibration and insufficient phylogenetic resolution in Myristicaceae phylogeny makes it difficult to precisely examine the degree to which ecological diversification events align with Pleistocene climatic fluctuations in the region. Consequently, it will be important to collectively consider the phylogeographic structure found in some taxa of Myristicaceae in the region, the contemporary population structure in all taxa, and the spatial distribution of climatic responses and gene flow to fully evaluate the impacts of local habitat specialization and climatic variation on speciation patterns, and the potential responses of Myristicaceae lineages to future climate change.

At large spatial scales, georeferenced occurrence information and high-resolution climate data and other environmental layers have been examined in a phylogenetic context and subjected niche evolution analysis to suggest that divergence (e.g., Graham *et al.* 2004; Evans *et al.* 2009; McCormack *et al.* 2010) and conservatism (e.g., Peterson *et al.* 1999; Kozak & Wiens 2006; McCormack *et al.* 2010) in the climate niche can each promote speciation by different mechanisms. In the present study, we used these approaches to understand range wide niche evolution among endemic Myristicaceae in Western Ghats, India. First, as expected an analysis of geographically exclusive environmental variables had variable contribution to the Maxent generated ENMs for the parapatric species of Myristicaceae (Fig. 4-3, Table 4-5). However, a few environmental variables appeared to be extremely important. At least one or a combination of the variables BIO7, AET, AI and BIO12 was a major contributor to the models generated for all five species. These variables deal with temperature, moisture availability and evapotranspiration (Appendix C5). However, the importance of individual variables must be interpreted with caution because of a high level of intervariable correlation (McCormack *et al.* 2010). As temperature, moisture availability, productivity and precipitation related variable are some of the critical variables important in limiting distribution of species in wetland tropical forests. However, niche models developed for five Western Ghats Myristicaceae in the present study significantly differ from the niche models developed by (Priti *et al.* 2016). This difference in modelling results might be due to following reasons 1) we had high coverage of distribution records and 2) we used other environmental variables (edaphic, hydrologic aridity and evapotranspiration variables) along with bioclim variables.

The greatest amount of niche overlap observed between species pairs inhabiting similar habitats such as either flooded habitat or terra firme habitat (Appendix C16). In general, our analysis of genetic distance versus niche overlap indicated that niche overlap increases with increasing genetic distance i.e. niche differences decreases with genetic divergence (Appendix C17). This pattern, i.e., two ecologically similar species that are parapatric across mutually habitable space and phylogenetically divergent, suggests that phylogenetically related species are prevented from invading similar habitat by competitive exclusion (Graham *et al.* 2004; Kozak & Wiens 2006). Because competitive interactions are likely to be strongest among close relatives (Darwin 1859; Elton 1946; Vamosi *et al.* 2009; Burns & Strauss 2011) and at the most local spatial scales (Weiher and Keddy, 1999; Cavender-Bares *et al.* 2006). 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 (Table 4-3). In other words, these results suggest that convergent 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 (Fig. 4-4 and Table 4-6). However, there was strong support for niche conservatism among taxa occurring in similar habitat such as either seasonally flooded habitat or terra firme habitat (Fig. 4-4 and

Table 4-6). 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 range wide environmental niche evolution. 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.

4.6 Conclusion

This study represents a first attempt to understand 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 hypothesis will likely refine our understanding of mechanisms promoting flooded habitat specialization and even change some of our conclusions for global 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 habitat. The seasonally flooded habitat in lowland tropical rainforest of Asia including Western Ghats, India mainly dominated by Myristicaceae and at least 17% 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 promote 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 has played a key role in the diversification of many groups within the global and Western Ghats endemic Myristicaceae. 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 specialist (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.

Table 4-1: Habitat association test for trees (>10 cm dbh) and seedlings of five endemic species of Myristicaceae in Western Ghats, India.

Species	**Stage**	**Seasonally flooded forest (swamp) N= 42**			**Terra firme forest (non-swamp) N=29**		
		N	***p***	**Association**	**N**	***P***	**Association**
Gymnacranthera canarica	Adult	1077	1.000	(+)***	2	0.000	(-)***
	Seedling	1362	1.000	(+)***	1	0.000	(-)***
Knema attenuata	Adult	30	0.042	(-)*	253	0.986	(+)*
	Seedling	9	0.000	(-)***	300	1.000	(+)***
Myristica malabarica	Adult	13	0.032	(-)*	168	0.991	(+)**
	Seedling	5	0.000	(-)***	258	1.000	(+)***
Myristica dactyloides	Adult	11	0.002	(-)**	126	0.975	(+)*
	Seedling	14	0.012	(-)*	187	0.970	(+)*
Myristica fatua	Adult	1061	1.000	(+)***	0	0.000	(-)***
	Seedling	1885	1.000	(+)***	0	0.000	(-)***

Notes: 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 (þ) or negative ( ) association.

* *P* , 0.05; ***P* , 0.01; ****P* , 0.001 (one-tailed); NS, not significant.

Table 4-2: Ancestral state estimates for habitat affinity and aerial root at the root of Myristicaceae

Trait	States	Parsimony		Maximum likelihood		MCMC		SIMMAP	
		Global	**WG endemic**	**Global**	**WG endemic**	**Global**	**WG endemic**	**Global**	**WG endemic**
Habitat affinity	Swampy	1	1	0.90	0.80	0.95	0.85	0.65	0.55
	Non-swampy	0	0	0.10	0.20	0.5	0.15	0.35	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

Table 4-3: The statistics for phylogenetic signal in traits.

	Global		Western Ghats endemic	
	Habitat affinity	Aerial roots	Habitat affinity	Aerial roots
Phylogenetic dispersion D				
Estimated *D*	0.631	0.520	0.712	0.620
p random model	**0.250**	**0.312**	**0.421**	**0.271**
p Brownian model	0.005	0.023	0.012	0.020
Pagel's λ				
Lambda	0.152	0.090	0.230	0.121
p-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.

Table 4-4: The mean area under curve (AUC) and true skill statistics (TSS) values from 50 replicate models of Myristicaceae members endemic to Western Ghats, India.

Species	**AUC_{TRAIN}**	**AUC_{TEST}**	**TSS**	**MTSS threshold used for categorical classification**
Gymnacranthera canarica	0.993 (0.0001)	0.991(0.001)	0.975 (0.018)	0.071
Knema attenuata	0.983 (0.0002)	0.979 (0.002)	0.942 (0.019)	0.102
Myristica malabarica	0.991 (0.0004)	0.983 (0.004)	0.962 (0.021)	0.117
Myristica dactyloides	0.993 (0.0003)	0.990 (0.002)	0.950 (0.011)	0.076
Myristica fatua	0.996 (0.0002)	0.995 (0.001)	0.948 (0.015)	0.067

Note: Values in parenthesis represent standard deviation. MTSS, maximum training sensitivity plus specificity.

Table 4-5: Environmental variables with the percent contribution and permutation importance in predicted distribution of species using ecological niche model (ENM).

Variables	***G. canarica***		***K. attenuate***		***M. malabarica***		***M. dactyloides***		***M. fatua***	
	% contribution	**Permutation importance**	**% contribution**	**Permutation importance**	**% contribution**	**Permutation importance**	**% contribution**	**Permutation importance**	**% contribution**	**Permutation importance**
AET	**13.5**	**25.1**	1.1	**5.3**	4.6	**6.3**	**3.3**	**2.6**	2	2
AI	**6.6**	1.6	**4.8**	0.2	**10.8**	0.2	**11.3**	0.6	**4.5**	0
Aspect	0.1	0.2	0.1	0.2	0.7	0.9	0.3	0.5	0.1	0
CTI	0	0.4	0.1	0.3	0.2	0.6	0.3	0.8	0	0
DEM	**6**	**3.2**	1.2	**4**	0.7	1.7	**7.9**	**3.6**	0.5	0
FA	0	0	0	0	0.1	0.1	0.1	0	0	0
FD	0.1	0.2	0.2	0.8	0.4	0.5	0.2	0.3	0.2	0
Slope	0.1	0.5	0	0.1	0.1	0.2	0.2	0.3	0.1	0
AWC	0.4	0.9	2.1	0.9	2.2	1.3	**3.2**	0.6	**13.2**	0.5
BIO 1	0.6	0.6	0.6	0.6	**2.8**	**2.8**	0.5	**2.9**	0	0
BIO 12	**4.2**	2.1	**8**	0.4	**7.5**	1	0.9	0.1	0	0
BIO 14	0.7	**3.6**	0.6	1.1	0.8	1.3	1.1	0.9	**3.4**	0
BIO 15	0.3	**12.3**	0.9	**9.3**	0.6	**4.9**	0.7	**4.2**	**2.8**	1.3

BIO 18	**4.5**	2.1	**5**	**5.7**	**3.2**	**2.7**	1.6	1.2	0.8	1.4
BIO 19	0.7	1.3	1	0.4	1.6	1.1	**8.2**	1.5	**17.7**	0
BIO 5	2.4	0.2	0.7	1.8	5.3	0.1	1.6	0.3	0	0.1
BIO 6	**10.9**	**2.6**	1.6	1	**12**	1.7	2.3	1.3	0.4	0
BIO 7	**42.2**	**42**	**62.9**	**65.8**	**45**	**72.1**	**49.2**	**77.3**	**53.3**	**94.5**
PET	0.1	0.1	1.2	1.1	0.7	0.4	0.4	0.8	0	0
PH	**6.3**	1	**7.8**	0.9	0.7	0.3	**6.7**	0.2	0.8	0

Variables with more than 2.5% contribution and permutation are given in bold. For variables abbreviations see Appendix C5.

Table 4-6: 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 parapatric endemic 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**
G. canarica/K. attenuate	**9.67±0.163 D**	**15.87±0.348 C**	6.45±0.644	3.40±0.019	4.33±0.025	3.53±0.041	3.18±0.059
	(11.16, 8.47)	(15.56, 15.67)	(6.96, 6.75)	(3.34, 3.26)	(4.40, 4.56)	(3.60, 3.47)	(3.12, 3.21)
G. canarica/M. malabarica	**9.47±0.041 D**	**15.66±0.130 C**	6.89±0.229	3.39±0.029	4.25±0.100	3.57±0.072	3.22±0.028
	(11.22, 9.14)	(15.58, 15.68)	(6.78, 6.96)	(3.40, 3.35)	(4.50, 4.40)	(3.50, 3.56)	(3.18, 3.12)
G. canarica/M. dactyloides	**9.47±0.037 D**	**16.48±0.949 D**	**6.83±0.282 D**	3.40±0.018	4.37±0.015	3.56±0.067	3.09±0.156
	(11.83, 9.14)	(15.61, 15.68)	(7.16, 6.76)	(3.35, 3.27)	(4.39, 4.56)	(3.58, 3.47)	(3.10, 3.21)
G. canarica/M. fatua	**9.04±0.463 C**	**15.25±0.274 C**	**8.06±0.948 D**	3.39±0.021	4.32±0.032	3.52±0.026	3.32±0.070
	(8.47, 9.14)	(15.37, 15.68)	(6.42, 6.75)	(3.23, 3.27)	(4.50, 4.56)	(3.60, 3.46)	(3.04, 3.21)
K. attenuata/M. malabarica	**9.63±0.204 C**	**16.01±0.218 D**	6.24±0.416	3.37±0.010	4.23±0.074	3.61±0.031	3.16±0.031
	(11.23, 11.16)	(15.58, 15.56)	(6.78, 6.96)	(3.40, 3.34)	(4.50, 4.40)	(3.50, 3.56)	(3.18, 3.18)
K. attenuata/M. dactyloides	**9.63±0.200 C**	**16.83±0.601 D**	**6.19±0.363 C**	3.38±0.002	4.34±0.041	3.60±0.026	3.03±0.097
	(11.83, 11.16)	(15.61, 15.56)	(7.16, 6.96)	(3.50, 3.46)	(4.40, 4.40)	(3.60, 3.56)	(3.10, 3.12)
K. attenuata/M. fatua	**9.21±0.626 C**	**15.60±0.623 C**	**7.42±1.592 D**	3.38±0.002	4.30±0.006	3.56±0.016	3.26±0.129
	(8.47, 11.16)	(15.37, 15.56)	(6.42, 7.0)	(3.23, 3.34)	(4.50, 4.40)	(3.60, 3.56)	(3.05, 3.12)
M. malabarica/M. dactyloides	**9.43±0.003 C**	**16.61±0.819 D**	**6.60±0.052 C**	3.37±0.012	4.27±0.116	3.63±0.005	3.06±0.128
	(11.83, 11.23)	(15.61, 15.60)	(7.20, 6.78)	(3.35, 3.40)	(4.40, 4.50)	(3.60, 3.50)	(3.10, 3.18)
M. malabarica/M. fatua	**10.33±0.422 D**	**15.69±0.405 C**	**6.72±1.177 C**	3.38±0.008	4.32±0.068	3.57±0.048	3.19±0.098
	(8.47, 11.23)	(15.38, 15.6)	(6.42, 6.80)	(3.23, 3.40)	(4.50, 4.50)	(3.60, 3.50)	(3.04, 3.18)
M. dactyloides/M. fatua	**9.01±0.426 D**	**16.20±1.224 D**	**7.78±1.229 D**	3.38±0.003	4.34±0.048	3.59±0.041	3.16±0.226
	(8.47, 11.83)	(15.37, 15.61)	(6.42, 7.17)	(3.23, 3.35)	(4.57, 4.40)	(3.60, 3.60)	(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	Precipitation	Hydrological	Hydrological	Hydrological	Soil PH or

	temperature or aridity or evapotranspiration	elevation or evapotranspiration		variables	variables	variables or soil PH	precipitation or evapotranspiration

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

See Appendix C5 for variable descriptions. Parentheses indicate opposite sign. Values in italics reflect variables with particularly high contributions to a given PC axis

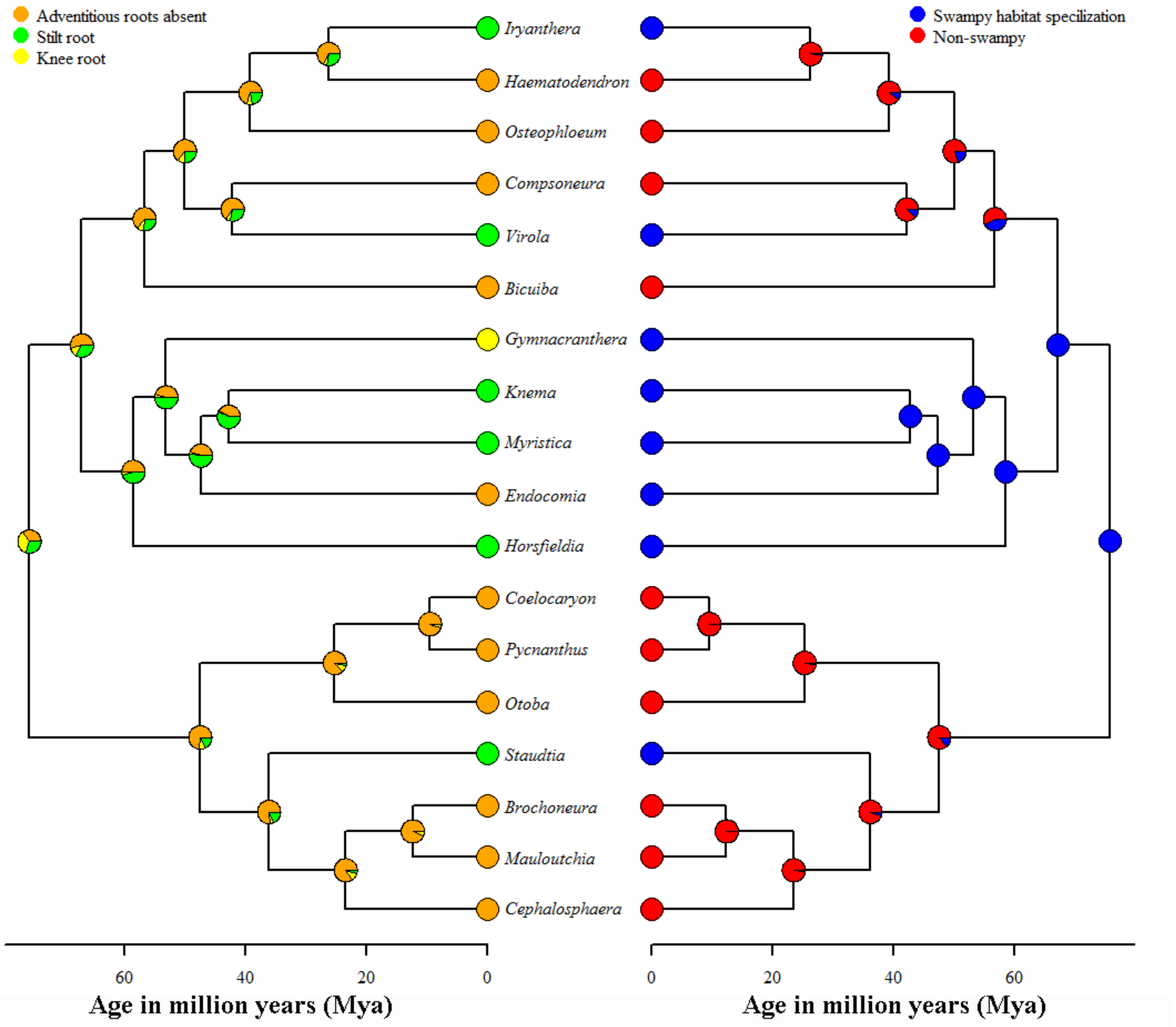

Figure 4-1: Ancestral reconstruction of habitat type and aerial roots in global Myristicaceae based on best likelihood model of stochastic mapping. The circles represent the mean posterior probability distribution of traits calculated from 1000 separate character maps.

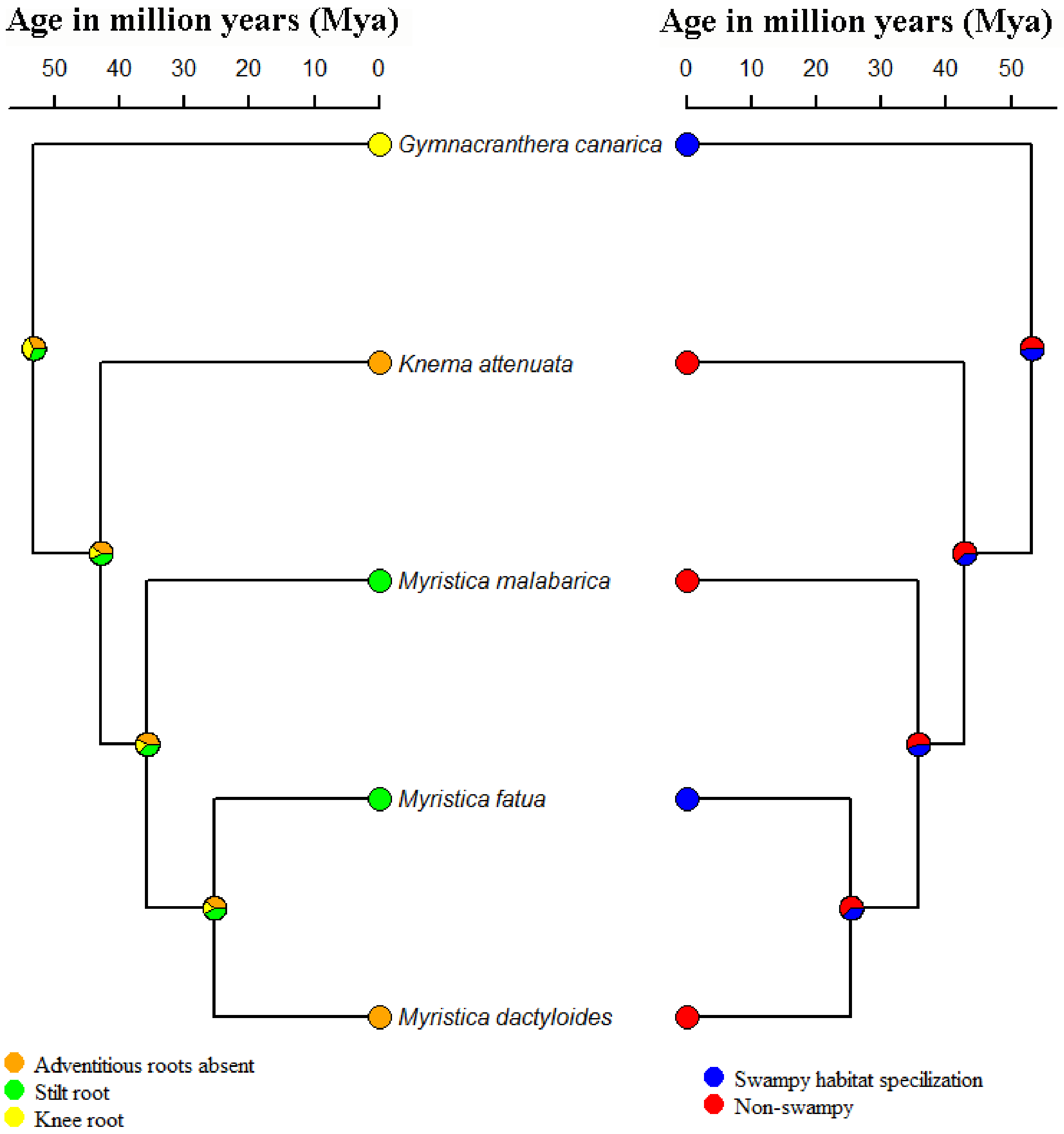

Figure 4-2: Ancestral reconstruction of habitat type and aerial roots in Western Ghats endemic Myristicaceae based on best likelihood model of stochastic mapping. The circles represent the mean posterior probability distribution of traits calculated from 1000 separate character maps.

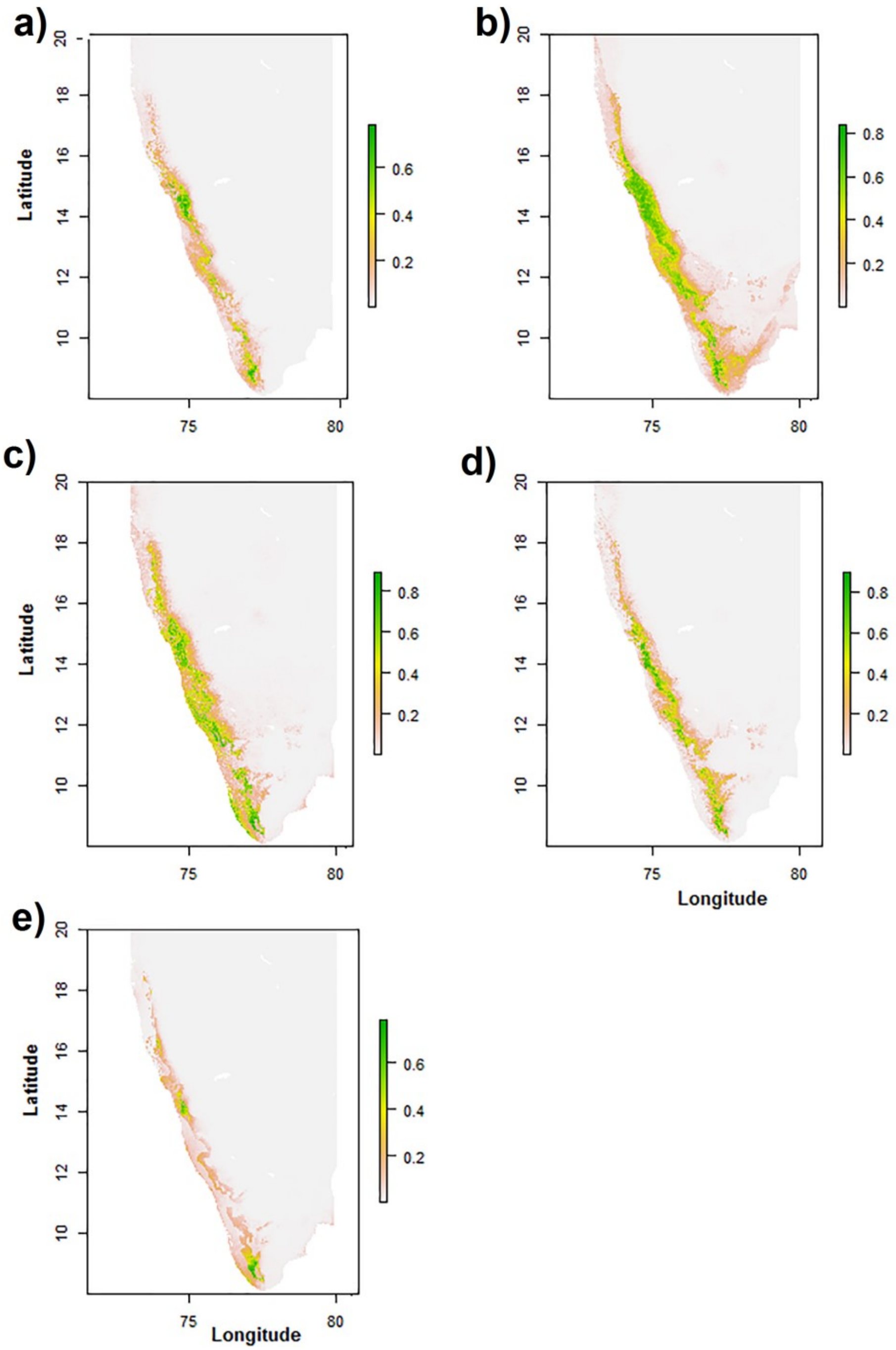

Figure 4-3: Habitat suitability maps of five endemic species from Western Ghats, India a) *Gymnacranthera canarica* b) *Knema attenuata* c) *Myristica dactyloides* d) *Myristica malabarica* and e) *Myristica fatua.*

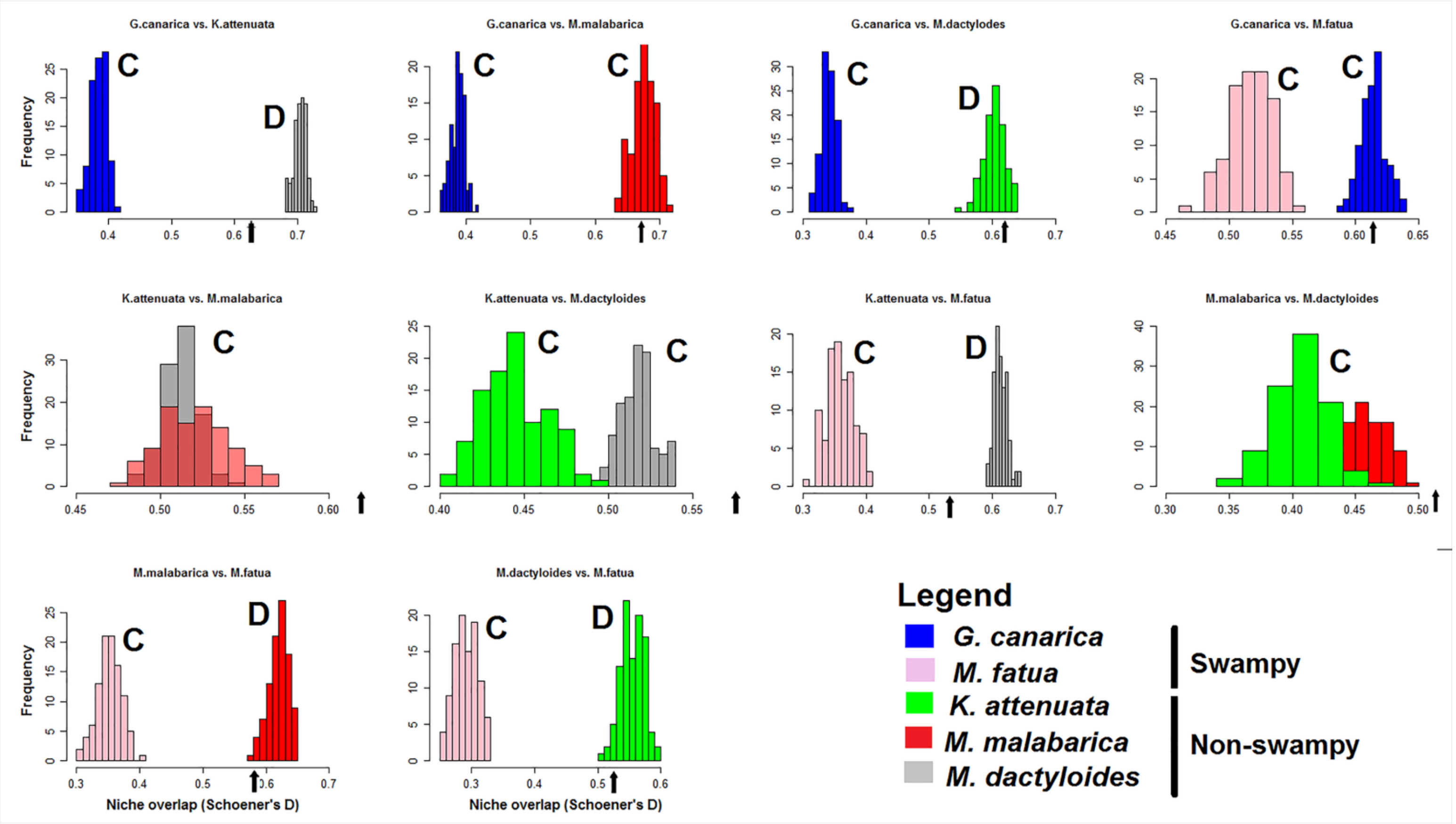

Figure 4-4: Tests of niche divergence and conservatism for Western Ghats endemic Myristicaceae from niche models. Niche-overlap values (arrows) compared to a null distribution of background divergence. Each pairwise comparison produces two reciprocal analyses, one in which the niche model for species 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).

CHAPTER 5

General Conclusion

5.0 Major findings, discussion and contribution to literature

The recent strong theoretical development in community ecology and advancement in functional trait analytical methods, community phylogenetic and comparative phylogenetic methods, availability of high resolution climate data and algorithms to model species ecological niche have provided newer and deeper insights into processes determining assembly and coexistence of diverse plant communities in tropical forest both from ecological and evolutionary perspective. The traditional species count data and richness pattern provide limited insights into multitude of factors determining biodiversity pattern, mainly because assembly mechanisms cannot be identified using such data. The number of assembly processes act on and alter the functional strategy and phylogenetic relatedness of species in ecological communities leaving distinct signatures of functional trait pattern and phylogenetic imprint. Therefore, functional trait pattern and phylogenetic relatedness of co-occurring species in communities can serve as proxy to identify the potential biotic and abiotic processes structuring communities accounting for ecological (functional difference) and evolutionary differences (phylogenetic relatedness) of species. Further, the comparative phylogenetic methods can help in understanding evolution of key functional traits conferring adaptation and specialization to different habitats in deep evolutionary time scale. Finally, the ecological niche modeling tools help to identify niche differences and similarity among co-occurring species and how such niche differences promote diversity and coexistence of cooccurring species in communities. Here using an integrative approach, that combine community phylogenetic and comparative phylogenetic methods, functional trait metrics and niche evolution analysis in a single framework to investigate the mechanisms determining assembly and habitat specialization of tropical tree communities distributed across broad scale (precipitation and dryness) environmental gradient and in different habitat types such as flooded and non-flooded habitat in Western Ghats biodiversity hotspot, India.

5.1 Tree communities in tropical forests of Western Ghats are assembled by non-neutral processes

The tropical forest of Western Ghats harbor rich and highly diverse tree species, the tree species composition notably changes across the landscape along a gradient of moisture (precipitation and dry period) and in different habitat types. Although, numerous vegetation ecological studies are carried out in the region, these studies are unable to provide deeper insights into the potential biotic and abiotic processes structuring tropical forest communities along a broadscale environmental gradient and in different habitat types. The high-resolution tree species composition data collected along a gradient of moisture (precipitation and dry period) and in habitats characterized by seasonal flooding gradient spanning large spatial scale by researchers at French Institute, Pondicherry, India and from my own field survey can be used to address questions related to assembly processes and evolution of habitat specialization in tropical forest tree communities in Western Ghats, India. This study investigated the importance of the most influential assembly mechanisms i.e. the neutral and niche-based community assembly processes in tropical tree communities of Western Ghats. Here I mainly investigated assembly mechanisms structuring tropical tree communities distributed along a gradient of moisture (precipitation and dry period) and in habitats characterized by seasonal flooding gradient using community phylogenetic and functional trait metrics. I find that 1) tree communities in dry deciduous forest (habitat with lower precipitation and longer dry period) are more phylogenetically related and possessed similar functional traits related to light harvesting, reproduction, and growth than expected under various null expectations, while tree communities in wet evergreen forest (habitat with higher precipitation and shorter dry period) are phylogenetically distantly related and possessed different functional traits than expected under various null expectations and, 2) similarly I also found that, tree communities in flooded habitat possess similar functional strategies related to flooding tolerance, light harvesting, reproduction, and growth than expected under various null expectations. These results indicate that, tree communities in dry deciduous forest and flooded habitat are likely structured by environmental filtering (Webb *et al*. 2002; Hardy & Senterre 2007), while niche partitioning likely dominated in wet evergreen forests (Kraft *et al*., 2008; Kraft & Ackerly, 2010). The similar pattern of stronger evidence for habitat filtering in assembly of species is observed in tree communities of flooded habitat in Amazonian forest and other tropical forest habitat (Engelbrecht *et al*. 2007; Kraft *et al*. 2008; Paine *et al*. 2011; Katabuchi *et al*. 2012; Fortunel *et al*. 2014). Thus, our results further confirm and extends on previous research showing the importance of habitat filtering in tropical forest habitats and demonstrate that, spatially varying environmental gradient and diverse habitat types not only assemble species with divergent strategies but also shift the community phylogenetic and functional composition across the gradient. Overall, this study provides additional evidence to the body of literature that tropical tree community assemblages are not neutral but are dictated by niche-based processes.

5.2 Human disturbance leaves distinct signatures of taxonomic and phylogenetic structure in tree communities along an environmental gradient.

The forests of Western Ghats have been and still subjected to variety of human impact including commercial logging, extraction of fuelwood and fencing poles, lopping of leaves, cattle grazing dry-season fires and encroachment (Daniels *et al*., 1995). It has been noted that, increasing levels of disturbance lead to reduction in forest biomass, an opening of the forest canopy and a reduction in soil moisture. Despite strong influence of climatic variables, these environmental changes favor deciduous species and replace shade-tolerant and moisture-loving evergreen species (Puri *et al*. 1983; Pasal 1988). 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 (Verdu & 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). Though, numerous studies have quantitatively assessed the impact of human disturbance on taxonomic composition and turnover of tree species in tropical forest, whether human disturbance alter assembly mechanisms and leave distinct signatures of evolutionary imprint in tree communities of tropical forest has not been addressed. In this study I address this question and find that despite strong influence of climatic variables, the human disturbance reduces phylogenetic diversity in species rich wet evergreen forests but did not affect phylogenetic turnover of tree communities in deciduous forest.

The result of distinct phylogenetic imprint influenced by human disturbance in evergreen forest tree communities has important implication for conservation and management of tropical forest in Western Ghats biodiversity hotspot. The reduction of phylogenetic diversity in tree communities due to human disturbance in species rich evergreen forest can also reduce ecosystem services provided by them. If such historical factors continue increase, they can completely alter basic biotic and abiotic processes and may replace highly diverse evergreen tree communities with low diversity deciduous tree communities. As our results indicate that, tree communities distributed along spatially varying environmental gradient in Western Ghats forest strongly structured by both climatic variables and historical human disturbance, thus both climate change and human disturbance likely to impact structure of tropical forest tree communities in Western Ghats biodiversity hotspot.

5.3 The convergent and correlated evolution of key functional traits conferring flooding tolerance promote ecological dominance in tree communities in flooded habitat.

Although, the tropical forests are known to harbor species rich and hyper diverse ecological communities, in many tropical forest habitats only few species entirely dominate while a large majority of species remain rare. For example, recent study by ter Steege *et al*. 2013 showed that despite having high species diversity (~16,000 tree species) only 227 (1.4% of total) tree species entirely dominate Amazonian forest. The relative importance of neutral versus deterministic (ecological (niche based) and evolutionary (phylogenetic)) processes in determining dominance and rarity of species among suite of co-occurring species in ecological communities have been extensively debated in literature (Hubbell, 2001; Pitman *et al*. 2001; McGill *et al*. 2005; Morlon *et al*. 2009; Cornwell & Ackerly 2010, Maire *et al*. 2012; Seabloom *et al*. 2015).

Here using a integrates analyses of functional traits with that of community level phylogenetic comparative analyses, I investigated the relative importance of neutral (stochastic) versus non-neutral (niche based) in dominance and rarity pattern of species in tree communities distributed across flooding gradient. The results suggest that species functional difference alone predict the relative abundance of species independent of traits evolutionary relationship among co-occurring species in a community and non-neutral niche-based processes such as habitat filtering strongly affect the dominance and rarity of species in flooded forest (freshwater swamp) tree community. For the first time in this study, I have documented the strong connection between species functional difference (functional traits) and abundance of species after accounting for traits evolutionary relationship among co-occurring species in tree communities of tropical forest both at local plot and landscape scale and as well as shifts in the trait–abundance relationship across an ecological gradient (flooding gradient). Interestingly, earlier studies ignored the evolutionary relationship of traits when determining relationship between species functional difference and abundance (Cornwell & Ackerly 2010; Maire *et al*. 2012). This study also showed that, ecologically important traits determining the assembly and abundance pattern of species in flooded forest (freshwater swamp) tree communities have a convergent evolutionary history and they have mainly evolved in lineages specialized to adapt in flooded or waterlogged condition in habitat. Overall, the findings from the present study strongly support the idea that non-neutral, niche-based processes play an important role in determining abundance distribution of species within communities both at local and landscape scale and challenge the ongoing debate about whether dominance and rarity of species in communities are exclusively structured by stochastic processes (McGill *et al*. 2006, 2007; Shipley *et al*. 2006).

5.4 Flooded habitat specialization has evolved early in the evolution of primitive plant family Myristicaceae

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 (Pepper & Norwood, 2001; Rajakaruna *et al*. 2003; Patterson & Givnish, 2004; Cavender-Bares *et al*. 2004; Fine *et al*. 2005; Emery *et al*. 2012). However, these studies are mostly conducted to investigate edaphic habitat specialization in plants (Pepper & Norwood, 2001; Rajakaruna *et al*. 2003; Patterson & Givnish 2004; Cavender-Bares *et al*. 2004; Fine *et al*. 2005). Seasonal flooding during heavy rains creates heterogeneous landscape of seasonally flooded and terra-firme (non-flooded) forest in lowland tropical rain forest. Despite knowing the fact that two habitats differ in micro habitat variables (flooding gradient, edaphic variables) and species composition, relatively little attention has been paid to understand how habitats with difference in seasonal water stress promote habitat specialization and limit species distribution both at small and large spatial scale (Prance, 1979; Lopez & Kursar 2003; Parolin *et al*. 2004). There are hardly any studies which attempted to understand the habitat specialization of plants either across moisture gradient or flooding gradient among sister lineages in the phylogenetic context (Emery *et al*. 2012).

This study represents a first attempt to understand 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. The comparative phylogenetic analysis of habitat association data and functional trait conferring flooding tolerance (adventitious roots) demonstrate that, the habitat specialization has evolved early in the evolution of Myristicaceae. The ancestral Myristicaceae were probably evolved in flooded habitat and subsequently shifted to non-flooded habitat. I find similar results for both global and Western Ghats endemic Myristicaceae. However, one of the limitation of this study is that there are many taxa missing from our phylogenetic tree due to unavailability of DNA sequence data (at least 80% 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. This means that the ancestral states that we have inferred could change with additional data. However, our results are robust given the available data and reconstruction of character states in many ways agrees with deep phylogenetic history of species and traits.

5.5 Flooding gradient promote range wide niche evolution and ecological speciation in Western Ghats plant lineages.

This study is the first to investigate the role of flooding gradient in ecological speciation of tropical plant lineages. Specifically, in this study I investigated the role of flooding gradient in promoting ecological speciation accompanied by range-wide climatic niche evolution among sister taxa of Myristicaceae endemic to Western Ghats, India. The seasonally flooded habitat in lowland tropical rainforest of Asia including Western Ghats, India mainly dominated by Myristicaceae and at least 17% of species surveyed globally exclusively occur in seasonally flooded habitat and has evolved specialized morphological traits (aerial roots) to adapt in flooded condition. In the preset study, I first used georeferenced occurrence information, high-resolution climate data and other environmental layers in a phylogenetic context to understand range wide niche evolution among endemic Myristicaceae in Western Ghats, India. The study results indicate that sister taxa inhabiting similar habitat are phylogenetically divergent and show similar range wide climatic niche whereas sister taxa inhabiting different habitat (flooded and non-flooded) are phylogenetically closely related and differ in range wide climatic niche. In other words, these results suggest that convergent evolution of range wide environmental niche and local habitat niche plays a major role in ecological speciation of Myristicaceae in Western Ghats. 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.

Further, the comparative phylogenetic analyses indicate that association with seasonally flooded habitat and associated morphological traits such as aerial roots has evolved independently multiple times in both global and Western Ghats endemic Myristicaceae members, consistent with the hypothesis that ecological speciation is driving contrasting habitat (flooded and non-flooded) divergence. The presence of multiple putative sympatric sister taxa with divergent habitat association with and without seasonal flooding in Western Ghats is consistent with the hypothesis of ecological speciation scenario. The study by Emery *et al*. 2012 investigated 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. In 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 (Oliveira *et al*. 2014). These examples, together with the results from this study point to an active role for semi-aquatic habitat specialization in the diversification process of closely related lineages both in tropical forest and in temperate region.

5.6 Future research

The future work should focus on understanding the role of historical biogeographic processes such as in-situ speciation, extinction, dispersal on assembly of tree flora in Western Ghats, India. Further, the geographic breaks in Western Ghats such as Palghat Gap and Shencottah Gap have been thought to act as a biogeographic barrier to exchange of biota between on either side of the gap and many biogeographers and naturalist have argued that the assembly of flora in the Western Ghats has been shaped by this barrier. The future work should also focus to understand the role of these geographic breaks on assembly of tree flora in Western Ghats. The Indian Biodiversity Information Network (IBIN) is a database developed by multi-institutional collaborative effort, host vegetation data collected from entire Western Ghats using grid-based approach. In total, it hosts vegetation data collected from 3000 grids spanning 8 to 21^0 latitudes. Such meta data can be used to address many questions related to assembly of tree flora in Western Ghats.

One should also gather functional trait data for all Western Ghats tree flora to understand the role of functional difference in assembly of tree flora in Western Ghats. Such data also can be used to understand the ecosystem services provided by tropical forest across the Western Ghats landscape.

The evergreen forest is very sensitive to human disturbance compare to deciduous forest. My study results also indicated that human disturbance significantly alters taxonomic and phylogenetic structure of evergreen tree communities. The future work should focus to understand how altered taxonomic and phylogenetic structure of tree communities due to human disturbance impact ecosystem services provided by tropical forest of Western Ghats.

As results from this study suggested, the structure and composition of tree communities in tropical forest is influenced by climatic factors as well as human disturbance. Therefore, the future climate change and land use change due to anthropogenic disturbance expected to alter the structure of tropical forest to the larger extant. The future studies should model how projected climate change and future land use changes due to anthropogenic disturbance modify the extant of evergreen and deciduous tropical forest in Western Ghats biodiversity hotspot.

In the present study, I revealed mechanisms determining ecological dominance, assembly and habitat specialization in tree communities distributed across flooding gradient in lowland tropical forests of Western Ghats. 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.

The recent studies suggest that, the fragmented distribution of freshwater swamps (flooded habitat) in Western Ghats possibly influenced by Late Pleistocene climatic fluctuations (Kumaran *et al*. 2013; Kumaran *et al*. 2014). Thus, the current island-like distribution of freshwater swamp (seasonally flooded) habitat in Western Ghats is markedly different from the ecological context in which much of the diversification of swampy tree flora especially Myristicaceae likely might have occurred. Therefore, it will be important to collectively study the phylogeographic structure found in some taxa of Myristicaceae in the region, the contemporary population structure in all taxa, and the spatial distribution of climatic responses and gene flow to fully evaluate the impacts of local habitat specialization and climatic variation on speciation patterns, and the potential responses of Myristicaceae lineages to future climate change.

There is growing interest in understanding potential role of ecological (biotic and abiotic) and evolutionary processes structuring biodiversity pattern all over the world, as such information is crucial for conservation and management of biodiversity. Fortunately, the recent advancement in community phylogenetic and comparative phylogenetic methods, ease of obtaining and analyzing functional trait data, availability of open source high resolution climate data and species distribution data can be used to gain deeper insights into processes structing biodiversity pattern. Despite having some methodological limitations and constrained by assumption, these tools can provide additional perspective on mechanism of species assembly and diversity pattern in ecological communities accounting for ecological difference and evolutionary relationship of cooccurring taxa, and as I have shown here, potential ecological and evolutionary processes structuring assembly and diversity pattern of tree communities in tropical forest of Western Ghats biodiversity hotspot. The work presented in this thesis identify potential assembly mechanisms in tropical tree communities of Western Ghats distributed across broad scale environmental gradient and in habitat characterized by flooding gradient. Further, this study highlights the impact of human disturbance on ecological and evolutionary stability of tropical forest ecosystem. The study also identifies the vital role of flooding gradient in ecological speciation of tropical lineages. Despite hosting taxonomically, ecologically and evolutionary distinct and diverse tropical tree communities, the tropical forest of Western Ghats are expected experience greater threat in the phase of future climate change and ever increasing human population in the biodiversity hotspot. Therefore, the tropical forest of Western Ghats, especially the evergreen forest should be given high priority for conservation.

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Appendices

Appendix A

Supporting Information — Chapter 2

Appendix A1: The details of variables used to predict the proportion abundance and distribution pattern of deciduous and evergreen tree species with their summary statistics in central Western Ghats, India

Note: non-collinear environmental variables are indicated in bold.

Layer	**Variables**	**Reference**	**Psuedo R^2**				
			Abundance deciduous	**Abundance evergreen**	**Richness deciduous**	**Richness Evergreen**	**NRI**
Bio1	Annual Mean Temperature (°C*10)	http://www.worldclim.org/current)	0.005	0.004	0.050	0.002	0.020
Bio2	Mean Diurnal Range (Mean (period max-min)) (°C*10)		0.390	0.403	0.184	0.317	0.163
Bio3	Isothermality (Bioclim2/Bioclim7) (°C*10)		0.259	0.264	0.100	0.251	0.186
Bio4	Temperature Seasonality (SD*100)		0.415	0.424	0.198	0.369	0.208
Bio5	Max Temperature of Warmest month (°C*10)		0.405	0.407	0.356	0.336	0.067
Bio6	Min Temperature of Coldest month (°C*10)		0.060	0.064	0.002	0.053	0.089
Bio7	Temperature Annual Range (Bioclim5-Bioclim6)		0.383	0.395	0.177	0.326	0.182
Bio8	Mean Temperature of Wettest Quarter (°C*10)		0.012	0.011	0.070	0.008	0.013
Bio9	Mean Temperature of Driest Quarter (°C*10)		0.008	0.009	0.010	0.010	0.067
Bio10	Mean Temperature of Warmest Quarter (°C*10)		0.061	0.058	0.134	0.045	0.001
Bio11	Mean Temperature of Coldest Quarter (°C*10)		0.003	0.004	0.016	0.005	0.050
Bio12	Annual Precipitation (mm)		0.585	0.590	0.450	0.544	0.219
Bio13	Precipitation of Wettest Period (mm)		0.599	0.601	0.456	0.574	0.237
Bio14	Precipitation of Driest Period (mm)		0.001	0.001	0.006	0.019	0.010

Bio15	Precipitation Seasonality (Coefficient of Variation)		0.308	0.305	0.178	0.321	0.169
Bio16	Precipitation of Wettest Quarter (mm)		0.594	0.598	0.446	0.562	0.231
Bio17	Precipitation of Driest Quarter (mm)		0.001	0.001	0.033	0.007	0.090
Bio18	Precipitation of Warmest Quarter (mm)		0.141	0.143	0.241	0.064	0.000
Bioc19	Precipitation of coldest Quarter (mm)		0.549	0.552	0.598	0.550	0.160
DryMo	Number of dry months	Ramesh et. al. 2010b	0.092	0.093	0.151	0.045	0.000
AET	Annual evapo-transpiration	http://www.cgiar-csi.org/data/global-aridity-and-pet-database)	0.147	0.149	0.093	0.127	0.067
PET	Potential evapo-transpiration		0.470	0.479	0.350	0.367	0.097
AI	Global aridity index		0.594	0.599	0.470	0.540	0.206

Appendix A2: Traits, and ecological importance of each trait and source of the data.

Traits	No of species sampled	Strategy correlation or function	Data source
Maximum attainable DBH	210 (100%)	Energy and water uptake (1)	8,9,10,11,12,13,14,15
Leaf size	210 (100%)	Competition for light (1)	9,10,17,18
Seed size	200 (95%)	Dispersal strategy (3)	8,9,10,12,18,19,20,21,22,23,24,25,26,27,28,29,30,31,32,33,34,35,36,37,38,39,40
Seed mass	200 (95%)	Dispersal and regeneration strategy (1,3)	19,20,21,22,23,25,29,32,34,41,42 43,44,45,46,47
Wood density	195 (93%)	Allocation of resources for growth and mechanical strength (4)	16,17,43,48,49,50,51,52,53,54,55

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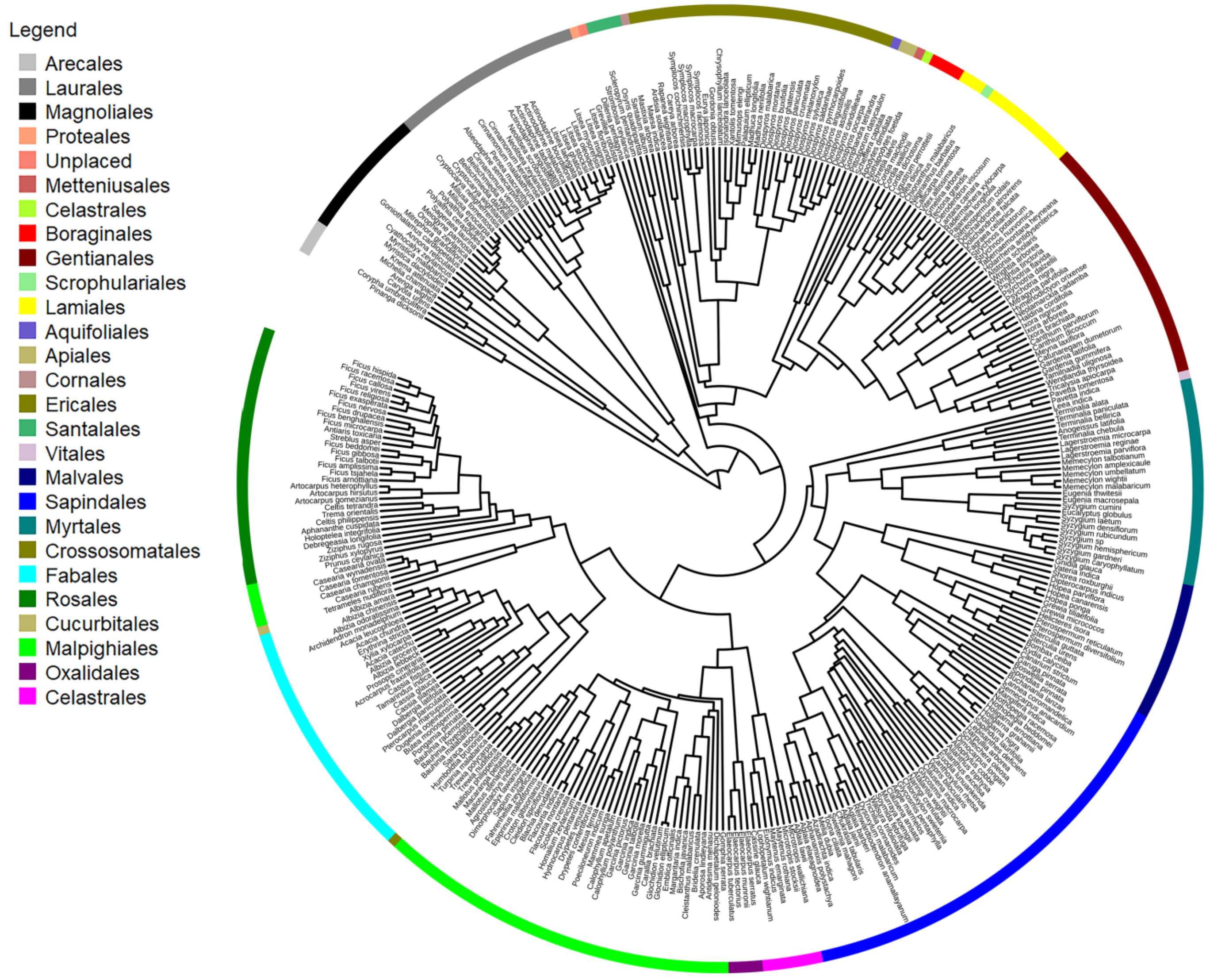
Appendix A3: The dated phylogenetic tree used for community phylogenetic and comparative phylogenetic analysis. The dated tree was obtained using Bayesian analysis in BEAST. The color strip around the circle indicate order of the taxa. In set, the dated phylogeny was developed for 339 tropical tree species occurring in the plots.



Appendix A4: Sequence data used to create a phylogeny for tree species found in 96 1-ha plots in Western Ghats, India. TBA represent sequences generated in the present study, but not yet deposited to NCBI.

		Gene fragments		
Species Name	**Related species sequence used**	**RBCL**	**MATK**	**PSBA**
Acacia catechu		KF532043.1	KF531964.1	GQ434968.1
Acacia chundra	*Acacia dealbata*	KF532044.1	KF531966.1	KF532005.1
Acacia leucophloea		JX195515.1	KR530247.1	JX195530.1
Acrocarpus fraxinifolius		KR528593.1	HM163957.1	KR532956.1
Actinodaphne angustifolia	*Actinodaphne Pilosa*	KP094296.1	KP093382.1	KP095527.1
Actinodaphne bourdillonii	*Actinodaphne omeiensis*	HM019449.1	HM019309.1	HM019379.1
Actinodaphne malabarica	*Actinodaphne acuminate*	KJ594563	KJ687706.1	KJ686998.1
Actinodaphne tadulingami	*Actinodaphne henryi*	KR528601.1	KR530255.1	KR533092.1
Aegle marmelos		AB505961.1	AB762358.1	JX856815.1
Aglaia barberi		GQ248542.1	GQ248073.1	GQ248239.1
Aglaia elaeagnoidea		AB925562.1	AB924932.1	KR533405.1
Aglaia jainii	*Aglaia lawii*	KR528623.1	KR533436.1	KR530276.1
Aglaia lawii		KR528617.1	AB925000.1	KR533390.1
Agrostistachys indica		AB925297.1	AB924687.1	
Ailanthus excelsa	*Ailanthus altissima*	KR528647.1	EF489111.1	KC816435.1
Ailanthus triphysa		KR528651.1	EU042844.1	KR533472.1
Albizia amara		JX856628.1	JX517531.1	JQ230170.1
Albizia chinensis		KP095051.1	KR530302.1	KP095325.1
Albizia lebbeck		JX571776.1	GU134994.1	GU135326.1

Albizia odoratissima		KR528666.1	KR530314.1	KR532933.1
Albizia procera		KJ082111.1	KC689800.1	KR532920.1
Allophylus cobbe	*Allophylus racemosus*	KF496609.1	KJ012459.1	KJ426599.1
Alseodaphne semecarpifolia		KR528689.1	KR530334.1	AF268799.1
Alstonia scholaris		EU916739.1	JN228931.1	JX856820.1
Annona reticulata		KM068871.1	KM068850.1	HG963681.1
Anogeissus latifolia	*Anogeissus sericea*	JF747605.1		
Antiaris toxicaria		KF496469.1	KR530358.1	GQ435322.1
Antidesma menasu	*Antidesma fordii*	HQ415204	HQ415370	HQ415551
Aphanamixis polystachya		JX856634.1	AY128178.1	KR533416.1
Aphananthe cuspidate		KR528736.1	KR530373.1	KR533044.1
Apodytes dimidiate		JX572309.1	KR530375.1	
Aporosa lindleyana	*Aporusa yunnanensis*	HQ415224.1	HQ415388.1	HQ415570.1
Archidendron monadelphum	*Archidendron lucidum*	HQ415101	HQ415282	HQ415452
Ardisia solanacea		KR528774.1	KR530404.1	KR533734.1
Arenga wightii		JF344836.1	JF344976.1	JF345043.1
Artocarpus gomezianus	*Artocarpus tonkinensis*	KR528798.1	KR530423.1	KR532827.1
Artocarpus heterophyllus	*Artocarpus altilis*	HM446760	HM446658	HM446889
Artocarpus hirsutus	*Artocarpus styracifolius*	HQ415055	HQ415243	HQ415407
Atalantia wightii	*Atalantia monophyla*	AB505920.1	AB762381.1	
Azadirachta indica		AJ402917.1	EF489115.1	KP675876.1
Bambusa arundinacea	*Bambusa vulgaris*	JQ734486.1	EU434243.1	GU063075.1
Bauhinia foveolate	*Bauhinia purpurea*	AF387976.1	JN881391.1	JX856839.1
Bauhinia malabarica	*Bauhinia sps(psba)*	JF265551.1	JN881454.1	JX856840.1

Bauhinia racemose	*Bauhinia acuminate*	AY126644.1	JN881392.1	JX856830.1
Beilschmiedia dalzellii	*Beilschmiedia pendula*	GQ981679.1	EU153824.1	EU153945.1
Beilschmiedia wightii	*Beilschmiedia tsangii*	KP094802	KP093862	KP095540
Bischofia javanica		KF496300.1	EF135508.1	KR533571.1
Blachia denudate	*Blachia siamensis*	AY794888.1	AB268040.1	
Bombax ceiba		KP088494.1	JX495673.1	
Boswellia serrata	*Boswellia sacra*	GU246021.1	AY594461.1	JF919223.1
Bridelia crenulate		HQ415195.1	HQ415363.1	JX856845.1
Buchanania lanzan	*Buchanania sessilifolia(matk)*	KF381150.1	KJ708851.1	
Butea monosperma		JX141401.1	JN008175.1	KJ436379.1
Callicarpa tomentosa	*Callicarpa bodinieri*	KR528878.1	HQ427330.1	KR533829.1
Calophyllum apetalum	*Calophyllum longifolium*	GQ981683	HQ331555.1	GQ982164
Calophyllum polyanthum	*Calophyllum membranaceum*	KR528883.1	KP093729	HQ415450
Canarium strictum	*Canarium zeylanicum*	FJ466638.1	KF521891.1	AY635379.1
Canthium dicoccum		AB925751.1	KP093419.1	KP095438.1
Canthium parviflorum	*Canthium horridum*	KR528912.1	KR530519.1	HQ415572.1
Carallia brachiate		HQ415233	HQ415397	HQ415579
Careya arborea		AF077655.1	AB925162.1	
Caryota urens		JQ734494.1	JF344998.1	JF345069.1
Casearia championii	*Casearia arborea*	GQ981686	HM446663	HM446896
Casearia ovata	*Casearia glomerate*	HQ415115	HQ415293	HQ415465
Casearia rubens	*Casearia sylvestris*	HM446768	HM446664	HM446898
Casearia tomentosa	*Casearia velutina*	HQ415116.1	HQ415294.1	HQ415466.1
Casearia wynadensis	*Casearia guanensis*	KJ082174.1	GQ981953.1	GQ982169.1

Cassia fistula		U74195.1	AM086830.1	GQ435368.1
Cassia glauca		JQ301853.1	JQ301873.1	HQ161758.1
Cassia siamea		JQ301862.1	AM086897.1	HG963781.1
Cassine glauca	*Cassine schinoides*	KF432042.1	DQ217536.1	
Catunaregam dumetorum	*Catunaregam spinose*	KP094947	KP094000	KP095441
Celtis philippensis		JF738837.1	AY263925.1	KR532807.1
Celtis tetrandra	*celtis sinensis*	JF317479.1	JF317420.1	HQ427097.1
Chionanthus malabaricus	*Chionanthus domingensis*	HM446772	KJ012507.1	HM446902
Chloroxylon swietenia		AF066802.1		
Chrysophyllum lanceolatum		KJ594653.1	KP094145.1	KP095281.1
Chukrasia tabularis		KR528988.1	KR530583.1	KR533370.1
Cinnamomum keralaense	*Cinnamom camphora*	JX414038.1	JX185547.1	GU135428.2
Cinnamomum malabathrum	*Cinnamom montanum*	KF878112.1	KP093991.1	KJ426655.1
Cinnamomum verum		JX414039.1	EF590398.1	AF268784.1
Clausea anisate	*Clausena anisate*	AB505910.1	AB762395.1	AM500899.1
Clausena indica	*Clausena smyrelliana*	GQ436740.1	KF159531.1	KM895207.1
Cleidion spiciflorum	*Cleidion brevipetiolatum*	KR529022.1	KR530616.1	KR533956.1
Cleistanthus malabaricus	*Cleistanthus sumatranus*	AB925565.1	KR530621.1	KR533570.1
Clerodendron viscosum	*Clerodendrum floribundum*	KM895703.1	KM894594.1	KM895131.1
Cordia dichotoma		JX141399.1	KP093718.1	KP095981.1
Cordia macleodii	*Cordia monoica*	JF265368.1	KR735050.1	KR735905.1
Cordia wallichii	*Cordia dichotoma*	KF496651.1	KP093718.1	JF427954.1
Corypha umbraculifera		AJ404761.1	HQ720271.1	
Croton gibsonianus	*Croton tiglium*	KP094474	KP093547	KP095635

Cryptocarya neilgherrensis	*Cryptocarya chinensis*	KP094541	KP093613	KP095542
Cryptocarya wightiana	*Cryptocarya floydii*	KM896015.1	KM894920.1	KM895367.1
Cyathocalyx zeylanicus		HM173796.1	HM173739.1	HM173710.1
Dalbergia latifolia		KM510270.1	KM276432.1	JX856873.1
Dalbergia paniculate	*Dalbergia hupenia*	KF381155.1	KM276462.1	GU396817.1
Debregeasia longifolia		KR529093.1	KR530679.1	KR534042.1
Dichapetalum gelonioides	*Dichapetalum sp*	KR529102.1	AB936038.1	KR534143.1
Dillenia pentagyna	*Dillenia indica*	FJ860350.1	KF224977.1	JX852696.1
Dimocarpus longan		AF153353.2	AY724286.1	JN407058.2
Dimorphocalyx lawianus	*Dimorphocalyx australiensis*	KF496685.1		
Diospyros angustifolia	*Diospyros malabarica*	EU980707.1	**FJ238151.1**	JX856876.1
Diospyros assimilis	*Diospyros kaki*	KP094640	KP093703	KP095200
Diospyros buxifolia	*Diospyros morrisiana*	EU980658.1	KJ708884	HQ427083.1
Diospyros candolleana	*Diospyros eriantha*	KP094503	KP093576	KP095198
Diospyros crumenata	*Diospyros sp*	KC628653.1	KC627925.1	KC668123.1
Diospyros ghatensis	*Diospyros morrisiana*	KP094462	KP093535	KP095202
Diospyros malabarica		EU980707.1	**FJ238151.1**	JX856876.1
Diospyros melanoxylon	*Diospyros virginiana*	EU980774.1	DQ924064.1	FJ238227.1
Diospyros montana	*Diospyros sp*	EU980717.1	DQ924042.1	JX856877.1
Diospyros oocarpa	*Diospyros sintenisii*	KJ082272.1	KJ012568.1	KJ426703.1
Diospyros paniculate	*Diospyros morrisiana*	KP094462	KP093535	KP095202
Diospyros pyrrhocarpoides	*Diospyros malabarica*	JX856690.1	FJ238151.1	JX856876.1
Diospyros saldanhae	*Diospyros glaucifolia*	HQ427239	HQ427382	HQ427082.1
Diospyros sylvatica	*Diospyros ebenum*	EU980677.1	EU980944.1	FJ238239.1

Dipterocarpus indicus	*Dipterocarpus tempehes*	KJ594685	KJ708907	KR338464.1
Dolichandrone atrovirens	*Dolichandrone spathacea*	AY289683.1	KJ784600.1	
Dolichandrone falcata	*Dolichandrone crispa*	KF432028.1		
Drypetes confertiflorus	*Drypetes alba*	HM446793	KJ012572.1	HM446925
Drypetes venusta	*Drypetes leteriflora*	AY663638.1	KJ012574.1	KJ426710.1
Dysoxylum malabaricum	*Dysoxylum caulostachyum*	KJ594693.1	KJ708914.1	AB057503.1
Ehretia laevis	*Ehretia amoena*	KF496326.1	JF270754.1	JX856878.1
Elaeocarpus munronii	*Elaeocarpus chinensis*	KP094451	KP093525	KP095766
Elaeocarpus serratus	*Elaeocarpus sylvestris*	KP094623	KP093686	KP095774
Elaeocarpus tectorius	*Elaeocarpus nitentifolius*	KP094932	KP093987	KP095772
Elaeocarpus tuberculatus	*Elaeocarpus sikkimensis*	KR529220.1	KR530773.1	KR532904.1
Emblica officinalis		JX125081.1	AY936594.1	GU598547.1
Epiprinus mallotiformis	*Croton lachnocarpus*	KP094558	KP093630	KP095633
Erythrina stricta		KR529253.1	KR530796.1	KR534091.1
Eucalyptus globulus		EF590530.1	AY521535.1	EF590698.1
Eugenia macrosepala	*Eugenia uniflora*	AF294255.2	GU135006.1	GU135338.2
Eugenia thwaitesii	*Eugenia pseudopsidium*	JQ626267.1	KJ012594.1	KJ426734.1
Euodia lunuankenda	*Tetradium fraxinifolium*	KF912881.1	KP793206.1	HG971146.1
Euonymus indicus	*Euonymus laxiflorus*	KP094502	KP093575	KP095173
Eurya japonica	*Eurya muricate*	Z80207.1	AF380081.1	HQ427071.1
Fagraea ceilanica	*Fagraea racemose*	DQ131693.1	AJ010516.1	
Fahrenheitia zeylanica	*Croton billbergianus*	GQ981717	JQ587440.1	GQ982201
Ficus amplissima	*Ficus caulocarpa*	JQ773663.1	JQ773517.1	JQ774307.1
Ficus arnottiana	*Ficus tinctorial*	JQ773786.1	JF953747.1	JQ774225.1

Ficus beddomei	*Ficus formosana*	HQ890844.1	KR530825.1	JQ774290.1
Ficus benghalensis	*Ficus benghalensis*	GU935060.1	GU935034.1	JX856886.1
Ficus callosa		JQ773669.1	JQ773522.1	JX185798.1
Ficus drupacea	*Ficus henryi*	JX571831.1	JX495713.1	JX185797.1
Ficus exasperata	*Ficus hirta*	JF941541.1	JF953736.1	JQ774219.1
Ficus gibbosa	*Ficus curtipes*	JQ773826.1	JQ773518.1	JQ774166.1
Ficus hispida		KP094194	KP093285	KP095828
Ficus microcarpa		KP094631.1	AB925064.1	KP095829.1
Ficus nervosa		HQ415156	HQ415329	HQ415505
Ficus racemosa		EU516328.1	KC508603.1	GU935097.1
Ficus religiosa	*Ficus religiose*	GU935073.1	GU935045.1	JQ774205.1
Ficus talbotii	*Ficus ampelas*	JF941521.1	JQ773505.1	JQ774149.1
Ficus tsjahela	*Ficus tinctorial*	JQ773786.1	JQ773605.1	JQ774225.1
Ficus virens		JQ773809.1	JQ773627.1	KP095847.1
Flacourtia indica		GU135218.1	JF270789.1	KR534141.1
Flacourtia montana	*Flacourtia indica*	AF454736.2	KP094010.1	GU135386.2
Garcinia gummigutta		TBA	TBA	TBA
Garcinia indica		JX141417.1	TBA	TBA
Garcinia morella		TBA	TBA	TBA
Garcinia pictorius		TBA	TBA	TBA
Garcinia talbotii	*Garcinia madruno*	JQ626234.1	JQ587259.1	JX997356.1
Gardenia gummifera	*Gardenia jasminoides*	KF381165.1	KC576965.1	JX312218.1
Gardenia latifolia	*Gardenia sootepensis*	KF381163.1	KC576966.1	JX675230.1
Garuga pinnata		KR529366.1	KR530880.1	KR533359.1

Glochidion ellipticum	*Glochidion_puberum*	HQ415189	HQ415359	HQ415538
Glochidion velutinum	*Glochidion_wrightii*	HQ415187	HQ415357	HQ415536
Glycosmis macrocarpa	*Glycosmis parviflora*	JX144166.1	KP093766.1	KP095943.1
Glycosmis pentaphylla		FJ434178.1	AB762391.1	GQ435452.1
Gmelina arborea		KR529394.1	JQ589429.1	KR533822.1
Gnidia glauca		AM162511.1	FJ572797.1	
Gomphandra tetrandra		KR529402.1	KR530907.1	KR533661.1
Gomphia serrata		AB925353.1	AB233803.1	
Goniothalamus cardiopetalus		KM818524.1	KM818575.1	KM818692.1
Gordonia obtusa	*Gordonia lasianthus*	AF380042.1	AF380085.1	HM100515.1
Grevillea robusta		KM895690.1	EU169631.1	KM895122.1
Grewia micrococos	*Grewia villosa*	EU213491.1	JF270803.1	EU213835.1
Grewia tiliaefolia	*Grewia flavescens*	EU213488.1	JF270797.1	EU213832.1
Haldina cordifolia		X83639.1		
Harpullia arborea		JF738925.1	GQ248130.1	GQ248309.1
Helicteres isora		KF496517.1	KJ012633.1	KJ426772.1
Holarrhena antidysenterica		AJ002884.1	EF456361.1	JQ279751.1
Holigarna arnottiana	*Trichoscypha patens*	KC628299.1	KC627664.1	KC667843.1
Holigarna grahamii	*Trichoscypha preussii*	KC628192.1	KC627584.1	KC667753.1
Holigarna nigra	*Trichoscypha klainei*	KC628636.1	KC627911.1	KC668107.1
Holoptelea integrifolia		KF381141.1	KC539622.1	JX856899.1
Homalium zeylanicum	*Homalium cochinchinense*	HQ415194	HQ415362	HQ415542
Hopea canarensis	*Hopea mengarawan*	KJ594748.1	KJ708955	AB452463.1
Hopea parviflora		JX163307.1	JX163312.1	JX502816.1

Hopea ponga		JX163308.1	JX163313.1	AB452461.1
Humboldtia brunonis		JX163310.1	EU361970.1	
Hydnocarpus pentandra		AJ418799.1	EF135551.1	
Hymenodictyon orixense	*Hymenodictyon parvifolium*	KC737707.1	JF270827.1	
Isonandra lanceolata	*Isonandra villosa*	JX856715.1		
Ixora arborea	*Ixora chinensis*	HQ415123	HQ415301	HQ415473
Ixora brachiata	*Ixora coccinea*	HM164167.1	HM119544.1	AM939409.1
Ixora nigricans	*Ixora nematopoda*	AB925882.1	AB925250.1	KC667804.1
Knema attenuata			TBA	TBA
Kydia calycina	*Kydia.sp*	KR529483.1	EF207261.1	KR533636.1
Lagerstroemia microcarpa	*Lagerstroemia indica*	AY905412.1	KP089119.1	HG963877.1
Lagerstroemia parviflora	*Lagerstroemia floribunda*	JX856721.1	AB925059.1	JX856902.1
Lagerstroemia reginae	*Lagerstroemia tomentosa*	JX856719.1	KR530989.1	KJ686934.1
Lannea coromandelica		AB925480.1	AB924865.1	
Lantana camara		JQ594382.1	JQ589438.1	JQ618443.1
Leea indica		KF496447.1	KR531025.1	KR533778.1
Lepisanthes deficiens	*Lepisanthes senegalensis*	KR529535.1	EU720654.1	KR533492.1
Ligustrum perrottetii	*Ligustrum sinense*	JF942297.1	JF954389.1	GU135317.2
Litsea floribunda		KP094769	KP093830	
Litsea ghatica	*Litsea cubeba*	KP094358	KP093440	KP095557
Litsea insignis	*Litsea glutinosa*	KP094179	KP093272	KP095559
Litsea laevigata	*Litsea monopetala*	KP094520	KP093592	KP095561
Litsea mysorensis	*Litsea rotundifolia*	KP094181	KP093274	KP095564
Litsea oleoides	*Litsea szemaois*	KR529607.1	KR531102.1	KR533127.1

Litsea stocksii	*Litsea panamanja*	KR529592.1	KR531086.1	KR533122.1
Lophopetalum wightianum		KJ594776.1	KJ708988.1	
Macaranga peltata	*Macaranga bracteate*	HQ415215	HQ415380	HQ415562
Madhuca longifolia		JQ673542.1	JQ673568.1	AM179726.1
Madhuca neriifolia	*Madhuca microphylla*	AF421096.1	KJ708992.1	AM179727.1
Maesa indica		KR529646.1	KP093445.1	KR533742.1
Mallotus philippensis		HQ415221	HQ415385	**HQ415567**
Mallotus stenanthus	*Mallotus_hoookerianus*	HQ415222	HQ415386	HQ415568
Mammea suriga	*Mammea Americana*	AF518376.1	AY625052.1	KC667890.1
Mangifera indica		JN114819.1	AY594472.1	HG963847.1
Margaritaria indica	*Margaritaria nobilis*	JQ593116.1	FJ235279.1	HM446955.1
Mastixia arborea	*Mastixia pentandra*	AF384109.1	JF308673.1	JF321233.1
Maytenus emarginata	*Maytenus laevigata*	KJ082414.1	KJ012676.1	KJ426816.1
Maytenus rothiana	*Maytenus oblongata*	JQ626259.1	JQ626557.1	FJ038887.2
Meiogyne pannosa	*Meiogyne bidwillii*	JQ723865.1	JQ723778.1	KM924983.1
Melia dubia	*Melia azedarach*	U38859.1	AY128194.1	GU135311.2
Memecylon amplexicaule		KP202253.1	AB924757.1	KJ488998.1
Memecylon malabaricum		KP202253.1	KF895404.1	KJ488995.1
Memecylon talbotianum		KM871216.1	KF895408.1	KJ488996.1
Memecylon umbellatum		KM871205.1	KF895406.1	KJ488997.1
Memecylon wightii		KF003022.1	KF895405.1	KJ488994.1
Mesua ferrea		AY625024.1	HQ331661.1	GQ435381.1
Meyna laxiflora	*Canthium coromandelicum*	Z68851.1	HM119520.1	
Michelia champaca		AB623325.1	KJ510875.1	GQ435216.1

Microtropis stocksii	*Microtropis discolor*	KR529744.1	KR531212.1	KR533588.1
Microtropis wallichiana	*Microtropis fokienensis*	KJ440002.1	HQ393850.1	KP095175.1
Miliusa eriocarpa	*Miliusa balansae*	KR529747.1	KR531215.1	KR533260.1
Miliusa tomentosa	*Miliusa horsfieldii*	KF496583.1	AY518849.1	JQ690448.1
Mimusops elengi		JN114822.1	JN114760.1	AM179741.1
Mitragyna parvifolia	*M.rubrostipulata*	JX856731.1	AY538390.1	JX856911.1
Mitrephora grandiflora	*Mitrephora wangii*	KR529780.1	KR531248.1	KR533271.1
Murraya koenigii		KF381128.1	AB762390.1	JX856914.1
Myristica dactyloides			TBA	TBA
Myristica malabarica		JF738610.1		
Naringi crenulata		AB505914.1	AB762385.1	
Neolamarkia cadamba		KC737738.1	KR531271.1	KR533887.1
Neolitsea scrobiculata	*Neolitsea cambodiana*	JF942602.1	JF954699.1	KP095587.1
Neolitsea zeylanica	*Neolitsea aurata (psba)*	KJ594815.1	KJ709012.1	JN045547.1
Nilgirianthus barbatus				
Nothapodytes foetida			KJ563186.1	
Nothopegia beddomei				
Nothopegia racemosa				
Olea dioica		KP094844	**JX863045.1**	KP095520
Orophea zeylanica	*Orophea kerrii*	AY319008.1	AY518818.1	JQ690420.1
Osyris quadripartita	*Osyris wightiana*	HF568790.1	AY042623.1	KC503280.1
Ougeinia oojeinensis				
Pajanelia longifolia				
Palaquium ellipticum	*Palaquium microphyllum*	KJ594831.1	KJ709027.1	HF542902.1

Pavetta indica	*Pavetta staudtii*	AB925508.1	AB924889.1	KC688786.1
Pavetta tomentosa	*P.abyssinica*	Z68863.1	HM119556.1	AM939414.1
Persea macrantha	*Persea Americana*	AY337727.1	JQ588149.1	JQ513882.1
Pinanga dicksonii		KJ594849	KJ709045	
Pittosporum dasycaulon	*Pittosporum pentandrum*	JX572857.1	KM894453.1	GU135390.2
Poeciloneuron indicum		AY625023.1	HQ331673.1	
Polyalthia cerasoides		KR529914.1	KR531373.1	KR533231.1
Polyalthia fragrans	*Polyalthia lateritia*	JX227915.1	JX227890.1	KF709064.1
Pongamia pinnata		AY289676.1		JX506559.1
Prosopis cineraria	*Prosopis pallida*	KJ082517.1	EF165248.1	KJ426892.1
Prunus ceylanica		HQ235417.1	HQ235133.1	HQ188760.1
Psychotria dalzellii	*Psychotria pubescens*	KJ082528.1	KJ012738.1	KJ426903.1
Psychotria flavida	*Psychotria maleolens*	KJ082525.1	KJ012737.1	KJ426901.1
Psychotria nigra	*Psychotria domingensis*	KJ082524.1	KJ012736.1	KJ426900.1
Pterocarpus marsupium	*P.rohrii*	JN083733.1	JN083553.1	GQ982349.1
Pterospermum diversifolium	*Pterospermum lanceifolium*	KR529955.1	KR531415.1	KP095700.1
Pterospermum reticulatum	*Pterospermum menglunense*	AY082360.1	KR531423.1	KR533632.1
Radermachera xylocarpa	*R.microcalyx*	KR529978.1	KR531436.1	KR533838.1
Rapanea wightiana	*Rapanea howittiana*	KM895546.1	KM894463.1	KM895041.1
Reinwardtiodendron anamallayanum	*Reinwardtiodendron kinabaluens*	DQ238054.1	LC052214.1	
Sageraea laurina	*Sageraea lanceolate*	AY319050.1	AY518799.1	JX544787.1
Santalum album		JX856758.1	AY042650.1	GQ435377.1
Sapindus laurifolia	*Sapindus trifoliatus*	JQ673550.1	AY724323.1	KR533371.1
Sapium insigne	*Sapium baccatum*	KP752388.1	KR531442.1	KR534123.1

Saraca asoca	*sarac declinate*	JQ673549.1	KC592386.1	JX856941.1
Schefflera capitata	*Schefflera heptaphylla*	KP094267	KP093353	KP095131
Schleichera oleosa		AY724367.1	AY724329.1	
Scleropyrum pentandrum	*Scleropyrum wallichianum(psba)*	AB925837.1	AB925198.1	KR533323.1
Scolopia crenata	*Scolopia chinensis*	KP095040	KP094086	KP095690
Semecarpus anacardium	*semecarpus reticulatus*	JF738945.1	AB925248.1	KR533334.1
Shorea roxburghii	*Shorea robusta*	KM267142.1	KJ611242.1	JX856943.1
Spondias pinnata	*Spondias sp*	KP774626.1	JQ586474.1	KJ026795.1
Sterculia guttata	*Sterculia lanceolate*	KP094342	KP093424	KP095703
Sterculia urens	*Sterculia pruriens*	JX856768.1	JQ626433.1	FJ038995.2
Stereospermum colais		KR530043.1	JN183984.1	**JQ899437.1**
Streblus asper	*Streblus indicus*	AB925449.1	GQ434235.1	GQ435323.1
Strombosia ceylanica	*Strombosia schefflera*	KJ594898.1	KJ709095.1	KC688809.1
Strychnos nuxNAvomica		L14410.1	AB636281.1	GQ435195.1
Strychnos potatorum		KF381125.1	JF270953.1	JX856949.1
Swietenia mahagoni		FN599465.1	EU042835.1	JX856954.1
Symplocos cochinchinensis		KR530061.1	HQ415341	HQ415519
Symplocos macrocarpa	*S.anomala*	KR530055.1	KR531500.1	HQ427076.1
Symplocos macrophylla		HQ415168	AY630674.1	HQ415517
Symplocos racemosa		AB925775.1	AB925051.1	HQ415516
Syzygium caryophyllatum	*Syzygium buxifolium*	KP094792	KP093852	KP095749
Syzygium cumini		GU135224.1	GU135062.1	GU135329.2
Syzygium densiflorum	*Syzygium championii*	KP095089	KP094126	KP095751
Syzygium gardneri		HQ415137	AB925274.1	HQ415487

Syzygium hemisphericum	*Syzygium hancei*	KP094796	KP093856	KP095753
Syzygium laetum	*Syzygium nervosum*	KP094155	KP093248	KP095745
Syzygium rubicundum	*Syzygium rehderianum*	KP094241	KP093329	KP095759
Syzygium sp.	*Syzygium jambos*	KP094169	KP093262	KP095755
Tabernaemontana heyneana	*Tabernaemontana arborea*	GQ981892	GQ982109	GQ982379
Tamarindus indica		AB378728.1	EU362056.1	KJ426962.1
Tamilnadia uliginosa		KF964888.1	JQ673573.1	
Tectona grandis		KJ082606.1	KJ012800.1	JQ618438.1
Terminalia alata	*Terminalia muleri*	AB925702.1	AB925073.1	GU135389.2
Terminalia bellirica		JF747600.1	KC130324.1	FJ381879.1
Terminalia chebula		JF747602.1	KT274005.1	FJ381883.1
Terminalia paniculata		KT274015.1	GU135121.1	JX856971.1
Tetrameles nudiflora		AF206828.1	AY968458.1	KR532878.1
Toona ciliata		KF496355.1	**EF138920.1**	KM895079.1
Trema orientalis		JF265631.1	JF270972.1	KJ687242.1
Trewia nudiflora		AY663648.1	EF582668.1	
Tricalysia apiocarpa	*Tricalysia achoundongiana*	KC628422.1	KC627760.1	KC688806.1
Trichilia connaroides		KR529425.1	HM446750	HM447009
Turpinia malabarica	*Turpinia occidentalis*	KJ082627.1	KJ012815.1	KJ426981.1
Vateria indica	*Vateria copallifera*	KJ594927	AB246431.1	KR338463.1
Vepris bilocularis	*Vepris soyauxii*	KC628323.1	KC627533.1	KC667699.1
Vitex altissima	*Vitex negundo*	KF796632.1	AB284176.1	DQ304781.1
Wendlandia thyrsoidea	*Wendlandia uvariifolia*	AM117283.1	KR531641.1	KP095472.1
Wrightia arborea	*Wrightia coccinea*	AJ002891.1	DQ660555.1	JX856976.1

Wrightia tinctoria		JX856804.1	GQ220745.1	JX856977.1
Xantolis tomentosa	*Xantolis siamensis*			DQ344151.1
Xylia xylocarpa		AB925419.1	AB924808.1	
Zanthoxylum rhetsa	*Zanthoxylum gilletii*	KP325138.1	KC627917.1	JX139454.1
Ziziphus rugosa	*Ziziphus reticulata*	HQ325599.1	KJ012830.1	EU075105.1
Ziziphus xylopyrus	*Ziziphus mauritiana*	JX573106.1	JX518013.1	JX856980.1

Appendix A5: The details of three loci used for phylogeny reconstruction. The length of each genomic region (number of base pairs), the models selected with JModelTest and missing data for each locus.

Gene	Length (bp)	Selected model	Present/Missing data
MatK	845	TVM+G	326/13
Rbcl	496	TVM+G	318/21
psbA-trnH	397	GTR+I+G	291/48

Appendix A6: Calibration points and age constraints used in divergence time estimations.

Fossil	Minimum age (Ma)	Reference
Myrtales	88.2	Takahashi et al. (1999)
Malvales	65.5	Wheeler et al. (1987, 1994)
Magnoliales	112.0	Massoni *et al*. 2015
Laurales	108.8	Crane *et al*. (1994)
Ericales	91.2	Nixon & Crepet (1993)
Fabales	59.9	Herendeen (1992)
Lamiales	44.3	Call & Dilcher (1992)
Arecales	64.0	Pan *et al*. (2006) (77)
Malphigiales	49.0	Jarmillo & Dilcher (2001)
Sapindales	65.0	Knobloch & Mali (1986)
Santalales	51.9	Collinson *et al*. (1993)

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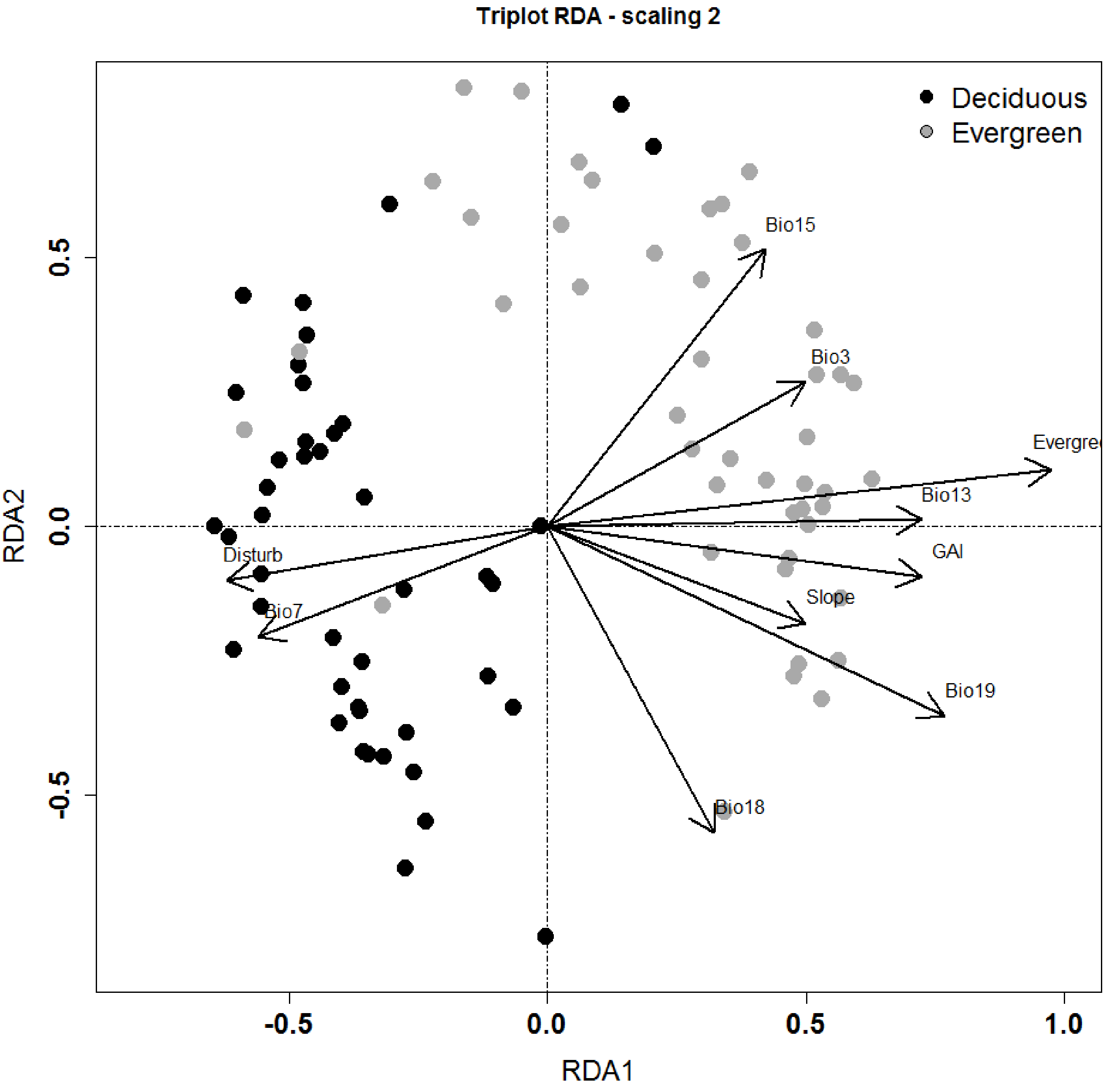
Appendix A7: Redundancy analysis (RDA) conducted on the abundance matrix of 339 tree species in ninety-six 1-ha plots in the central Western Ghats of Karnataka, India.



Appendix A8: The results of the GLM regression analyses of relative abundance of deciduous and evergreen species with the environmental variables

Variable	**Coefficient (DEC/EVG)**	**Pseudo R^2 (DEC/EVG)**	**AIC (DEC/EVG)**
Abundance (DEC/EVG)			
Bio2	0.624/0.624	0.390/0.410	49.547/47.041
Bio3	-0.509/0.514	0.259/0.264	68.186/67.076
Bio4	0.644/-0.651	0.415/0.424	45.519/43.57
Bio5	0.637/-0.638	0.405/0.407	47.044/46.316
Bio7	0.619/-0.628	0.383/0.395	50.541/48.313
Bio12	-0.765/0.768	0.585/0.59	12.48/11.041
Bio13	-0.774/0.775	0.599/0.601	9.171/8.371
Bio15	-0.555/0.553	0.308/0.305	61.64/61.572
Bio16	-0.77/0.773	0.594/0.598	10.525/9.124
Bio19	-0.741/0.743	0.549/0.552	20.488/19.526
PET	0.686/-0.692	0.47/0.479	35.954/34.027
GAI	-0.77/0.774	0.594/0.599	10.505/8.919

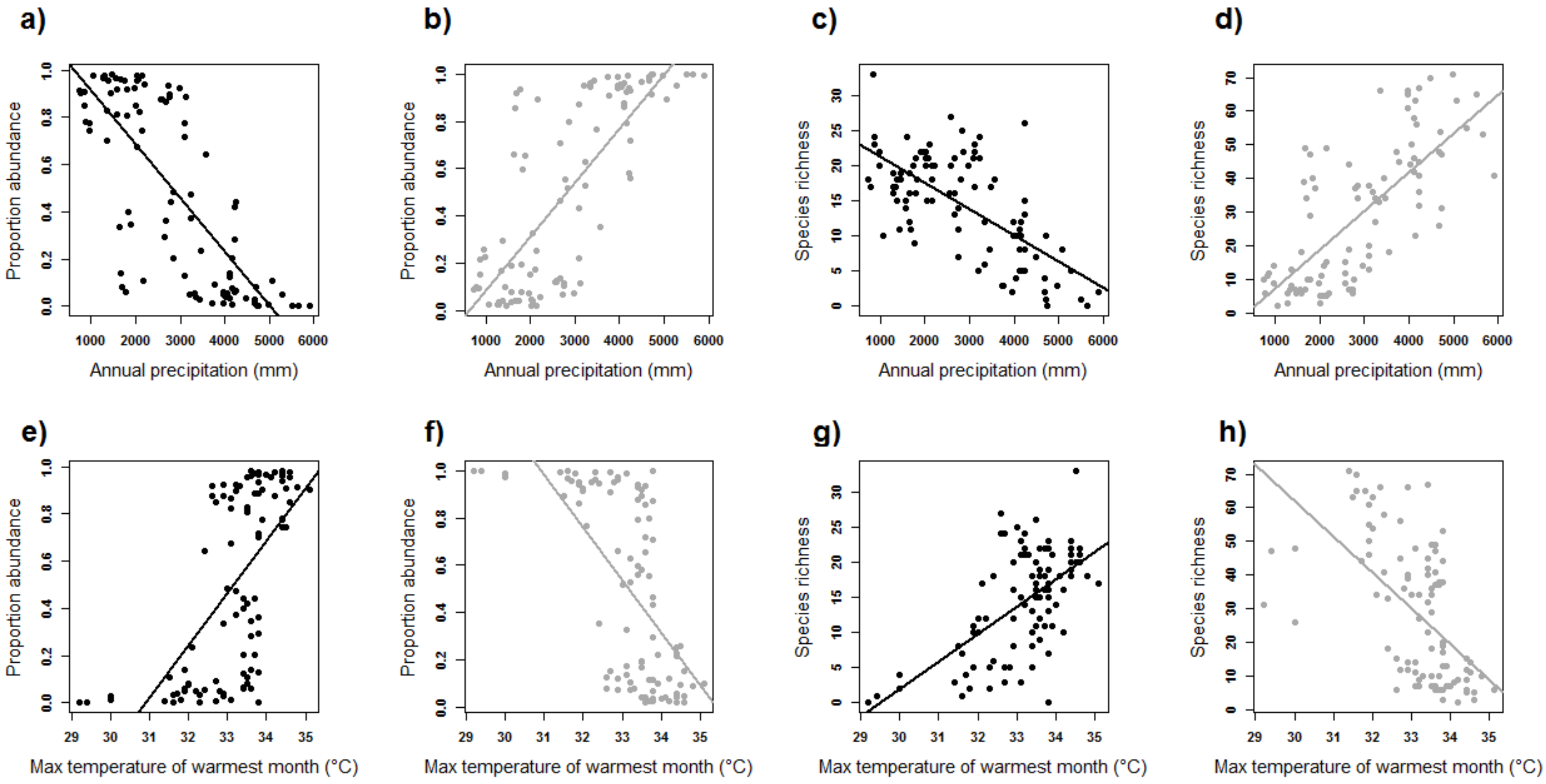
Note: Regression coefficients are standardized to compare the effect of variables by standardizing the predictor variables included in the GLM formula. Pseudo-R^2 values are calculated as: (null deviance – residual deviance)/null deviance.

Appendix A9: The results of the GLM regression of species richness of deciduous and evergreen species with the environmental variables

Variable	**Coefficient (DEC/EVG)**	**Pseudo R^2 (DEC/EVG)**	**AIC (DEC/EVG)**
Species richness (DEC/EVG)			
Bio2	0.624/-0.563	0.184/0.317	640.406/822.054
Bio3	0.514/0.501	0.1/0.251	649.821/830.972
Bio4	-0.651/-0.607	0.198/0.369	638.802/814.481
Bio5	-0.638/-0.58	0.356/0.336	617.67/819.328
Bio7	-0.628/-0.571	0.177/0.326	641.192/820.863
Bio12	0.768/0.738	0.45/0.544	602.564/783.279
Bio13	0.775/0.757	0.456/0.574	601.515/776.838
Bio15	0.553/0.567	0.178/0.321	641.072/821.471
Bio16	0.773/0.75	0.446/0.562	603.315/779.463
Bio19	0.743/0.741	0.598/0.55	572.334/782.064
PET	-0.692/-0.605	0.35/0.367	618.54/814.837
GAI	0.774/0.735	0.47/0.54	599.074/784.213

Regression coefficients are standardized to compare the effect of variables by standardizing the predictor variables included in the GLM formula. Pseudo-R^2 values are calculated as: (null deviance – residual deviance)/null deviance.

Appendix A10: Relationships between bioclimatic variables, proportion abundance and species richness of deciduous and evergreen tree species a to d: annual precipitation versus proportion abundance and species richness of evergreen and deciduous tree species, f to h: maximum temperature of warmest month versus proportion abundance and species richness of evergreen and deciduous tree species, i to l: anthropogenic disturbance versus proportion abundance and species richness of evergreen and deciduous tree species.



Appendix A11: The results of generalized linear model regression (GLM) between Net Relatedness Index (NRI) and environmental variables.

Variable	**Coefficient**	**Pseudo R^2**	**AIC**
Bio2	0.403	0.163	215.129
Bio3	-0.431	0.186	219.906
Bio4	0.456	0.208	204.594
Bio5	0.258	0.067	220.829
Bio7	0.427	0.182	212.349
Bio12	-0.467	0.219	185.945
Bio13	-0.487	0.237	183.352
Bio15	-0.411	0.169	214.110
Bio16	-0.481	0.231	185.746
Bio19	-0.400	0.160	193.769
PET	0.312	0.097	213.651
GAI	-0.454	0.206	186.473

Regression coefficients are standardized to compare the effect of variables by standardizing the predictor variables included in the GLM formula. Pseudo-R^2 values are calculated as: (null deviance – residual deviance)/null deviance. Bold numbers represent the best models explaining the observed NRI values. AICw = Akaike weight: low AICw value indicate greater support for the model.

Appendix A12: The results of the GLM regression of NTI with the environmental variables

Variable	**Coefficient**	**Pseudo R^2**	**AIC**
NTI			
Bio2	-0.019	0.000	204.027
Bio3	0.014	0.000	204.044
Bio4	0.013	0.000	204.046
Bio5	-0.007	0.000	204.058
Bio7	-0.010	0.000	204.053
Bio12	0.013	0.000	204.047
Bio13	-0.025	0.001	204.005
Bio15	-0.218	0.048	199.382
Bio16	0.002	0.000	204.062
Bio19	0.112	0.012	202.859
PET	-0.013	0.000	204.047
GAI	0.023	0.001	204.012

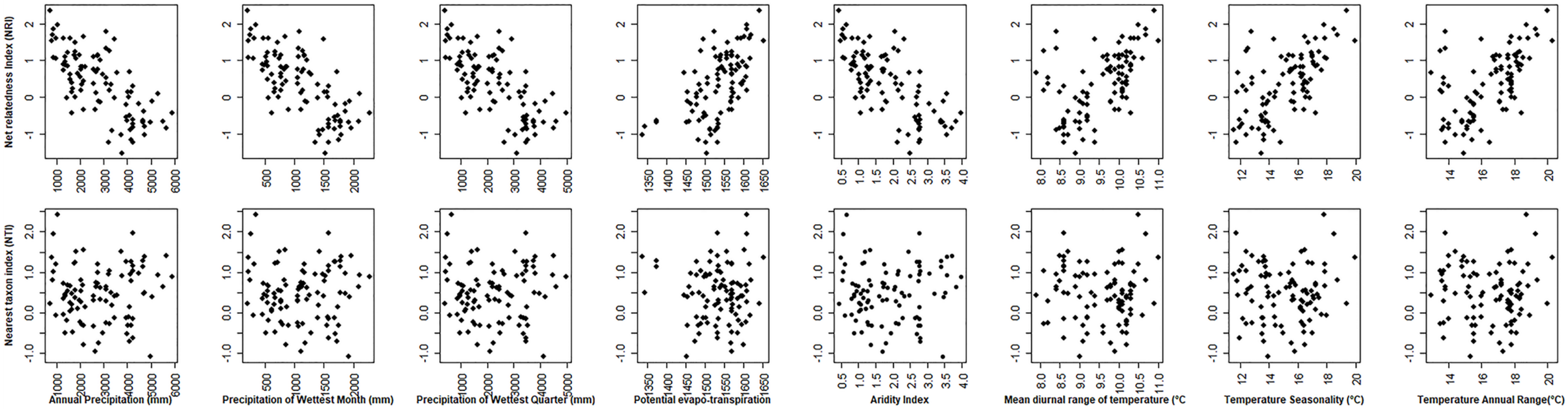
Regression coefficients are standardized to compare the effect of variables by standardizing the predictor variables included in the GLM formula. Pseudo-R^2 values are calculated as: (null deviance – residual deviance)/null deviance.

Appendix A13: The results of the T-tests between NTI values and the discrete habitat variables of forest type and level of disturbance.

Variable	Comparison	Mean	t	DF	P value	Clustered (%)	Overdispersed (%)
NTI							
Forest type	EVG/MD	0.451	0.183	74	0.855	21	2
	MD/DD	0.420	0.765	38	0.450	15	0
	DD/EVG	0.420	0.726	74	0.470	30	0
Level of Human disturbance	None/low	0.380	0.559	63	0.581	23	2
	Low/high	0.693	0.662	52	0.510	17	0
	High/none	0.379	1.264	71	0.210	16.5	0

Percentage values represent the proportion of sites that were significantly clustered and overdispersed assemblages per category. Abbreviations: DF: degrees of freedom, EVG: evergreen, DEC: deciduous, MD: moist deciduous, DD: dry deciduous. The formula for t-test used is $t = \bar{x}1- \bar{x}2/\sqrt{}((N1-1)s21+(N2-1)s22/N1+N2-2)(1/N1+1/N2)$, where $\bar{x}1$ and $\bar{x}2$ represent means of two different forest types or disturbance level; N1 and N2 are sample size and s21 and s22 are an estimator of the common variance of the two sample.

Appendix A14: The correlations between environmental variables and phylogenetic alpha diversity indexes (NRI or NTI). First panel NRI and second panel is NTI.

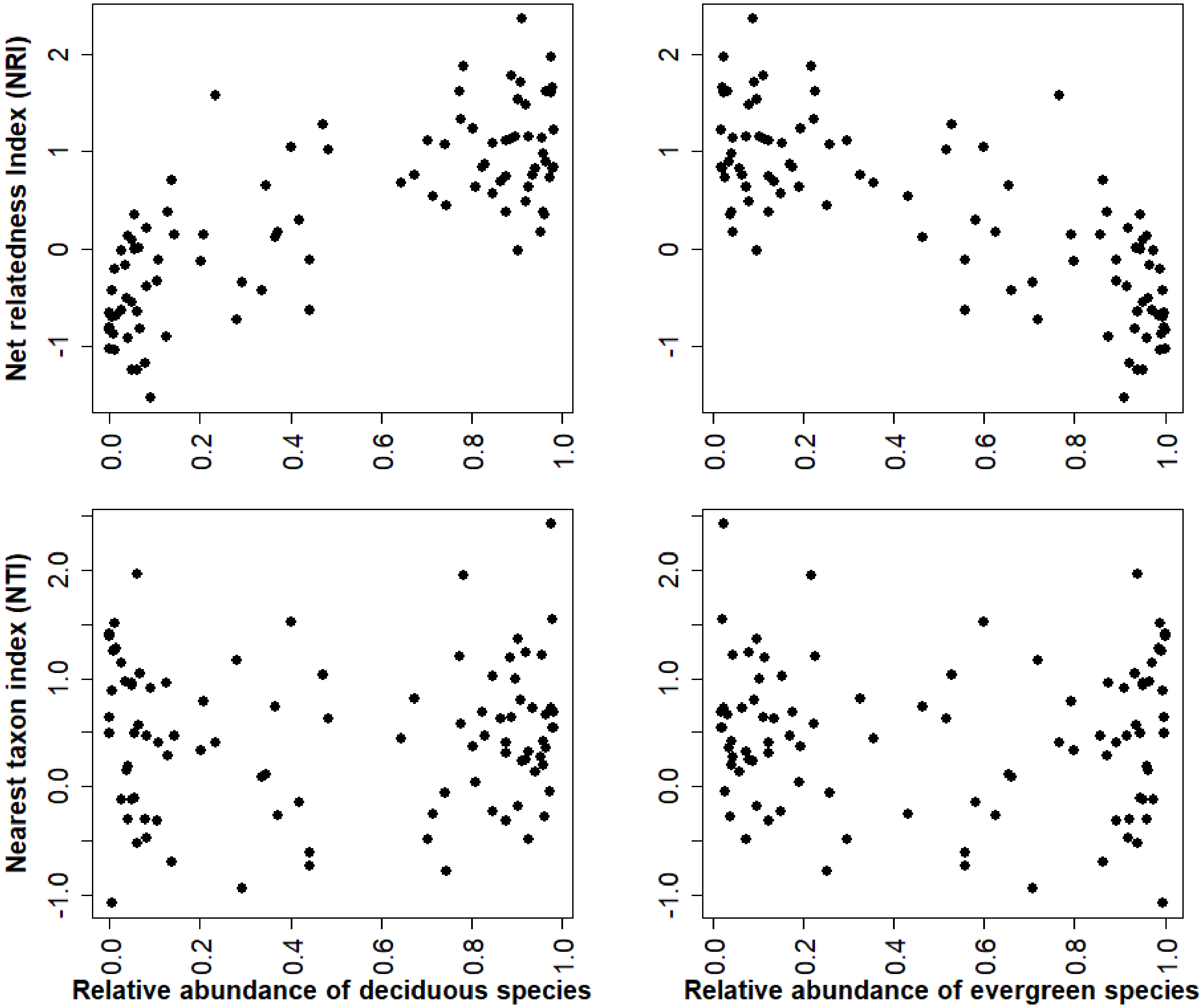


Appendix A15: The results of the GLM regression of NRI and NTI with the relative abundance of deciduous and evergreen tree species.

Variable	Coefficient	Pseudo R^2	AIC	AIC_w
Deciduous				
NRI	-0.563	0.609	161.859	0.000
NTI	0.501	0.000	204.027	42.168
Evergreen				
NRI	0.757	0.609	162.050	0.000
NTI	0.567	0.001	204.001	42.142

Regression coefficients are standardized to compare the effect of variables. Pseudo-R^2 values are calculated as: (null deviance – residual deviance)/null deviance. AICw = Akaike weight: low AICw value indicate greater support for the model.

Appendix A16: The relationship between phylogenetic alpha diversity and relative abundance (proportion) of deciduous species.

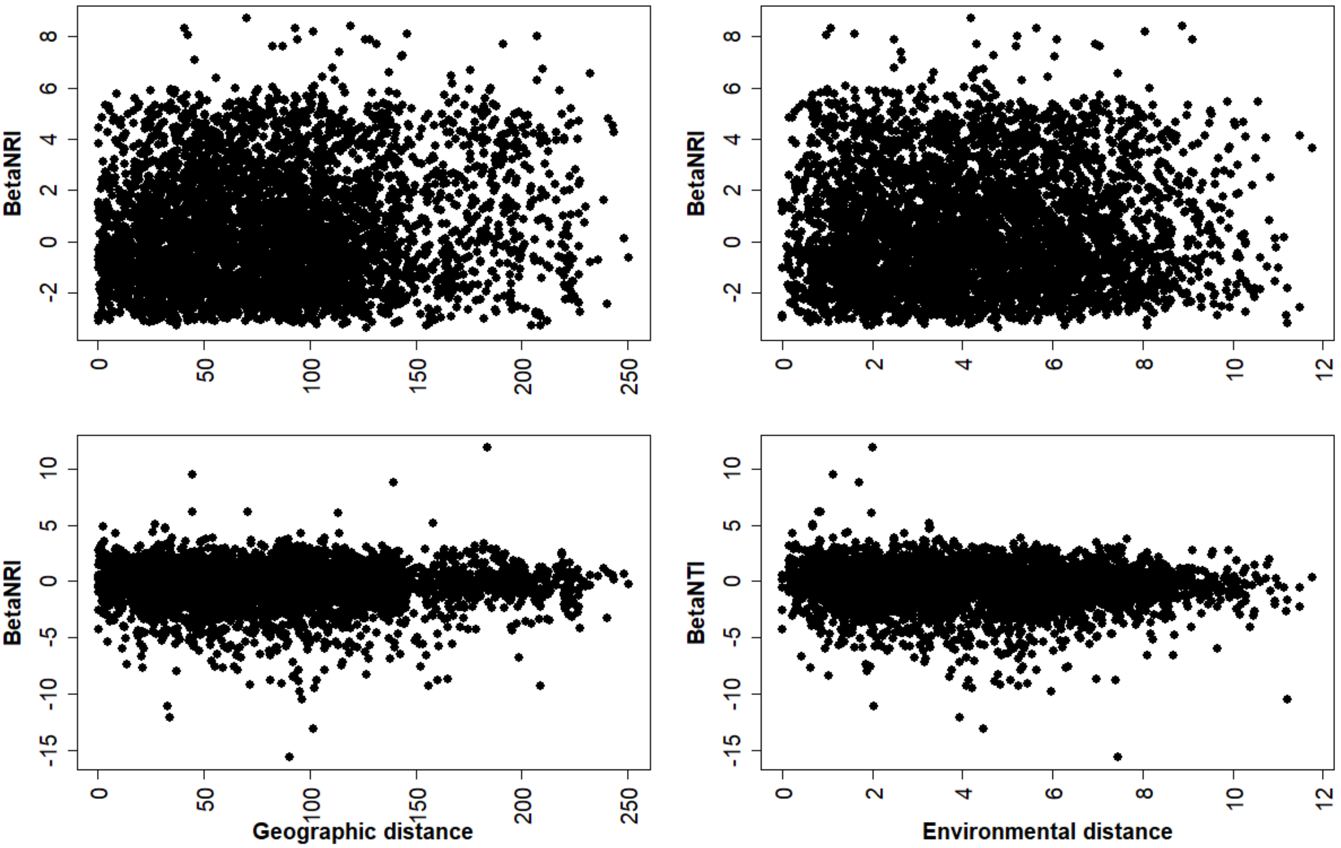


Appendix A17: The results of the GLM regression of NTI with the geographic and environmental distance

Variable	**Coefficient**	**Pseudo R^2**	**AIC**	**AIC$_w$**
NRI				
Geographic distance	0.112	20423.99	1976.917	0.013
Environmental distance	-0.008	18478.86	31.784	0.000
NTI				
Geographic distance	0.003	20479.66	2032.59	0.001
Environmental distance	-0.084	18447.07	0.000	0.007

Regression coefficients are standardized to compare the effect of variables. Pseudo-R^2 values are calculated as: (null deviance – residual deviance)/null deviance. AICw = Akaike weight: low AICw value indicate greater support for the model.

Appendix A18: plots depicting correlation between phylogenetic beta diversity metric, geographic distance and environmental distance.

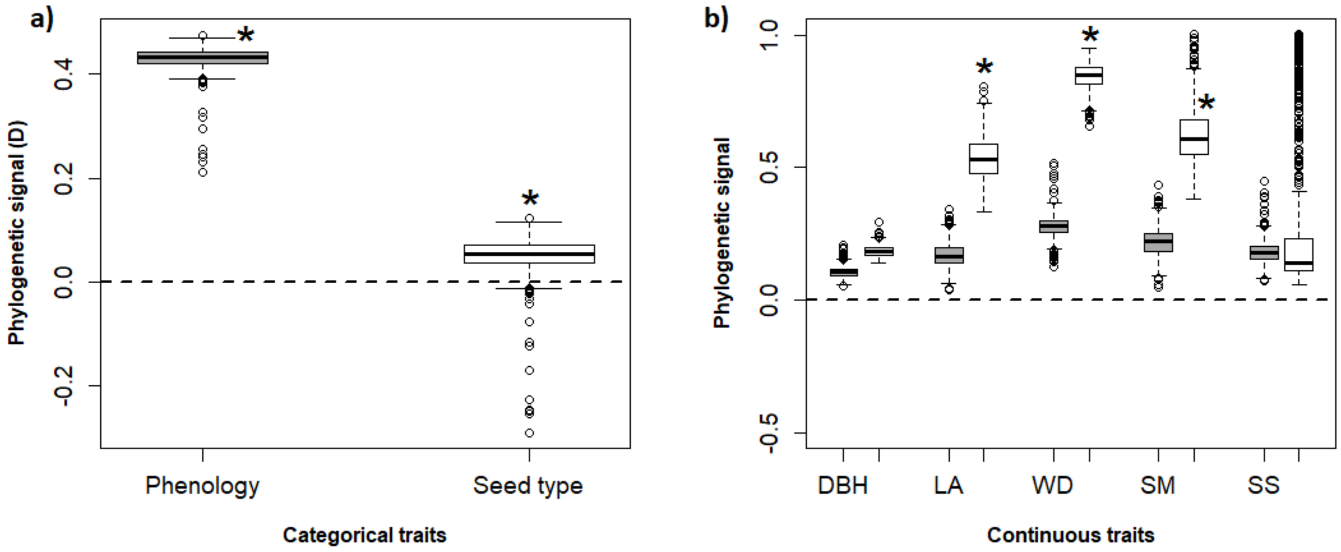


Appendix A19: Phylogenetic signal of traits across tree species from 96 plots in Western Ghats, India. The average and standard deviation values were obtained across 1000 Bayesian trees to account for phylogenetic uncertainty.

Continuous traits	**Bloomberg's K**		**Pagel's λ**		**Categorical traits**	**D statistic**		
	K (±SD)	**$P_{(rep=999)}$**	**λ (±SD)**	**$P_{(\lambda=0)}$**		**D (±SD)**	**P_{Random}**	**$P_{Brownian}$**
Leaf size	**0.169±0.043**	0.027	**0.534±0.077**	<0.001	Leaf phenology	0.430±0.021	0.023	0.025
Maximum DBH	0.105±0.02	0.340	0.184±0.02	<0.251	Seed dormancy type	**0.052±0.034**	<0.0001	<0.850
Seed size	0.180±0.042	0.125	0.244±0.239	<0.103				
Seed mass	**0.219±0.053**	0.001	**0.623±0.103**	<0.001				
Wood density	**0.277±0.038**	0.001	**0.844±0.048**	<0.001				

Note: Traits with significant phylogenetic signal are in bold.

Appendix A20: Boxplot showing phylogenetic signal for discrete and continuous functional traits used in the study. A) discrete traits and b) continuous traits. Asterisks represent significant phylogenetic signal in traits. Dashed line represents null hypothesis of no phylogenetic signal. Abbreviations: DBH=diameter at breast height, LA=leaf size, WD=wood density, SM=seed mass and SS= seed size.



Appendix A21: The results of the T-tests between functional trait metrics (Range and Variance) and the discrete habitat variables forest type. Significant results are indicated in bold.

Variable	Comparison	Mean	t	P value	Clustered (%)	Overdispersed (%)
DBH (Range)						
Forest type	EVG/MD	1.595	0.021	0.021	5	65
	MD/DD	2.569	0.697	0.500	5	85
	DD/EVG	2.130	1.268	0.210	5	90
DBH (Variance)						
Forest type	EVG/MD	2.814	3.062	0.0034	0	96
	MD/DD	2.203	1.452	0.324	0	95
	DD/EVG	2.528	1.396	0.167	0	95
Seed mass (Range)						
Forest type	EVG/MD	0.341	0.652	0.516	16	25
	MD/DD	0.147	0.265	0.792	30	15
	DD/EVG	0.260	0.279	0.788	25	35
Seed mass (Variance)						
Forest type	EVG/MD	0.663	0.784	0.435	2	34
	MD/DD	0.494	0.133	0.894	0	25
	DD/EVG	0.532	0.544	0.587	15	45

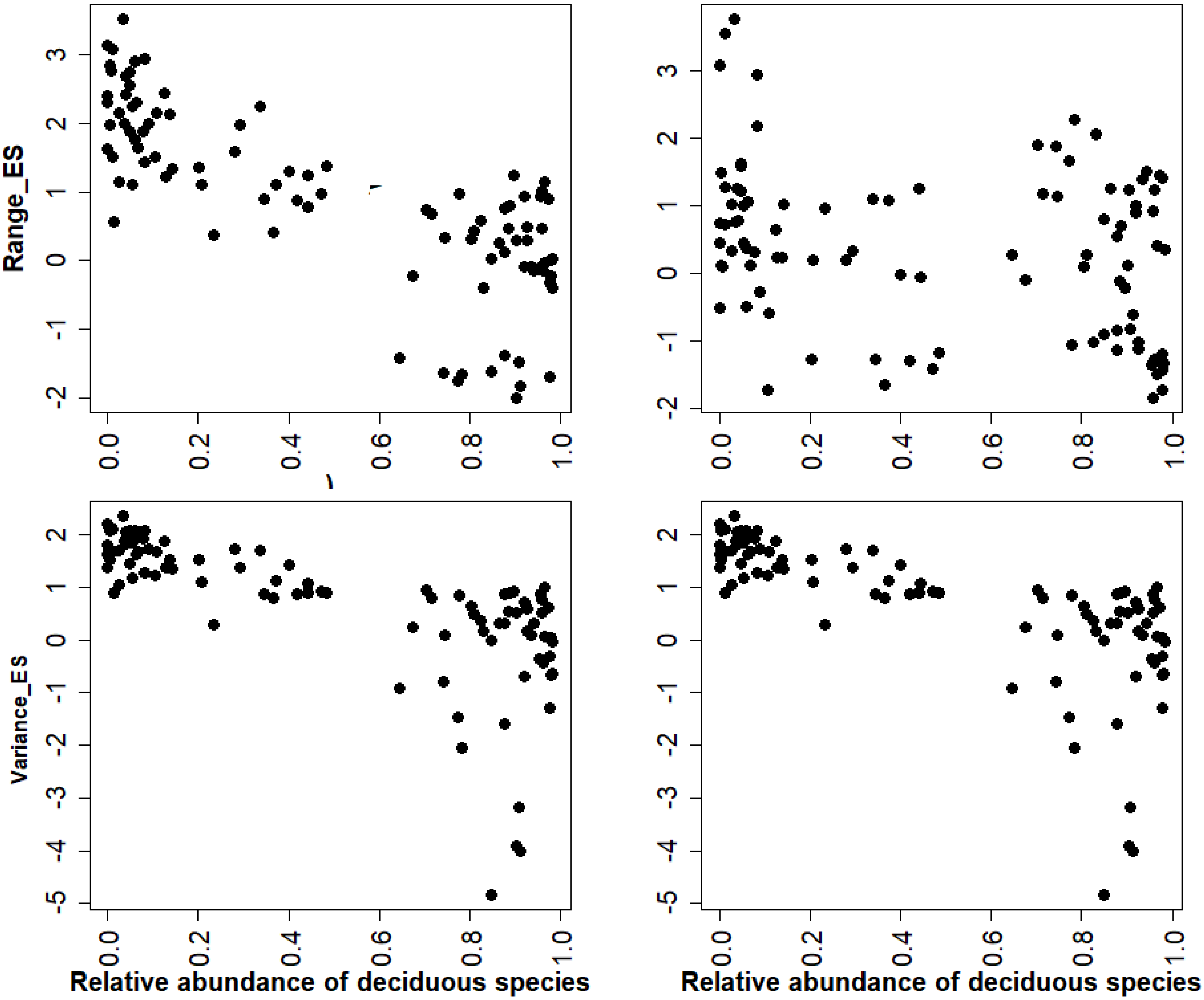
Percentage values represent the proportion of sites that were significantly clustered and overdispersed assemblages per category. Abbreviations: DF: degrees of freedom, EVG: evergreen, DEC: deciduous, MD: moist deciduous, DD: dry deciduous. The formula for t-test used is $t = \overline{x}1- \overline{x}2/\sqrt{((N1-1)s21+(N2-1)s22/N1+N2-2)(1/N1+1/N2)}$, where $\overline{x}1$ and $\overline{x}2$ represent means of two different forest types; N1 and N2 are sample size and s21 and s22 are an estimator of the common variance of the two samples

Appendix A22: The results of the GLM regression of range and variance of functional traits with the relative abundance of deciduous and evergreen tree species.

Variable	Coefficient	Pseudo R^2	AIC	AIC_w
Deciduous				
Leaf area (Range)	-0.607	0.596	238.254	0.000
Leaf area (Variance)	-0.580	0.458	276.575	1.235
Seed mass (Range)	-0.571	0.081	307.692	145.833
Seed mass (Variance)	0.738	0.092	255.994	94.136
Evergreen				
Leaf area (Range)	0.750	0.601	237.263	0.000
Leaf area (Variance	0.741	0.460	276.257	1.568
Seed mass (Range)	-0.605	0.087	307.037	145.179
Seed mass (Variance)	0.735	0.100	255.204	93.345

Regression coefficients are standardized to compare the effect of variables. Pseudo-R^2 values are calculated as: (null deviance – residual deviance)/null deviance.

Appendix A23: The relationship between functional trait metrics (Range and Variance) of leaf size and seed mass and relative abundance (proportion) of deciduous species. The first row is leaf size and second row is seed mass.

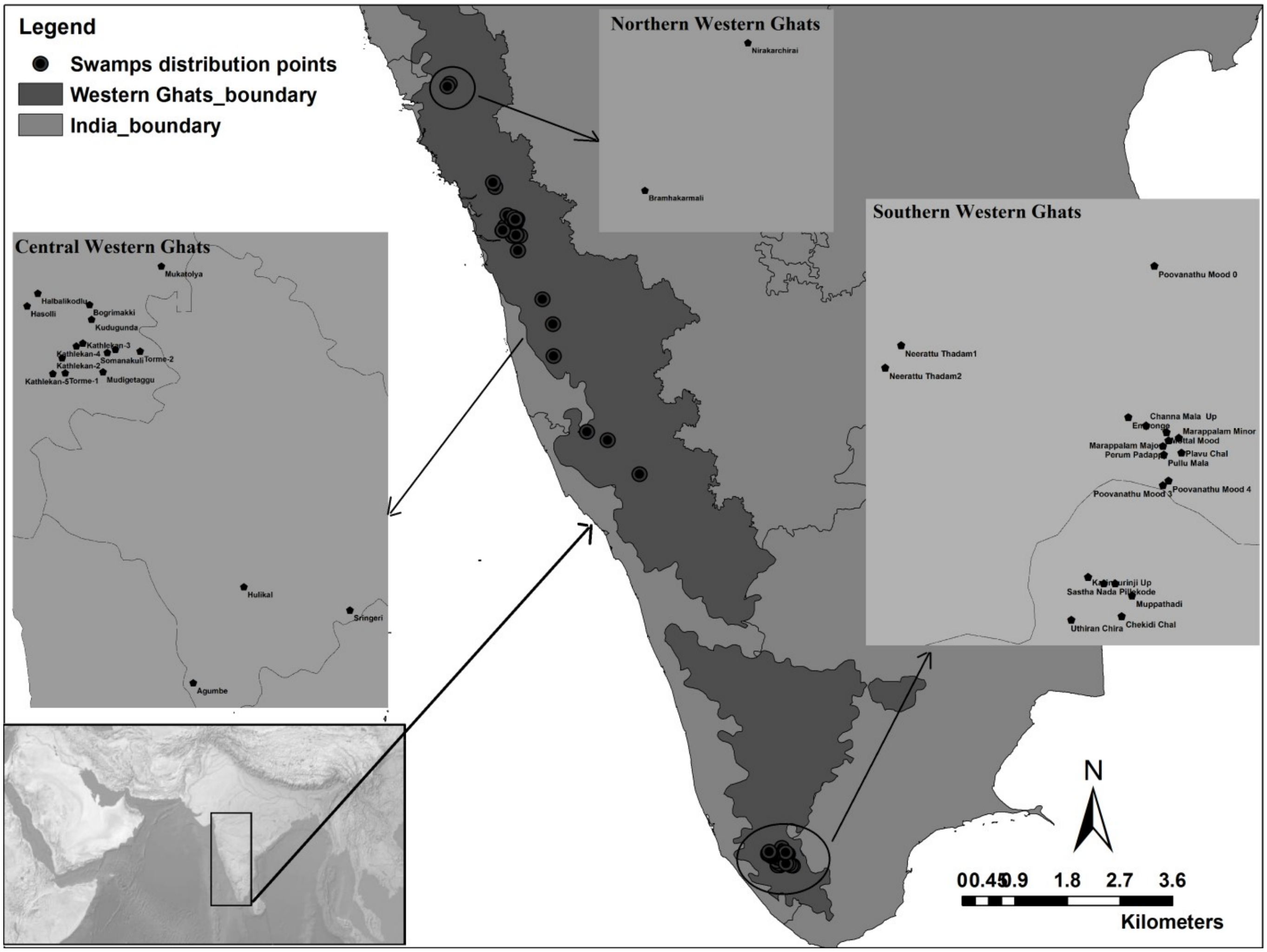


Appendix B

Supporting Information — Chapter 3

Appendix B1: Sampled location of 42 freshwater swamps and 29 terra-firme forest across Western Ghats biodiversity hotspot, India.

Note: refer Appendix B2 for geographic sub-division or region where sampling was done.

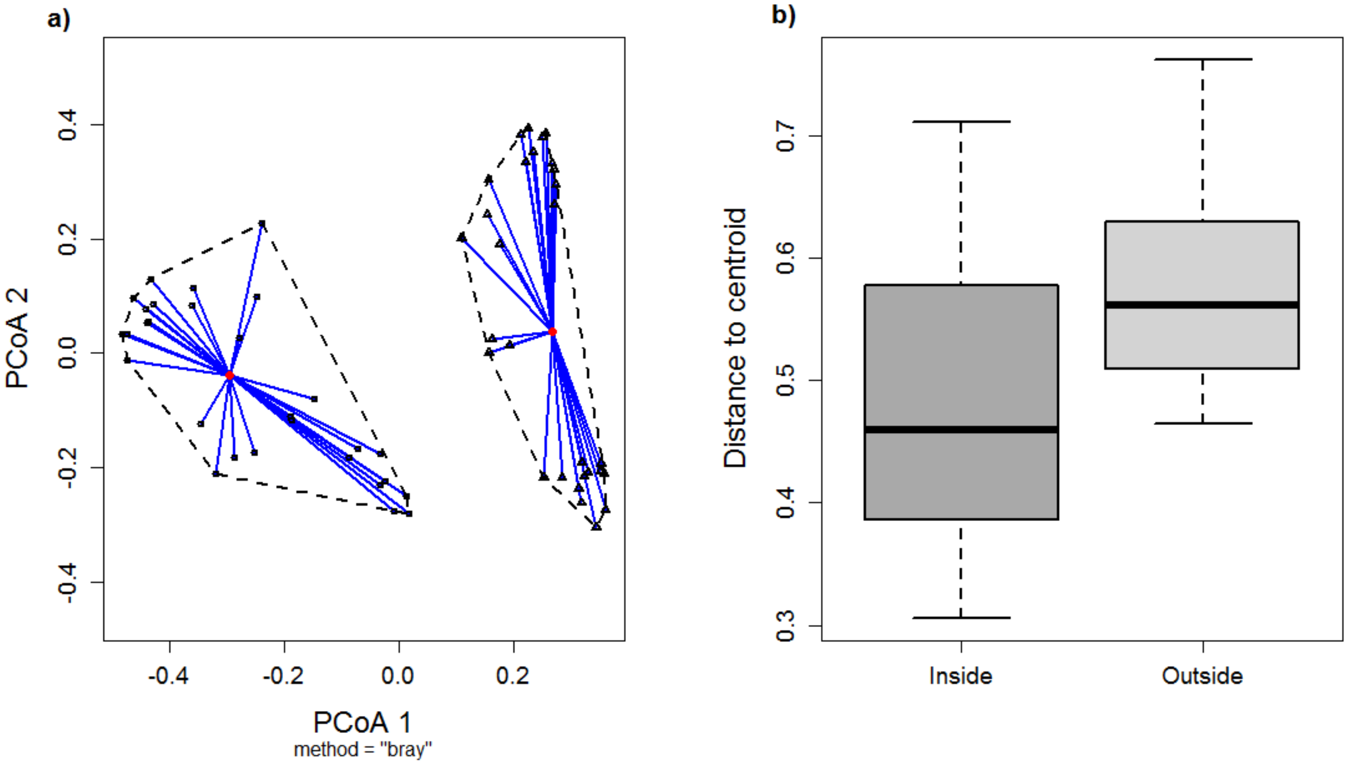


Appendix B2: Geographic description, total area and species richness of 42 swamps and 29 terra firme forest sampled in Western Ghats, India.

SI NO	Region (Provinance)	Name of swamp	Longitude	Latitude	Altitude (m)	Total area of swamp in (Ha)	Species richness (swamp/terra firme)
1	Southern Western Ghats (Kerala)	Chekadichal	77.060921	8.802753	222.000	3.61	13/22
2		Channamala	77.072784	8.882093	153.000	2.50	13/33
3		Emponge	77.064815	8.887532	153.000	3.23	15/31
4		Kanikurunji	77.051114	8.819454	222.000	3.95	12/12
5		Marapala major	77.089104	8.877313	153.000	1.31	11/31
6		Marapala minor	77.086248	8.878656	241.000	0.26	19/30
7		Mottal Mood	77.080923	8.881830	153.000	2.28	10/24
8		Muppalhadi	77.064307	8.811675	222.000	1.33	11/15
9		Neerattuthadam1	76.969605	8.916449	135.000	8.00	16
10		Neerattuthadam2	76.979605	8.926449	180.000	8.00	4
11		Perum Padappy	77.082255	8.875924	153.000	2.17	16/32
12		Pillekode	77.059372	8.815173	222.000	0.98	18
13		Plevukidnachal	77.087102	8.871814	349.000	3.58	15/17
14		Poovanathumood 0	77.078593	8.852787	154.000	3.24	7
15		Poovanathumood 3	77.080492	8.859325	175.000	0.76	9/24
16		Poovanathumood 4	77.080875	8.860595	175.000	1.22	16
17		Pulumala	77.080719	8.872284	175.000	1.50	13/16
18		Sashanada	77.053522	8.816829	222.000	1.71	29/19
19		Uthiranchira	77.040175	8.800738	190.000	1.45	7/12
20		Hulikal	74.998420	13.718280	517.000	1.50	47/60
21		Sringeri	75.482222	13.684444	658.000	1.00	32
22		Agumbe	75.116125	13.470813	664.000	2.50	27/63
23		Hebri	75.015405	13.585285	164.750	0.90	24
24		Belthangady	75.318532	13.078123	178.689	0.20	23

25	**Central Western Ghats (Karnataka)**	Subramanya	75.592346	12.742872	154.416	5.00	27/38
26		Sampanje	75.618740	12.456412	527.886	0.20	10
27		Makutta	75.723231	12.077411	145.284	0.04	19
28		Hosoli	74.676389	14.444167	414.000	5.60	25/21
29		Bogrimakki	74.831944	14.447222	507.000	0.40	19/25
30		Kathlekan 1	74.896389	14.335556	542.000	1.50	15/16
31		Kathlekan 2	74.763611	14.314167	547.000	2.50	14/22
32		Kathlekan 3	74.815556	14.351389	585.000	1.20	10/22
33		Kathlekan 4	74.799167	14.343889	565.000	5.25	14/22
34		Kathlekan 5	74.740290	14.275030	570.000	0.90	17/25
35		Mundigethaggu	74.865556	14.279333	560.000	0.90	5
		Somankuli	74.876389	14.327500	647.000	0.90	16
		Torme 1	74.674000	14.348700	580.000	0.50	26/24
		Torme 2	74.673000	14.348300	575.000	0.50	31/27
		Kudugunda	74.836944	14.410277	578.000	1.20	12/21
		Mukatoleya Kodlu	74.765700	14.278300	557.000	8.00	8/25
36	**Northern Western Ghats (Goa)**	Nirahankariprasham	74.190300	15.589560	187.000	0.05	14
37		Bramhakarmali	74.173270	15.565130	123.000	1.20	22

Appendix B3: Beta diversity of tree communities in paired plots inside (swamp) and outside (terra-firme forest or non-swamp) of freshwater swamps in Western Ghats. a) Distance between plots inside (left) and outside (right) of freshwater swamps; b) A boxplot of distances to the centroids of plots inside and outside of freshwater swamps. There was a significant difference in diversity between plots inside and outside of freshwater swamps, with outside plots having a higher beta diversity than inside plots (ANOVA: F1;56 = 9.830, P = 0.00274).



Appendix B4: Trait coverage, and example of the ecological significance of each trait, and data source.

Trait		No of species sampled	Strategy correlation or function	Data source
Continuous traits	Leaf size	210 (100%)	Energy and water uptake (1)	8,9,10,11,12,13,14,15
	Maximum height	210 (100%)	Carbon gain strategy via light capture (2)	9,10,17,18
	Maximum DBH	210 (100%)	Competition for light (1)	9,10,17,18
	Seed size	200 (95%)	Dispersal strategy (3)	8,9,10,12,18,19,20,21,22,23,24,25 ,26,27,28,29,30,31,32,33,34,35,36, 37,38,39,40
	Seed mass	200 (95%)	Dispersal and regeneration strategy (1,3)	19,20,21,22,23,25,29,32,34,41,42 43,44,45,46,47
	Wood density	195 (93%)	Allocation of resources for growth and mechanical strength (4)	16,17,43,48,49,50,51,52,53,54,55
Categorical traits	Adventitious root type	210 (100%)	Respiration and standing support under waterlogged condition (5)	6,8,9,10,56,57
	Flooding or inundation tolerance	210 (100%)	Ability to withstand water logged condition or depth of standing water (5, 6)	6,8,56,57
	Germination type	210 (100%)	Regeneration strategy in flooded condition (7)	8,13,18,19,20,21,22,41,58,59,60, 61,62,63,64,65,66,67,68
	Seed dormancy type	210 (100%)	Desiccation sensitivity and dispersal strategy (3,5)	8,13,18,19,20,21,22,41,58,59,60, 61,62,63,64,65,66,67
	Habitat preference	210 (100%)	-	6,8,9,10,51,52, 61,62

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Appendix B5: Trait correlations (Spearman's rho).

	DBH	**Leaf size**	**Seed size**	**Wood density**	**Seed mass**	**Categorical (PCoA 1)**
Height	0.85	0.2	0.23	-0.05	0.25	0.45
DBH		0.14	0.12	-0.02	0.13	0.28
Leaf size			0.06	-0.36	0.07	0.19
Seed size				-0.04	0.77	0.5
Wood density					0.02	-0.17
Seed mass						0.54

Appendix B6: The details of three genes used for phylogeny construction. The length of each gene (number of base pairs) is listed, as well as the models selected with JModelTest and missing data for each gene also given.

Gene	Length (bp)	Selected model	Present/Missing data
MatK	845	TVM+G	190/20
Rbcl	496	TVM+G	205/5
psbA-trnH	397	GTR+I+G	166/44

Appendix B7: Sequence data used to create a phylogeny for tree species found in 96 1-ha plots in Western Ghats, India. TBA represent sequences generated in the present study, but not yet deposited to NCBI.

Orginal species	Replaced species	RBCL	MATK	PSBA
Actinodaphne angustifolia	*Actinodaphne Pilosa*	KP094296.1	KP093382.1	KP095527.1
Actinodaphne hookeri	*Actinodaphne omeiensis*	HM019449.1	HM019309.1	HM019379.1
Actinodphne malabarica	*Actinodaphne acuminate*	KJ594563	KJ687706.1	KJ686998.1
Aglaia annamalayana	*Aglaia odoratissima*	GQ248543.1	GQ248074.1	GQ248240.1
Aglaia barberi	*Aglaia korthalsii*	GQ248542.1	GQ248073.1	GQ248239.1
Aglaia elaeagoidea	*Aglaia elliptifolia*	KJ688685.1		KJ687279.1
Aglaia lawii		AB925640.1	AB925000.1	
Aglaia roxburghiana	*Aglaia macrocarpa*	KJ594569	KJ708806	
Agrostistachys indica		AB925297.1	AB924687.1	
Agrostistachys meboldii	*Agrostistachys borneensis*	AB233856.1	AB233752.1	
Alangium salvifolium		JF308648.1	FJ644639.1	JF321228.1
Alstonia scholaris		EU916739.1	JN228931.1	JX856820.1
Anodendron paniculatum	*Anodendron affine*	EU916727.1	KP093971.1	KP095423.1
Antidesma menasu	*Antidesma fordii*	HQ415204	HQ415370	HQ415551
Apodytes dimidiate		AJ428895.1	AJ429311.1	
Aporosa acuminate	*Aporusa yunnanensis*	HQ415224.1	HQ415388.1	HQ415570.1
Aporosa bourdillonii	*Aporusa benthamiana*	KJ594594	KJ708826	
Aporosa cardiosperma	*Aporusa frutescens*	KJ594599	KJ708827	
Aporosa lindleyana	*Aporusa microstachya*	KJ594601	KJ708830	
Archidendron monadelphum	*Archidendron lucidum*	HQ415101	HQ415282	HQ415452
Arenga wightii		JF344836.1	JF344976.1	JF345043.1
Artocarpus heterophyllus	*Artocarpus altilis*	HM446760	HM446658	HM446889

Artocarpus hirsutus	*Artocarpus styracifolius*	HQ415055	HQ415243	HQ415407
Artocarpus integrifolia	*Artocarpus tonkinensis*	KP094622	KP093685	KP095807
Atalantia racemosa	*Atalantia monophyla*	AB505920.1	AB762381.1	
Baccaurea courtalensis	*Baccaurea macrocarpa*	KJ594624	KJ708847	
Bauhinia purpurea		JX856647.1	JN881391.1	JX856835.1
Beilschmiedia dalzellii	*Beilschmiedia pendula*	GQ981679.1	EU153824.1	EU153945.1
Beilschmiedia wightii	*Beilschmiedia tsangii*	KP094802	KP093862	KP095540
Bischofia javanica		AY663571.1	AB233813.1	GU135378.2
Bombax ceiba		KP088494.1	JX495673.1	
Bridelia retusa		HQ415195.1	HQ415363.1	JX856845.1
Calophyllum apetalum	*Calophyllum longifolium*	GQ981683	HQ331555.1	GQ982164
Calophyllum polyanthum	*Calophyllum membranaceum*	KP094666	KP093729	HQ415450
Canarium strictum		FJ466638.1		AY635379.1
Canthium angustifolium	*Canthium horridium*	HQ415226	HQ415390	HQ415572
Canthium dicoccum	*Canthium tetraphyllum*	JX572859.1	JF270895.1	AM939403.1
Carallia brachiate		HQ415233	HQ415397	HQ415579
Careya arborea		: AF077655.1	AB925162.1	
Caryota urens		JQ734494.1	JF344998.1	JF345069.1
Casearia championii	*Casearia arborea*	GQ981686	HM446663	HM446896
Casearia glomerata		HQ415115	HQ415293	HQ415465
Casearia ovata	*Casearia sylvestris*	HM446768	HM446664	HM446898
Casearia rubescens	*Casearia velutina*	HQ415116.1	HQ415294.1	HQ415466.1
Catunaregam dumetorum	*Catunaregam spinosa*	KP094947	KP094000	KP095441
Celtis philippensis		JF738837.1	AY263925.1	
Chionanthus malabaricus	*Chionanthus domingensis*	HM446772	KJ012507.1	HM446902
Chrysophyllum lanceolatum		KJ594653.1	KP094145.1	KP095281.1
Chrysophyllum roxburghii		KF496346.1	AB924896.1	DQ344101.1
Cinnamomum heyneanum		KF744230.1	JX185548.1	KF978095.1
Cinnamomum malabathrum		KF878112.1	KP093991.1	
Cinnamomum sulphuratum		JN988468.1	JX185550.1	JN988467.1
Clausena dentata	*Clausena smyrelliana*	GQ436740.1	KF159531.1	KM895207.1
Clausena indica	*Clausena anisate*	AB505910.1	AB762395.1	AM500899.1
Croton Malabaricus	*Croton tiglium*	KP094474	KP093547	KP095635
Cryptocarya wightiana	*Cryptocarya chinensis*	KP094541	KP093613	KP095542
Dalbergia latifolia		JX856687.1		JX856872.1
Dendrocnide sinuata		FJ432246.1	KF137981.1	
Dillenia pentagyna	*Dillenia indica*	FJ860350.1	KF224977.1	JX852696.1
Dimocarpus longan		AF153353.2	AY724286.1	JN407058.2
Dimorphocalyx beddomei	*Dimorphocalyx australiensis*	KF496685.1		
Diospyros angustifolia	*Diospyros malabarica*	EU980707.1	**FJ238151.1**	JX856876.1
Diospyros buxifolia		KJ594673	KJ708884	

Diospyros candolleana	*Diospyros eriantha*	KP094503	KP093576	KP095198
Diospyros crumenata	*Diospyros sp*	KC628653.1	KC627925.1	KC668123.1
Diospyros foliosa	*Diospyros kaki*	KP094640	KP093703	KP095200
Diospyros paniculata	*Diospyros morrisiana*	KP094462	KP093535	KP095202
Diospyros pruriens	*Diospyros virginiana*	EU980774.1	DQ924064.1	FJ238227.1
Diospyros saldanha	*Diospyros glaucifolia*	HQ427239	HQ427382	HQ427082.1
Diospyros sylvatica	*Diospyros ebenum*	EU980677.1	EU980944.1	FJ238239.1
Dipterocarpus indicus	*Dipterocarpus tempehes*	KJ594685	KJ708907	
Drypetes elata	*Drypetes alba*	HM446793	KJ012572.1	HM446925
Drypetes wightii	*Drypetes glauca*	HM446794		HM446926
Dysoxylum binectariferum		JX982144.1	JX982143.1	JX982146.1
Dysoxylum Malabaricum	*Dysoxylum caulostachyum*	KJ594693.1	KJ708914.1	AB057503.1
Elaeocarpus glandulosus	*Elaeocarpus chinensis*	KP094451	KP093525	KP095766
Elaeocarpus serratus	*Elaeocarpus sylvestris*	KP094623	KP093686	KP095774
Elaeocarpus tuberculatus	*Elaeocarpus nitentifolius*	KP094932	KP093987	KP095772
Epiprinus mallotiforms	*Croton lachnocarpus*	KP094558	KP093630	KP095633
Erythrina variegata		KF496750.1		GU396820.1
Erythroxylum lanceolatum	*Erythroxylum sinense*	KP095001	KP094048	KP095629
Eugenia macrocephala	*Eugenia uniflora*	AF294255.2	GU135006.1	GU135338.2
Euonymus angulatus	*Euonymus laxiflorus*	KP094502	KP093575	KP095173
Euonymus indicus	*Euonymus nitidus*	KP095097	KP094132	KP095174
Fahrenheitia zeylanica	*Croton billbergianus*	GQ981717	JQ587440.1	GQ982201
Ficus amplissima	*Ficus caulocarpa*	JQ773663.1	JQ773517.1	JQ774307.1
Ficus bedomi	*Ficus benghalensis*	GU935060.1	GU935034.1	JX856886.1
Ficus callosal		JQ773669.1	JQ773522.1	JX185798.1
Ficus hispida		KP094194	KP093285	KP095828
Ficus nervosa		HQ415156	HQ415329	HQ415505
Ficus tsjahela	*Ficus racemosa*	EU516328.1	KC508603.1	GU935097.1
Flacourtia montana		AF454736.2	KP094010.1	
Garcinia gummi-gutta		KF783270.1	KC627491.1	KC667808.1
Garcinia morella	*Garcinia_oblongifolia*	KP094229.1	KJ510946.1	KC667747.1
Garcinia talbotii	*Garcinia multiflora*	KJ594718	KJ708932	KP095628.1
Garcinia xanthochymus		AF518391.1	KC627616.1	KC667791.1
Gardenia obtuse	*Gardenia_jasminoides*	HQ415113	HQ415291	HQ415463
Glochidion ellipticum	*Glochidion_puberum*	HQ415189	HQ415359	HQ415538
Glochidion malabaricum	*Glochidion_wrightii*	HQ415187	HQ415357	HQ415536
Glochidion zeylanicum		HQ415188	FJ235237.1	HQ415537
Gnidia glauca		AM162511.1	FJ572797.1	
Gymnacranthera canarica		KJ594740.1	TBA	TBA
Helictres isora		KF496517.1	KJ012633.1	KJ426772.1
Holigarna arnottiana	*Trichoscypha patens*	KC628299.1	KC627664.1	KC667843.1

Holigarna ferruginea	*Trichoscypha preussii*	KC628192.1	KC627584.1	KC667753.1
Holigarna grahamii	*Trichoscypha klainei*	KC628636.1	KC627911.1	KC668107.1
Holigarna nigra	*Trichoscypha acuminate*	KC628423.1	KC627746.1	KC667871.1
Homalium zeylanicum	*Homalium cochinchinense*	HQ415194	HQ415362	HQ415542
Hopea canarensis	*Hopea mengarawan*	KJ594748.1	KJ708955	AB452463.1
Hopea parviflora		JX163307.1	JX163312.1	JX502816.1
Hopea ponga		JX163308.1	JX163313.1	AB452461.1
Hopea utilis	*Hopea racophloea*	JX163309.1	JX163314.1	JX502817.1
Humboldtia brunonis		JX163310.1	EU361970.1	
Hydnocarpus pentandra		AJ418799.1	EF135551.1	
Ixora brachiate	*Ixora chinensis*	HQ415123	HQ415301	HQ415473
Kingiodendron pinnatum		JF739130.1	EU361987.1	
Knema attenuate		AB925454.1	:	
Lagerstroemia lanceolata	*Lagerstroemia subcostata*	KJ688771.1		KJ686934.1
Lagerstroemia microcarpa	*Lagerstroemia indica*	AY905412.1	KP089119.1	HG963877.1
Lagerstroemia speciosa		JN114813.1		JX856902.1
Lansium anamallayanum	*Lansium domesticum*	AY128232.1	AY128191.1	
Leptonychia moacurroides	*Leptonychia echinocarpa*	KC628496.1	KC627813.1	KC688758.1
Litsea floribunda		KP094769	KP093830	
Litsea laevigata	*Litsea cubeba*	KP094358	KP093440	KP095557
Litsea mysorensis	*Litsea glutinosa*	KP094179	KP093272	KP095559
Litsea stocksii	*Litsea monopetala*	KP094520	KP093592	KP095561
Litsea travancorica	*Litsea rotundifolia*	KP094181	KP093274	KP095564
Lophopetalum wightianum		KJ594776.1	KJ708988.1	
Macaranga peltate	*Macaranga bracteate*	HQ415215	HQ415380	HQ415562
Madhuca longifolia		JQ673542.1	JQ673568.1	AM179726.1
Madhuca neriifolia	*Madhuca microphylla*	AF421096.1		AM179727.1
Mallotus philippensis		HQ415221	HQ415385	**HQ415567**
Mallotus stenanthus	*Mallotus_hoookerianus*	HQ415222	HQ415386	HQ415568
Mallotus tetracoccus		HQ415220	EF582683.1	HQ415566
Mangifera indica		JN114819.1	AY594472.1	HG963847.1
Mastixia arborea	*Mastixia pentandra*	AF384109.1	JF308673.1	
Meiogyne pannosa		JQ723865.1	JQ723778.1	
Melia dubia		U38859.1	AY128194.1	
Memecylon amplexicaule	*Memecylon edule*	AB925617.1	AB924757.1	KJ488998.1
Memecylon malabaricum		KP202253.1	KF895404.1	KJ488995.1
Memecylon randerianum	*Memecylon talbotianum*	KF887423.1	KF895408.1	KJ488996.1
Memecylon umbellatum		KF887424.2	KF895406.1	KJ488997.1
Memecylon wightii		KM871211.1	KF895405.1	KJ488994.1
Mesua ferrea		AY625024.1	HQ331661.1	GQ435381.1
Meyna laxiflora	*Canthium coromandelicum*	Z68851.1	HM119520.1	

Mimusops elengi		JN114822.1	JN114760.1	AM179741.1
Mitragyna parvifolia		JX856731.1		JX856911.1
Mitragyna tubulosa		KC737720.1	AY538390.1	
Myristica beddomei		AY298839.1	TBA	TBA
Myristica dactyloides		KF496610.1	TBA	TBA
Myristica fatua		GQ248653.1	TBA	TBA
Myristica malabarica		JF738499.1	TBA	TBA
Neolamarckia cadamba		KC737738.1		
Neolitsea zeylanica		KJ594815.1	KJ709012.1	
Neonauclea purpurea		KF496549.1		
Nothapodytes nimmoniana			KJ563186.1	
Nothopegia beddomei	*Drimycarpus racemosus*	JF738529.1		KF664316.1
Nothopegia racemosa	*Semecarpus schlechteri*	JF738726.1		
Olea dioica		KP094844	**JX863045.1**	KP095520
Palaquium elliipticum	*Palaquium microphyllum*		KJ709027.1	HF542902.1
Pandanus furcatus	*Pandanus pygmaeus*		JX286749.1	JN017056.1
Pandanus tectorius		AY952439.1	JN407168.1	JN407020.3
Pavetta indica		AB925508.1	AB924889.1	
Persea macrantha	*Persea americana*	AY337727.1	JQ588149.1	JQ513882.1
Phyllanthus emblica		AY765269.1	FJ235251.1	GU598547.1
Pinanga dicksonii		KJ594849	KJ709045	
Poeciloneuron indicum		AY625023.1	HQ331673.1	
Polyalthia fragrans	*Polyalthia lateritia*	JX227915.1	JX227890.1	KF709064.1
Pterygota alata		JX856756.1		JX856935.1
Reinwardtiodendron anaimalaiense	*Reinwardtiodendron kinabaluense*	DQ238054.1		
Rinorea bengalensis		**DQ834788.1**	DQ842611.1	HM483573.1
Sapindus trifoliatus		JQ673550.1	AY724323.1	
Schefflera capitate	*Schefflera heptaphylla*	KP094267	KP093353	KP095131
Schefflera venulosa	*Schefflera morototoni*	HM446870	HM446744	HM447000
Schleichera oleosa		AY724367.1	AY724329.1	GU135355.2
Scolopia crenata	*Scolopia chinensis*	KP095040	KP094086	KP095690
Semecarpus auriculata		KF496691.1	AY594479.1	GU080317.1
Semecarpus kathalekanensis		AB925880.1	AB925069.1	GU080309.1
Sterculia guttas	*Sterculia lanceolate*	KP094342	KP093424	KP095703
Stereospermum colais			JN183984.1	**JQ899437.1**
Strombosia ceylanica		KJ594898.1	KJ709095.1	
Strychnos nux-vomica		L14410.1	AB636281.1	GQ435195.1
Swietenia macrophylla		JX856777.1	EF489114.1	JX856954.1
Symplocos cochinchinensis		HQ415170	HQ415341	HQ415519
Symplocos macrophylla		HQ415168	AY630674.1	HQ415517
Symplocos racemosa		AB925775.1	AB925051.1	HQ415516

Syzygium canarana	*Syzygium acuminatissimum*	KP094421	KP093500	KP095743
Syzygium caryophyllatum	*Syzygium buxifolium*	KP094792	KP093852	KP095749
Syzygium cumini		GU135224.1	GU135062.1	GU135329.2
Syzygium gardneri	*Syzygium championii*	KP095089	KP094126	KP095751
Syzygium hemisphericum		HQ415137	AB925274.1	HQ415487
Syzygium heyneanum	*Syzygium hancei*	KP094796	KP093856	KP095753
Syzygium laetum	*Syzygium nervosum*	KP094155	KP093248	KP095745
Syzygium lanceolatum	*Syzygium rehderianum*	KP094241	KP093329	KP095759
Syzygium mundagam	*Syzygium jambos*	KP094169	KP093262	KP095755
Syzygium travancoricum	*Syzygium malaccense*	JF738887.1	DQ088590.1	KJ426954.1
Syzygium zeylanicum		AB925359.1	AB924926.1	AM489883.1
Tabernaemontana alternifolia	*Tabernaemontana arborea*	GQ981892	GQ982109	GQ982379
Tabernaemontana heyneana	*Tabernaemontana disticha*	FJ037967.1	GU973933.1	FJ038859.2
Terminalia bellirica		AF425714.1	KC130324.1	FJ381879.1
Terminalia elliptica		JX571903.1	JX495766.1	JX856969.1
Terminalia paniculate	*Terminalia muelleri*	AF425713.1	GU135121.1	JX856971.1
Tetrameles nudiflora		AF206828.1	AY968458.1	
Toona ciliate		KF496355.1	**EF138920.1**	KM895079.1
Trewia nudiflora		AY663648.1		
Trichilia connaroides	*Trichilia pallida*	HM446879	HM446750	HM447009
Vateria indica	*Vateria copallifera*	KJ594927	AB246431.1	
Vepris bilocularis	*Vepris soyauxii*	KC628323.1	KC627533.1	KC667699.1
Walsura trifolia	*Walsura chrysogyne*	KJ594932	KJ709133	
Xanthophyllum arnotianum	*Xanthophyllum hainanensis*	HQ415112	HQ415290	HQ415462

Appendix B8: Calibration points and age constraints used in divergence time estimations.

Fossil	Minimum age (Ma)	Reference
Myrtales	88.2	Takahashi *et al*. (1999)
Malvales	65.5	Wheeler *et al*. (1987, 1994)
Magnoliales	112.0	Massoni *et al*. 2015
Laurales	108.8	Crane *et al*. (1994)
Ericales	91.2	Nixon & Crepet (1993)
Pandanales	64.0	Muller (1981)
Burseraceae	50	Collinson & Cleal (2001)
Arecales	64.0	Pan *et al*. (2006)

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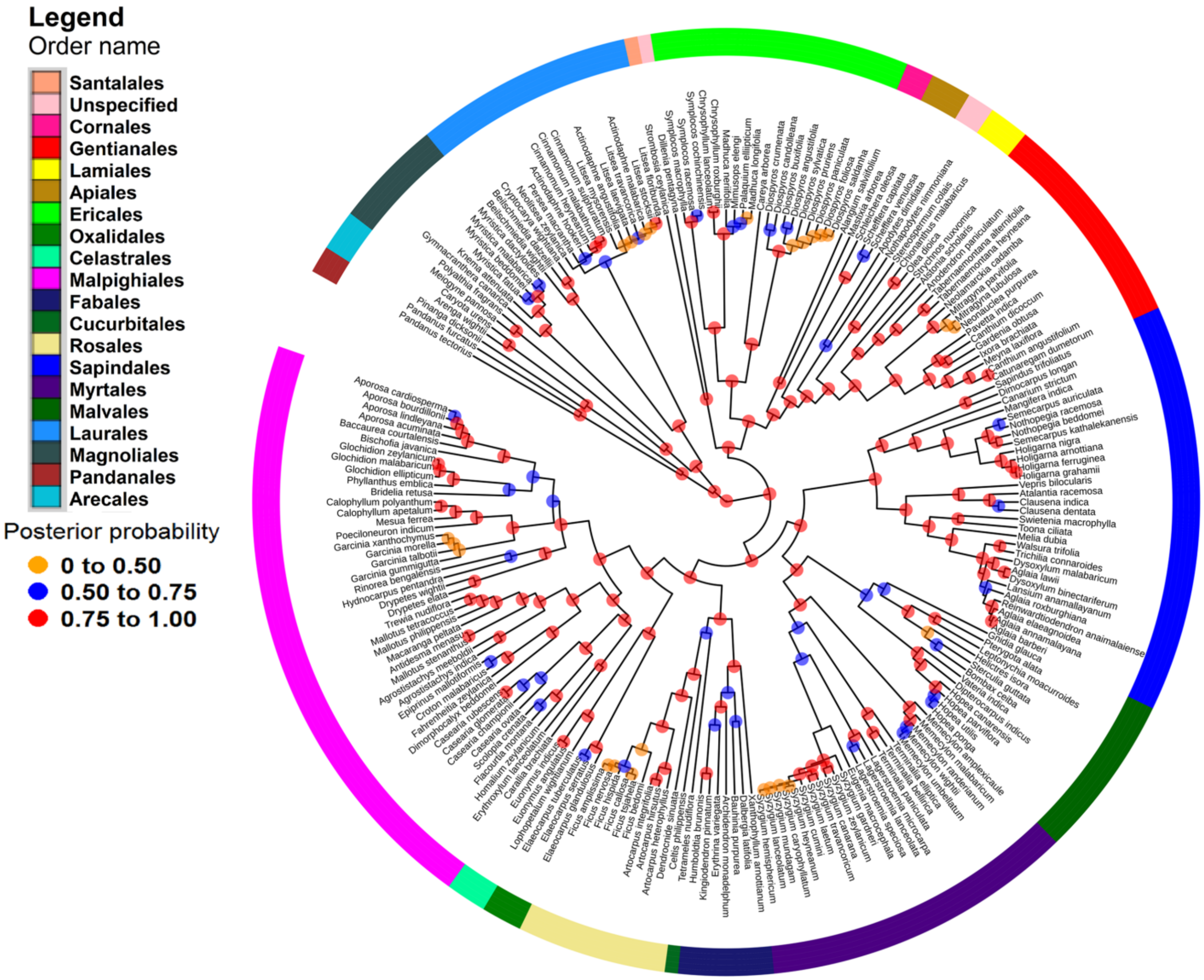
Appendix B9: Dated tree built using BEAST with three chloroplast genes (Rbcl, MatK and PsbA) and a backbone phylogeny enforced, using family level relationships from APG 111. Nodes with circles of different colors indicate estimated posterior probabilities from Bayesian analysis (MrBayes).



Appendix B10: The model fit of alternative models of correlated evolution between adventitious root and habitat specialization in freshwater swamp tree communities. The best fit model based on the Akaike Information Criterion (AIC) is shown in bold. ER=equal rates, ARD = all rates different.

Model	**parameters**	**-lnL**	**AIC**	**ΔAIC**
Individual character states (Independent model)				
Adventitious root, habitat specialization = ER	2	-159.434	322.867	36.923
Adventitious root =ER, habitat specialization = ARD	3	-159.434	322.867	36.923
Habitat specialization = ER, Adventitious root = ARD	3	-159.434	322.867	36.923
Adventitious root, habitat specialization = ARD	4	-133.777	275.555	40.08
Combined character states (Dependent model)				
ER	1	-119.560	247.120	30.809
ARD free	8	-101.961	219.923	3.612
The rate of transition to evolve adventitious root (only) to depend on the state of habitat specialization (model = ER)	6	-119.902	245.844	29.533
The rate of transition to evolve habitat preference to either swampy or non-swampy habitat (only) to depend on the presence or absence of adventitious root (model = ER)	6	-121.801	249.602	33.291
The rate of transition to evolve adventitious root (only) to depend on the state of habitat specialization (model = ARD)	8	-103.610	219.219	2.908
The rate of transition to evolve habitat preference to either swampy or non-swampy habitat (only) to depend on the presence or absence of adventitious root (model = ARD)	**8**	**-102.156**	**216.311**	**0**

Appendix B11. Model fits for ancestral reconstruction of adventitious root and habitat specialization, the best model based on Akaike Information Criterion (AIC) is highlighted (in bold).

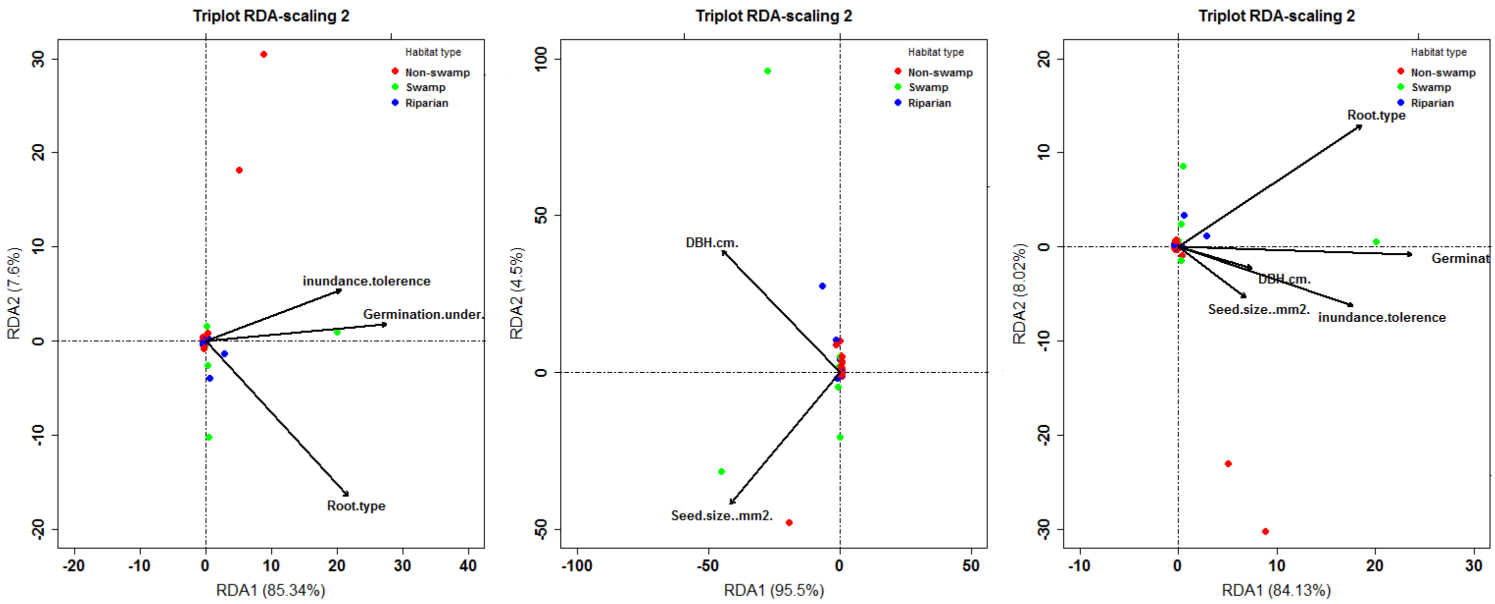
Model	**Adventitious root**		**Habitat specialization**	
	-lnL	**AIC**	**-lnL**	**AIC**
ER	-76.862	155.7256	-82.570	167.1414
SYM	-76.862	155.7256	-82.570	167.1414
ARD	-61.427	**126.8536**	-72.350	**148.701**
Ordered ASYM	-61.427	**126.8536**	-72.350	**148.701**

Appendix B12: Phylogenetic signal of traits across tree species from freshwater swamps and terra-firme forest.

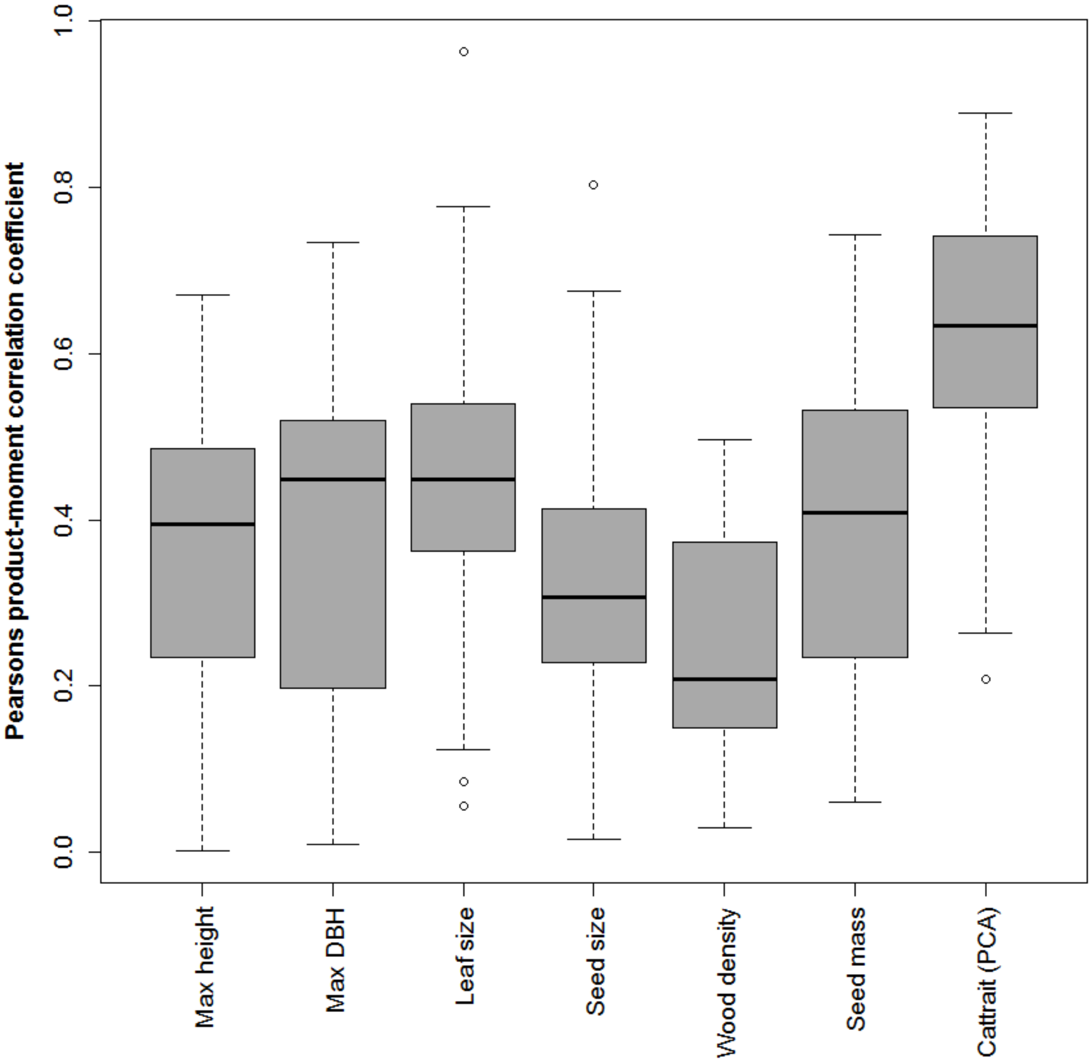
Continuous traits	**Bloomberg's K**		**Pagel's λ**		**Categorical traits**	**D statistic**		
	K	**$P_{(rep=999)}$**	**λ**	**$P_{(\lambda=0)}$**		**D**	**P_{Random}**	**$P_{Brownian}$**
Leaf size	0.108	0.027	**0.512**	<0.001	Adventitious root type	0.720	0.004	0.003
Maximum height	0.078	0.121	**0.586**	<0.001	Flooding or inundation tolerance	0.741	0.007	<0.001
Maximum DBH	0.054	0.234	0.276	0.061	Germination type	**-0.192**	0.354	0.932
Seed size	**0.174**	0.013	**0.974**	<0.001	Seed dormancy type	**-0.112**	0.342	0.810
Seed mass	**0.179**	0.001	**0.633**	<0.001	Habitat preference	0.680	0.002	0.001
Wood density	**0.139**	0.001	**0.792**	<0.001	-	-	-	-

Note: Traits with significant phylogenetic signal are in bold.

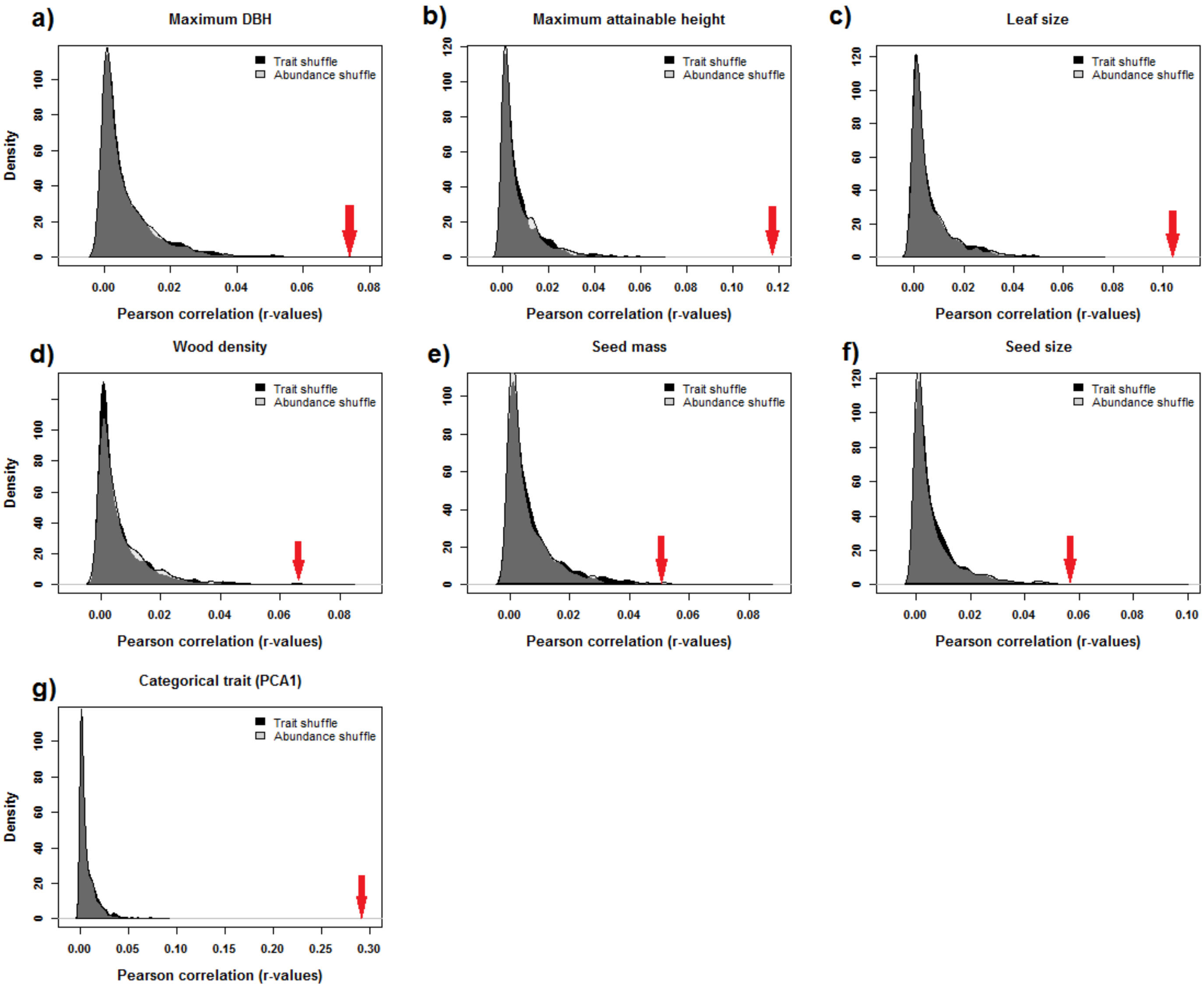
Appendix B13: Bi-plot from redundancy analysis of abundance of swamp tree species and functional traits (continuous and categorical). The arrows indicate continuous and categorical traits explaining significant variation in abundance of tree species occurring in swampy habitat.



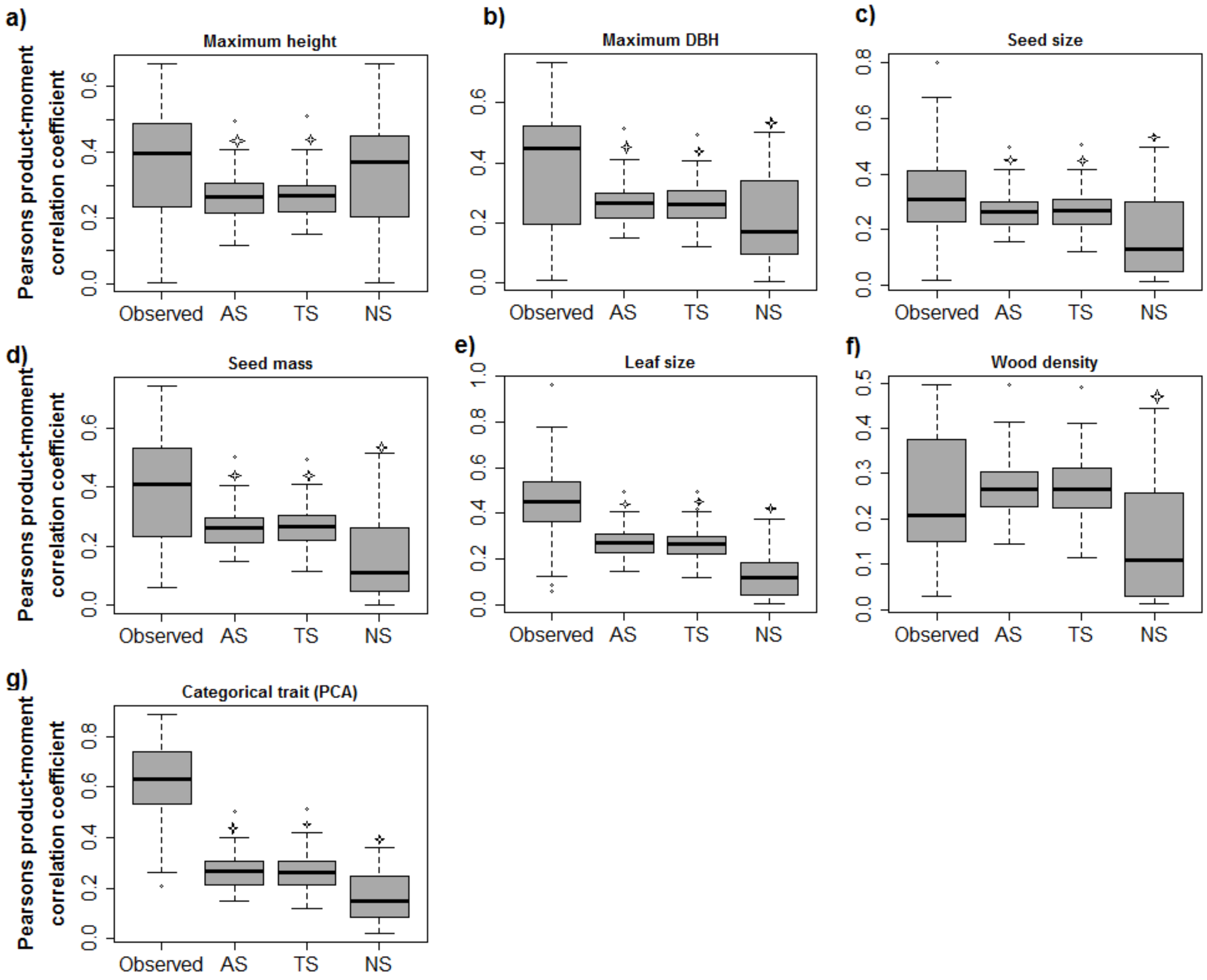
Appendix B14: Boxplots of the linear correlation between abundance and functional traits, based on results across 42 plots sampled from 42 different swamps. The boxplots are given only for observed.



Appendix B15: Density plots of the linear correlation between abundance and functional traits in swamps across landscape. The density plots are given for two different null models such as trait shuffle and abundance shuffle generated by 10000 randomizations. The red arrow indicates the position of observed r values.



Appendix B16: Boxplots of the linear correlation between abundance and functional traits, based on results across 42 plots sampled from 42 different swamps. The boxplots are given for both observed and three different null models generated by 10000 randomizations. The observed results which are significantly different (p<0.05) from null models are represented by stars.



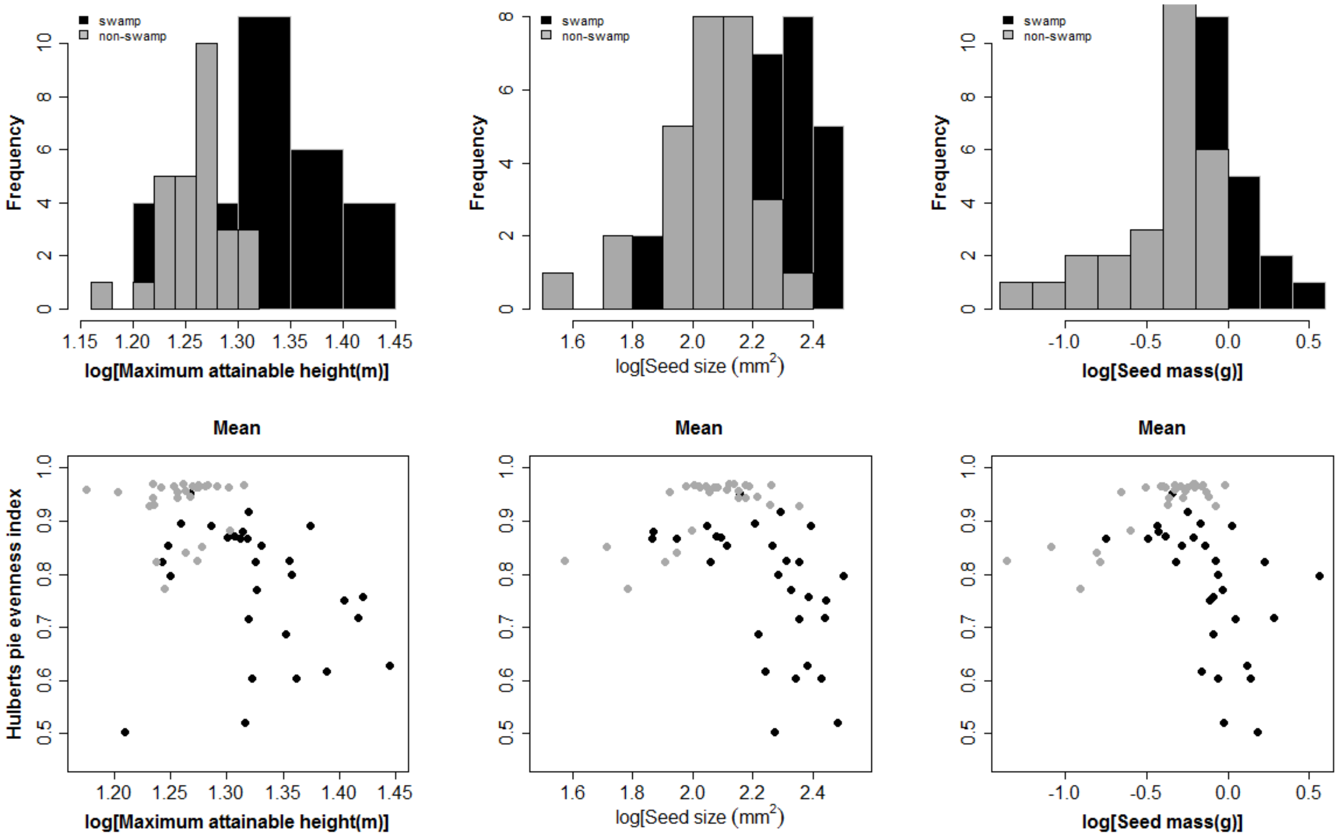
Appendix B17: Comparison of community trait structuring in swamp and non-swamp habitats. Average effect size (± 1 SE) of several community trait structure metric using an abundance-weighted null model (observed – expected / null SD). Wilcoxon signed-rank test of plot-wide null model results for swampy and non-swampy habitat. We report the absolute value of the effect size for mean, as test was two-tailed. Note: * Indicates trait metrics significantly different compare to null model expectation, p<0.0001***, p<0.001**, p<0.05*.

	Habitat type	
Traits and trait metrics	**Swamp (N=29)**	**Non-swamp (N=29)**
Maximum attainable height		
Mean	-0.879±0.137***	-0.394±0.124***
Range	-0.159±0.157	-0.440±0.141
Variance	-0.066±0.180	-0.252±0.122
SDNDr	-0.380±0.180	1.077±0.122***
Kurtosis	-0.286±0.176	-0.165±0.103*
Maximum DBH		
Mean	-0.853±0.147***	0.444±0.113***
Range	-0.904±0.154***	0.563±0.128**
Variance	-0.380±0.171**	0.475±0.116*
SDNDr	-0.580±0.132***	1.499±0.122***
Kurtosis	-0.417±0.145**	0.404±0.105*
Leaf size		
Mean	-0.802±0.117***	0.491±0.092***
Range	-0.626±0.163**	0.041±0.157**
Variance	-0.246±0.121**	0.348±0.104
SDNDr	-0.376±0.160**	1.119±0.191***
Kurtosis	-0.264±0.140*	0.036±0.153
Seed size		
Mean	-0.650±0.147***	0.455±0.105***
Range	0.025±0.177	-0.561±0.133***
Variance	0.177±0.153	-0.035±0.103
SDNDr	1.065±0.110***	0.891±0.145***
Kurtosis	0.337±0.117**	-0.260±0.090*
Seed mass		
Mean	-0.716±0.164***	0.462±0.116**
Range	-0.346±0.191	-0.036±0.161
Variance	-0.148±0.168	0.262±0.124
SDNDr	0.531±0.201	0.933±0.196***
Kurtosis	-0.102±0.183	-0.093±0.163
Wood density		
Mean	-0.716±0.164***	0.462±0.116***
Range	-0.346±0.191*	-0.036±0.161***

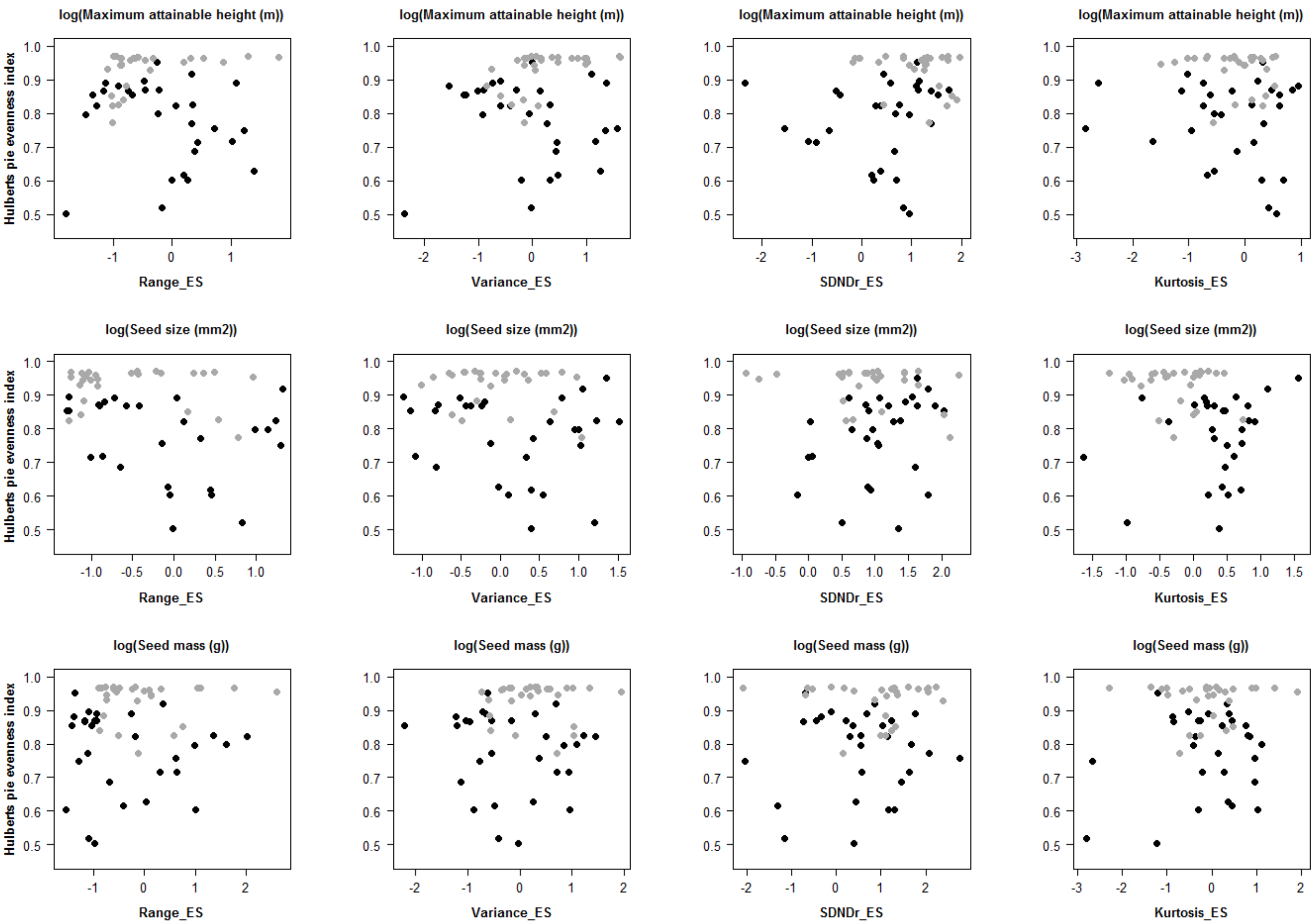
Variance	-0.148±0.168**	0.262±0.124**
SDNDr	0.531±0.201***	0.933±0.196***
Kurtosis	-0.102±0.183**	-0.093±0.163
Categorical trait (PCA1)		
Mean	-1.705±0.172***	1.048±0.124***
Range	-0.818±0.071***	1.390±0.153***
Variance	-0.530±0.142***	1.208±0.099***
SDNDr	1.572±0.093***	0.537±0.156*
Kurtosis	0.268±0.070**	0.182±0.191

Appendix B18: Community level trait pattern for tree communities in swampy and non-swampy habitat as a function of dominance (Hurlbert's pie) using local species pool null model. a) to c) observed distribution of traits among tree communities in swampy and non-swampy habitat. d) to f) trait mean plotted against Hulbert's pie (measure of dominance) respectively for maximum attainable height, seed size, and seed mass.

Note: Colored dots indicates habitat from which plots were sampled, swamp (black) and non-swamp (grey).



Appendix B19: Correlation between community level trait spacing metrics and Hulbert's pie (measure of dominance). Effect size of trait spacing metrics: first row (a) to d)) maximum attainable height, second row (e) to h)) seed size and third row (i) to l)) seed mass. Note: Colored dots indicates habitat from which plots were sampled, swamp (black) and non-swamp (grey).



Appendix B20: Average effect size (± 1 SE) of abundance-weighted null model tests (observed – expected / null SD) using regional species pool. Wilcoxon signed-rank test of plot-wide null model results for swampy and non-swampy habitat. We report the absolute value of the effect size for mean, as test was two-tailed. Note: * Indicates trait metrics significantly different compare to null model expectation, p<0.0001***, p<0.001**, p<0.05*.

Models	**Full model**		**Partial model**	
	Habitat type			
Traits and trait metrics	**Swamp (N=42)**	**Non-swamp (N= 29)**	**Swamp (N= 42)**	**Non-swamp (N= 29)**
Maximum DBH				
Mean	-2.321±0.152***	1.495±0.137***	-1.964±0.163*	-1.438±0.130***
Range	-0.541±0.180**	0.912±0.156***	-1.063±0.201*	0.749±0.160***
Variance	0.084±0.166	0.972±0.130***	-0.386±0.188*	0.736±0.133***
SDNDr	-0.241±0.161*	-0.014±0.195	-0.115±0.116*	0.122±0.187*
Kurtosis	-0.674±0.133***	-0.215±0.265	-0.640±0.145*	0.040±0.220*
Leaf size				
Mean	-1.725±0.144***	-0.865±0.125***	-1.224±0.115***	-1.168±0.139***
Range	0.235±0.105*	0.783±0.222**	0.272±0.131**	0.420±0.234*
Variance	0.476±0.112***	0.955±0.189***	0.546±0.110***	0.599±0.204**
SDNDr	-0.296±0.174**	0.091±0.252	-0.259±0.156	0.125±0.230
Kurtosis	-0.227±0.159*	-0.299±0.269	-0.443±0.158**	-0.204±0.235
Seed size				
Mean	-1.542±0.126***	-0.751±0.225**	-1.252±0.132*	-0.653±0.223**
Range	0.261±0.136***	-0.084±0.154	0.085±0.161*	-0.054±0.146
Variance	0.138±0.133	-0.002±0.141	-0.065±0.155*	0.008±0.135
SDNDr	0.611±0.119***	0.282±0.153	0.577±0.128	0.358±0.151**
Kurtosis	0.508±0.063***	0.139±0.113	0.526±0.076*	0.146±0.109*
Seed mass				
Mean	-1.824±0.117***	1.366±0.256***	1.554±0.124*	-1.197±0.260**
Range	-0.008±0.203	-0.825±0.277	-0.025±0.184	0.632±0.289
Variance	0.097±0.173	-0.667±0.180	-0.070±0.168	0.484±0.196
SDNDr	-0.052±0.192	-0.143±0.287	0.782±0.183	0.079±0.282
Kurtosis	-0.179±0.209	0.013±0.335	0.073±0.192	-0.050±0.328
Wood density				
Mean	1.349±0.127***	-0.548±0.217**	1.208±0.134***	-0.139±0.157
Range	0.6216±0.118***	-0.217±0.137	0.578±0.125***	-0.163±0.133
Variance	0.522±0.114***	0.109±0.154	0.526±0.117***	0.004±0.151
SDNDr	0.073±0.127	-0.002±0.156	0.072±0.125	-0.184±0.151
Kurtosis	0.424±0.117***	-0.394±0.174	0.344±0.121**	-0.088±0.051
Categorical trait (PCA1)				
Mean	-4.183±0.195***	-1.095±0.270**	-3.350±0.184***	-1.575±0.307***

Range	-1.511±0.078***	-0.083±0.128	-1.288±0.083***	0.575±0.140***
Variance	-1.894±0.142***	-0.069±0.149	-1.448±0.134***	-0.792±0.192***
SDNDr	2.071±0.074***	1.158±0.160***	1.783±0.083***	1.224±0.158***
Kurtosis	0.495±0.048***	0.270±0.226	0.505±0.055***	-0.040±0.255

Appendix B21: Results of ANOVA for community weighed trait mean values of functional traits among swampy and non-swampy habitat.

Response variable		**df**	**Sun of squares**	**Mean squares**	**F value**	**Prob (>F)**
Maximum attainable Height	**Habitat**	1	0.066141	0.066141	41.2976	<0.0001***
	Sites	1	0.008863	0.008863	5.5336	0.0223*
	Habitat*Site	1	0.020978	0.020978	13.0984	0.0006**
	Residuals	54	0.086485	0.001602		
Maximum DBH	**Habitat**	1	0.100911	0.100911	36.2531	<0.0001***
	Sites	1	0.133347	0.133347	47.906	<0.0001***
	Habitat*Site	1	0.026128	0.026128	9.3868	0.003**
	Residuals	54	0.15031	0.002784		
Leaf size	**Habitat**	1	0.20455	0.204545	32.7947	<0.0001***
	Sites	1	0.00812	0.008122	1.3022	0.2588
	Habitat*Site	1	0.00036	0.000356	0.0571	0.812
	Residuals	54	0.33681	0.006237		
Seed size	**Habitat**	1	0.62113	0.62113	22.2123	<0.0001***
	Sites	1	0.00503	0.00503	0.1798	0.67326
	Habitat*Site	1	0.27723	0.27723	9.9142	0.003**
	Residuals	54	1.51001	0.02796		
Seed mass	**Habitat**	1	1.4458	1.44575	20.3897	<0.0001***
	Sites	1	0.3006	0.30056	4.2389	0.044*
	Habitat*Site	1	0.7856	0.78562	11.0798	0.002*
	Residuals	54	3.8289	0.07091		

Wood density	**Habitat**	1	0.091989	0.091989	90.5377	<0.0001***
	Sites	1	0.002797	0.002797	2.7533	0.103
	Habitat*Site	1	0.000889	0.000889	0.8749	0.354
	Residuals	54	0.054866	0.001016		
Categorical trait (PCA1)	**Habitat**	1	2.12348	2.12348	93.1334	<0.0001***
	Sites	1	0.00336	0.00336	0.1473	0.703
	Habitat*Site	1	0.37094	0.37094	16.269	0.0001***
	Residuals	54	1.23122	0.0228		

Note: p<0.0001***, p<0.001**, p<0.05*

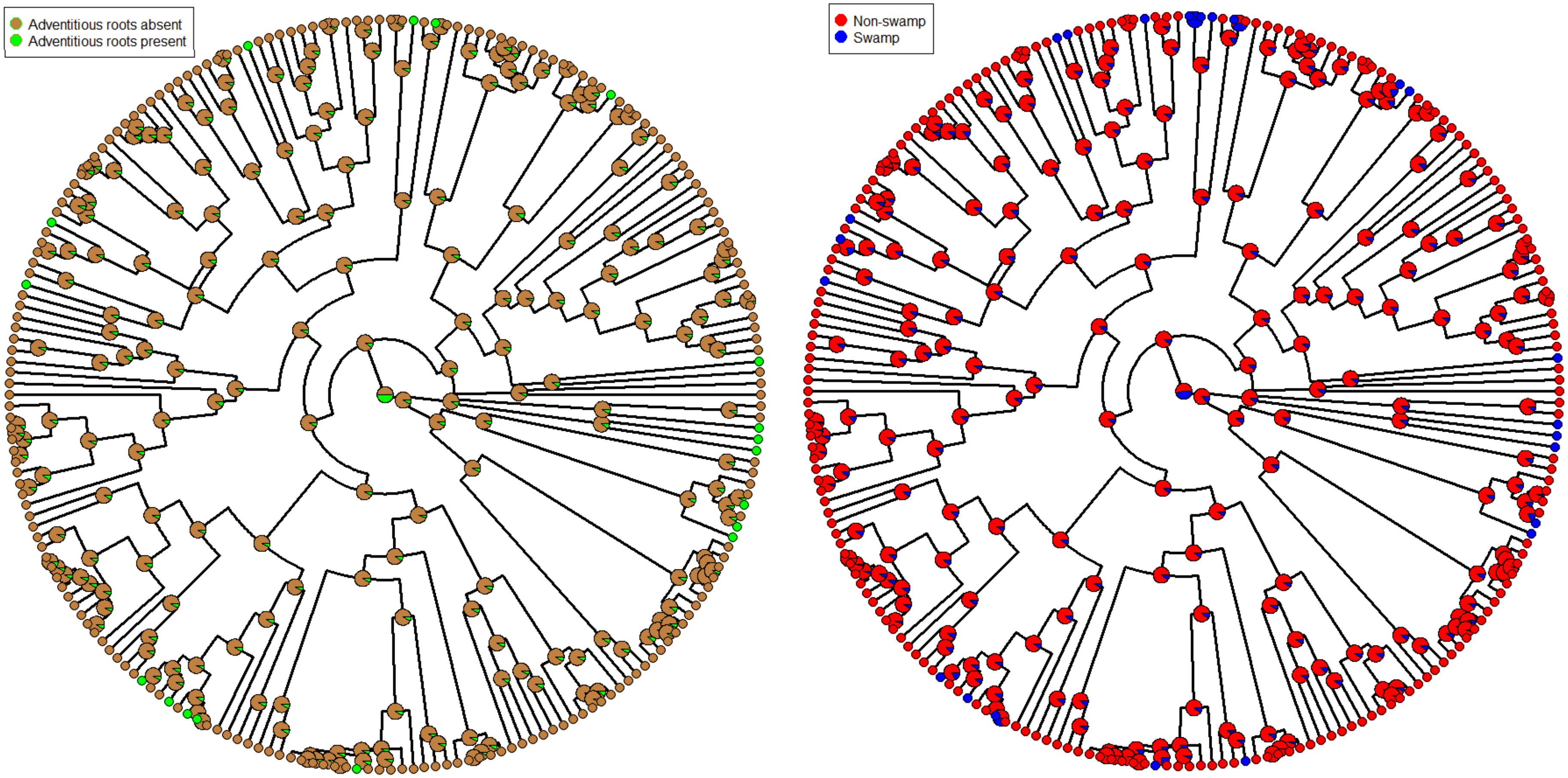
Appendix B22: The linear relationship between Hulbert's pie evenness index (measure of dominance) and functional trait spacing metrics using local species pool null models. R^2 is the Pearson product–moment correlation coefficient. The R^2 values >0.1 are in bold.

Trait	Trait metrics	R^2	p-value
Maximum attainable Height	Mean	**0.237**	<0.0001***
	Range_ES	-0.017	0.339
	Variance_ES	0.024	0.246
	SDNDr_ES	0.057	0.072
	Kurtosis_ES	-0.003	0.700
Maximum DBH	Mean	**0.266**	<0.0001***
	Range_ES	**0.212**	<0.0001***
	Variance_ES	**0.187**	0.0007**
	SDNDr_ES	**0.210**	0.0003**
	Kurtosis_ES	0.070	0.045*
Leaf size	Mean	**0.461**	<0.0001***
	Range_ES	0.062	0.061
	Variance_ES	**0.111**	0.012*
	SDNDr_ES	**0.170**	0.002*
	Kurtosis_ES	0.031	0.188
Seed size	Mean	**0.175**	0.002*
	Range_ES	0.087	0.026*
	Variance_ES	0.040	0.135
	SDNDr_ES	<0.0001	0.993
	Kurtosis_ES	0.040	0.139
Seed mass	Mean	**0.103**	0.014*
	Range_ES	0.007	0.550
	Variance_ES	0.007	0.543
	SDNDr_ES	0.018	0.312

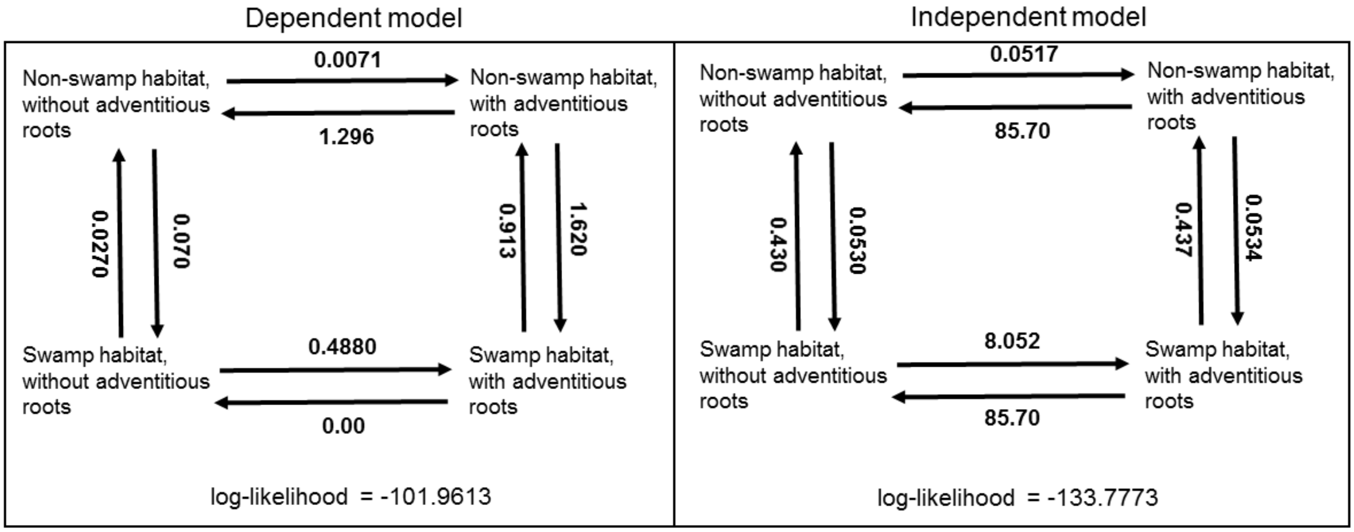
	Kurtosis_ES	0.010	0.456
Wood density	Mean	**0.302**	<0.0001***
	Range_ES	**0.273**	<0.0001***
	Variance_ES	**0.125**	0.007*
	SDNDr_ES	0.010	0.467
	Kurtosis_ES	**0.144**	0.004*
Categorical trait (PCA1)	Mean	**0.420**	<0.0001***
	Range_ES	**0.280**	<0.0001***
	Variance_ES	**0.170**	0.001**
	SDNDr_ES	0.0370	0.230
	Kurtosis_ES	0.0314	0.259

Note: p<0.0001***, p<0.001**, p<0.05* and ES = effect size.

Appendix B23: Ancestral reconstruction of adventitious roots and habitat type based on best likelihood model of stochastic mapping. a) adventitious roots b) habitat type. The circles represent the mean posterior probability distribution of traits calculated from 1000 separate character maps.



Appendix B24: Pagel's (1994) analysis of correlated evolution of traits for two traits- habitat (swampy or non-swampy) and adventitious roots (present or absent) given 4 different combination of characters. Arrows represent transition direction and values on arrows represent transition rates.

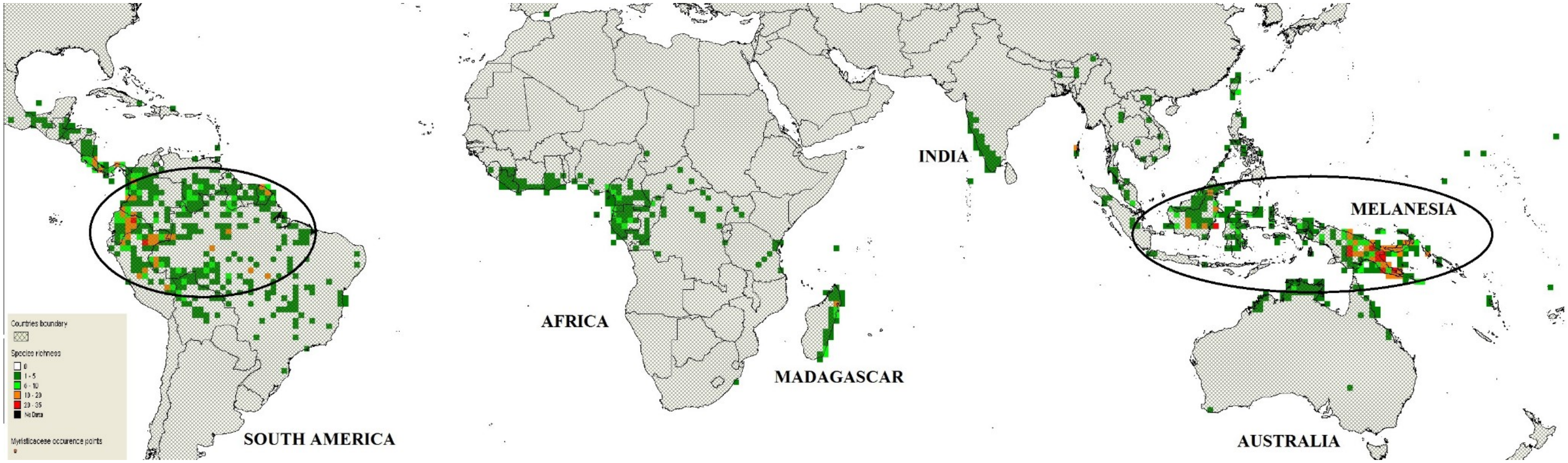


Appendix C

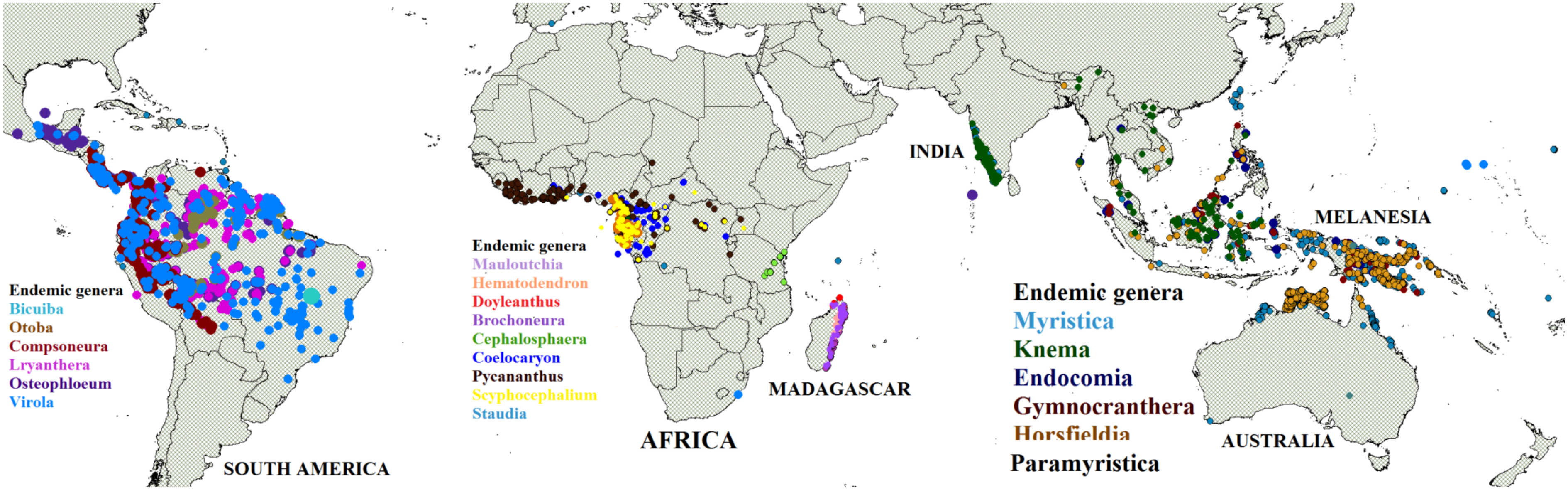
Supporting Information — Chapter 4

Appendix C1: Species richness map of Myristicaceae. Regions circled (South America and Melanesia) represent highest species diversity centers.

Note: Pixels colored in red and orange have highest species richness and pixels colored in light green and dark green have lower species richness. Circled area represents centers of diversity based on species richness.



Appendix C2: Global distribution map of Myristicaceae. Genera endemic to the region are marked in different coloring points on the map.



Appendix C3: Habitat type and morphological adaptation of five Myristicaceae members in Western Ghats, India

Species	Habitat type	Morphological adaptation		Total Number of occurrence records
		Stilt root	Knee root	
Gymnocranthera canarica	Swampy	Absent	Present	166
Knema attenuate	non-swampy	Absent	Absent	349
Myristica fatua	Swampy	Present (highly developed)	Absent	81
Myristica malabarica	Intermediate between swampy and non-swampy habitat (Non-swampy)	Absent, if present highly reduced	Absent	134
Myristica dactyloides	Non-swampy	Absent, if present highly reduced	Absent	125

Appendix C4: Taxa selected for the phylogenetic and trait analysis.

Genus	Total no of species	No of species in phylogenetic analysis	No of species in trait data	% of taxa represented in Phylogeny	% of taxa in trait data
Doyleanthus	1	0	5	0.00	50.00
Mauloutchia	10	3	4	30.00	66.67
Pycnanthus	6	1	2	16.67	100.00
Scyphocephalium	2	1	4	50.00	100.00
Staudtia	4	2	4	50.00	100.00
Brochoneura	4	3	1	75.00	100.00
Cephalosphaera	1	1	7	100.00	63.64
Coelocaryon	11	2	1	18.18	100.00
Haematodendron	1	1	4	100.00	100.00
Endocomia	4	1	7	25.00	53.85
Gymnacranthera	13	3	77	23.08	75.49
Knema	102	13	155	12.75	65.13
Myristica	238	13	100	5.46	71.43
Horsfieldia	140	11	1	7.86	100.00
Paramyristica	1	0	1	0.00	100.00
Bicuiba	1	1	9	100.00	40.91
Compsoneura	22	8	21	36.36	56.76
Lyranthera	37	4	1	10.81	50.00
Osteophloeum	2	1	2	50.00	18.18
Otoba	11	1	45	9.09	72.58
Virola	62	7	5	11.29	50.00
Total	**673**	**76**	**452**	**1.5**	**67.2**

Appendix C5: The details of variables used to predict the potential distribution of *Myristica* species in Western Ghats, India

Layer	**Reference**	**Variables**
Bioclimatic		
BIO 1	http://www.worldclim.org/current (Current) (http://www.ccafs-climate.org/data) (Future)	Annual Mean Temperature (°C*10)
BIO 2		Mean Diurnal Range (Mean (period max-min)) (°C*10)
BIO 3		Isothermality (Bioclim2/Bioclim7) (°C*10)
BIO 4		Temperature Seasonality (SD*100)
BIO 5		Max Temperature of Warmest month (°C*10)
BIO 6		Min Temperature of Coldest month (°C*10)
BIO 7		Temperature Annual Range (Bioclim5-Bioclim6)
BIO 8		Mean Temperature of Wettest Quarter (°C*10)
BIO 9		Mean Temperature of Driest Quarter (°C*10)
BIO 10		Mean Temperature of Warmest Quarter (°C*10)
BIO 11		Mean Temperature of Coldest Quarter (°C*10)
BIO 12		Annual Precipitation (mm)
BIO 13		Precipitation of Wettest Period (mm)
BIO 14		Precipitation of Driest Period (mm)
BIO 15		Precipitation Seasonality (Coefficient of Variation)
BIO 16		Precipitation of Wettest Quarter (mm)
BIO 17		Precipitation of Driest Quarter (mm)

BIO 18		Precipitation of Warmest Quarter (mm)
BIO 19		Precipitation of coldest Quarter (mm)
Global aridity and Evapo-Transpiration		
AET	http://www.cgiar-csi.org/data/global-aridity-and-pet-database	Annual evapo-transpiration
PET		Potential evapo-transpiration
AI		Global aridity index
Edaphic		
PH	http://webarchive.iiasa.ac.at/Research/LUC/External-World-soil-database)	Topsoil PH
AWC		Available water content
Topographic		
DEM	https://lta.cr.usgs.gov/gtopo30	Digital Elevation model
Aspect	https://lta.cr.usgs.gov/HYDRO1K	Direction of slope
Slope		Difference between two neighboring cells elevation
FA		Flow accumulation
FD		Flow direction
CTI		Compound topographic index

Note: The collinear variables with a Pearson's correlation coefficient ≥ 0.8 ($r^2 > 0.8$) is represented in bold

Appendix C6: Species GenBank accession numbers used in building the dated phylogenetic hypothesis for global Myristicaceae.

Genus	**Species**	**RBCL**	**MATK**	**NDHF**	**18S**	**TRNL**	**TRNK**	**TRNF**	**PSBA-TRNH**	**RPOC**	**RPOB**
Ambavia	*Gerrardii*	HM173806.1	AY220435.1	AY218168.1		JQ513889.1	AY218193.1	AY220358.1	AY578301.1		
Anaxagorea	*Phaeocarpa*	AY238952.1	AY238960.1	EF179279.1		AY231284.1			AY841426.1		
Liriodendron	*Tulipifera*	AB021077.1	AF123480.1	AF130230.1	AH001686.2	AY009086.1	AB021017.1		AB021047.1		
Magnolia	*Liliiflora*	KU853566.1	KU853528.1	AF107960.1	KJ567074.1		AB021012.1		KU853619.1		
Magnolia	*Quinquepeta*	KU853566.1	KU853528.1	AF107960.1			AB021012.1		AB021042.1		
Bicuiba	*Oleifera*					AY220416.1		AY220363.1			
Brochoneura	*Acuminate*		AY220442.1	AY218179.1		AY220404.1	AY218201.1				
Brochoneura	*Madagascariensis*					AY220418.1		AY220365.1			
Brochoneura	*Vouri*					AY220419.1		AY220366.1			
Cephalosphaera	*Usambarensis*		AY220443.1	AY218180.1		AY220420.1	AY218202.1	AY220367.1			
Coelocaryon	*Oxycarpum*		AY220444.1	AY218181.1		AY220421.1		AY220368.1			
Coelocaryon	*Preussii*	AY743437.1	AY743475.1	JQ437546.1				AY743456.1	KC688811.1		
Compsoneura	*Atopa*	EU090508.1	EU090469.1						EU090622.1	EU090582.1	EU090544.1
Compsoneura	*Capitellata*	EU090510.1	EU090471.1						EU090627.1	EU090583.1	EU090545.1
Compsoneura	*Debilis*	EU090515.1	EU090477.1						EU090631.1	EU090590.1	EU090552.1
Compsoneura	*Excelsa*	EU090520.1	EU090482.1						EU090636.1	EU090596.1	EU090557.1
Compsoneura	*Mexicana*	EU090529.1	EU090491.1						EU090645.1	EU090605.1	EU090565.1
Compsoneura	*Mutisii*	EU090534.1	EU090496.1						EU090650.1	EU090609.1	EU090570.1

Compsoneura	*Sprucei*	EU090540.1	AY220445.1	AY218182.1		AY220422.1	AY218204.1	AY220369.1	EU090656.1	EU090616.1	EU090576.1
Compsoneura	*Ulei*	EU090542.1	EU090505.1						EU090659.1	EU090618.1	EU090579.1
Endocomia	*Macrocoma*	JF738884.1									
Gymnacranthera	*Canarica*		TBA		JQ002591.1				TBA		
Gymnacranthera	*Farquhariana*	MF547519.1	AY220446.1	AY218183.1		AY220407.1	AY218205.1	AY220370.1	MF086600.1		
Gymnacranthera	*Paniculate*	JF738955.1									
Haematodendron	*Glabrum*		AY220447.1			AY220424.1	AY218206.1	AY220371.1			
Horsfieldia	*Amygdalina*	MF417801.1	MF547527.1		JQ002585.1				MF086598.1		
Horsfieldia	*Australiana*	KF496315.1									
Horsfieldia	*Basifissa*	FJ976140.1	GQ248135.1						GQ248315.1	GQ248951.1	GQ248789.1
Horsfieldia	*Hellwigii*	GQ248619.2							GQ248316.1	GQ248952.1	GQ248790.1
Horsfieldia	*Irya*	JF738509.1									
Horsfieldia	*Kingie*	KR529441.1	KR530947.1						KR533311.1		
Horsfieldia	*Polyspherula*	KU853180.1	KU853109.1								
Horsfieldia	*Prainii*	KR529443.1	KR530949.1		JQ002589.1				KR533289.1		
Horsfieldia	*Punctatifolia*		AY220448.1		AY218184.1	AB981751.1	AY218207.1	AY220372.1			
Horsfieldia	*Spicata*	JF738524.1									
Horsfieldia	*Sylvestris*	JF738855.1									
Hypodaphnis	*Zenkeri*	KC628659.1	KC627853.1			AJ247166.2		AF232036.1	KC668126.1		
Iryanthera	*Hostmanni*		AY220449.1			AY220426.1	AY218208.1	AY220373.1			
Iryanthera	*Lancifolia*		EU090506.1						EU090660.1	EU090660.1	EU090580.1
Iryanthera	*Sagotiana*	JQ625975.1	JQ626420.1			FJ039167.1			KX248655.1	FJ038730.1	

Knema	*Andamanica*		TBA		JN228265.1				TBA		
Knema	*Attenuate*	MF547520.1	TBA						TBA		
Knema	*Cinereal*	KJ594758.1	KJ708967.1								
Knema	*Elegans*	KR529456.1	KR530962.1						KR533290.1		
Knema	*Furfuracea*	KR529457.1	KR530964.1						KR533306.1		
Knema	*Globularia*	KR529464.1	KR530970.1						KR533300.1		
Knema	*Hookeriana*	KJ594760.1	KJ708969.1								
Knema	*Latericia*	L12653.2		AY394740.1	AF206946.1		AF040694.1	KU853245.1	AF129058.1		
Knema	*Laurina*		AY220450.1	AY218186.1		AY220427.1	AY220396.1	KU853217.1			
Knema	*Lenta*	KR529467.1	KR530973.1						KR533297.1		
Knema	*Linifolia*	KR529470.1	KR530976.1						KR533308.1		
Knema	*Patentinervia*	KJ594762.1	KJ708971.1								
Knema	*Tenuinervia*	KR529477.1	KR530983.1						KR533309.1		
Mauloutchia	*Chapelieri*	AF197594.1	AY220451.1	AY218187.1	DQ007409.1	AY220410.1	AY437812.1	AY220374.1			
Mauloutchia	*Heckelii*					AY220429.1		AY220375.1			
Mauloutchia	*Humblotii*					AY220430.1		AY220376.1			
Myristica	*Andamanica*	MF158639.1	MF547529.1		JQ002586.1				MF086596.1		
Myristica	*Bedomei*		TBA						TBA		
Myristica	*Cinnamomea*	KJ594812.1	KJ709010.1								
Myristica	*Dactyloides*		TBA						TBA		
Myristica	*Fatua*	MF186597.1	MF547526.1						GQ248350.1	GQ248985.1	
Myristica	*fatua1*		TBA						TBA		

Myristica	*Fragrans*		TBA						TBA		
Myristica	*Globose*	KF496610.1	GQ248166.1			KC428562.1			GQ248351.1	GQ248986.1	GQ248825.1
Myristica	*Hollrungii*	JF738724.1									
Myristica	*Maingayi*	AY220452.1	DQ401374.1	DQ406967.1			AY218211.1				
Myristica	*Malabarica*		TBA						TBA		
Myristica	*Markgraviana*	JF738507.1									
Myristica	*Yunnanensis*	KR529803.1	KR531268.1						KR533280.1		
Osteophloeum	*Platyspermum*	JQ625884.1	JQ626371.1								
Otoba	*Parvifolia*					AY220431.1		AY220377.1			
Pycnanthus	*Angolensis*		AY220453.1	AY218189.1		AY220432.1	AY220399.1	AY220378.1			
Staudtia	*Gabonensis*	KC628454.1	KC627785.1						KC667963.1		
Staudtia	*Kamerunensis*	KC628429.1	KC627748.1			AY220433.1		AY220379.1	KC667927.1		
Virola	*Koschnyi*	JQ592893.1	EU669473.1		KU204517.1			EU669559.1			
Virola	*Kwatae*	FJ038129.1	JQ626460.1						FJ039018.2	FJ038733.1	FJ038344.1
Virola	*Michelii*	JQ626059.1	AY220454.1				AY218213.1		KX249543.1	FJ038739.1	FJ038347.1
Virola	*Multicostata*	JQ625886.1							GQ428671.1		
Virola	*Multiflora*	GQ981913.1	GQ982125.1						GQ982401.1		
Virola	*Nobilis*	GQ981914.1	GQ982126.1						GQ982402.1		
Virola	*Sebifera*	EU090543.1	EU090507.1	AY218190.1					EU090661.1	EU090621.1	EU090581.1

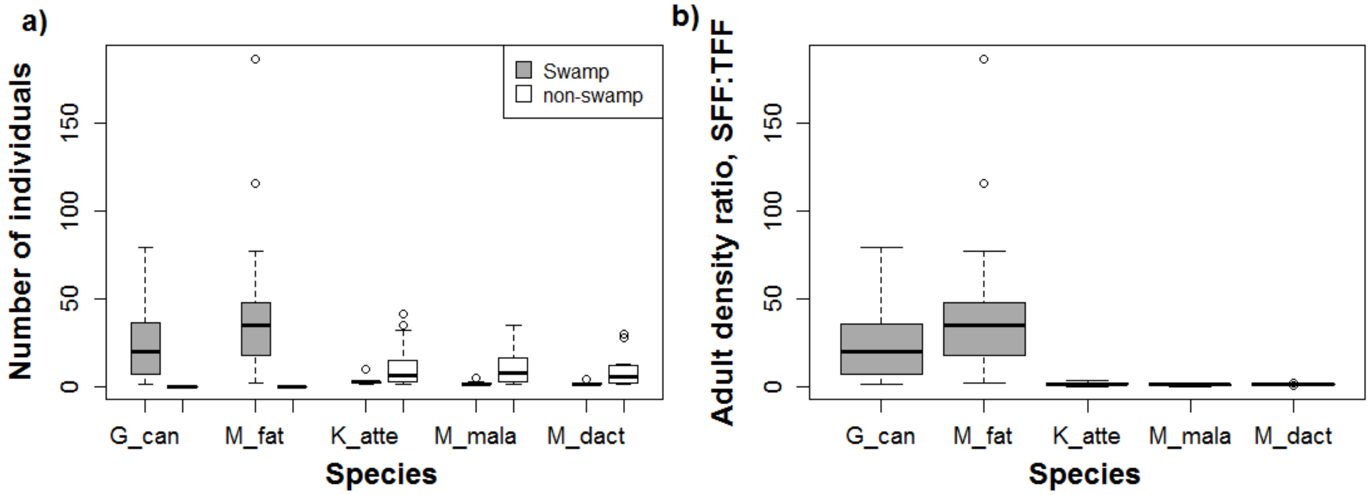
Appendix C7: The selected genes, % of missing data and chosen DNA evolution models based on JmodelTest results.

Gene	**Genome**	**Length (bp)**	**% species coverage**	**Selected model**
RBCL	Chloroplast	637	58/76 (76.3%)	TPM1uf+I
MATK	Chloroplast	1075	61/76 (80.3%)	TVM+G
NDHF	Nuclear	1984	17/76 (22.4%)	TVM+G
18S	Nuclear	1634	10/76 (13.2%)	TIM3+G
TRNL	Chloroplast	626	20/76 (26.3%)	TPM1uf+G
TRNK	Chloroplast	654	15/76 (19.7%)	GTR+I
TRNF	Chloroplast	508	16/76 (21.1%)	TPM1uf
PSBA-TRNH	Chloroplast	658	47/76 (61.8%)	GTR+I+G
RPOC	Nuclear	403	17/76 (22.4%)	TPM1uf
RPOB	Nuclear	508	17/76 (22.4%)	TPM1uf

Appendix C8: Model fits for ancestral reconstruction of habitat specialization and aerial roots, the best model based on Akaike Information Criterion (AIC) is highlighted (in bold).

Model	**aerial root**		**Habitat specialization**	
	-lnL	**AIC**	**-lnL**	**AIC**
ER	-74.862	141.526	-80.210	157.341
SYM	-74.862	141.526	-80.210	157.341
ARD	-63.427	**118.230**	-71.150	**135.121**
Ordered ASYM	-63.427	**118.230**	-71.150	**135.121**

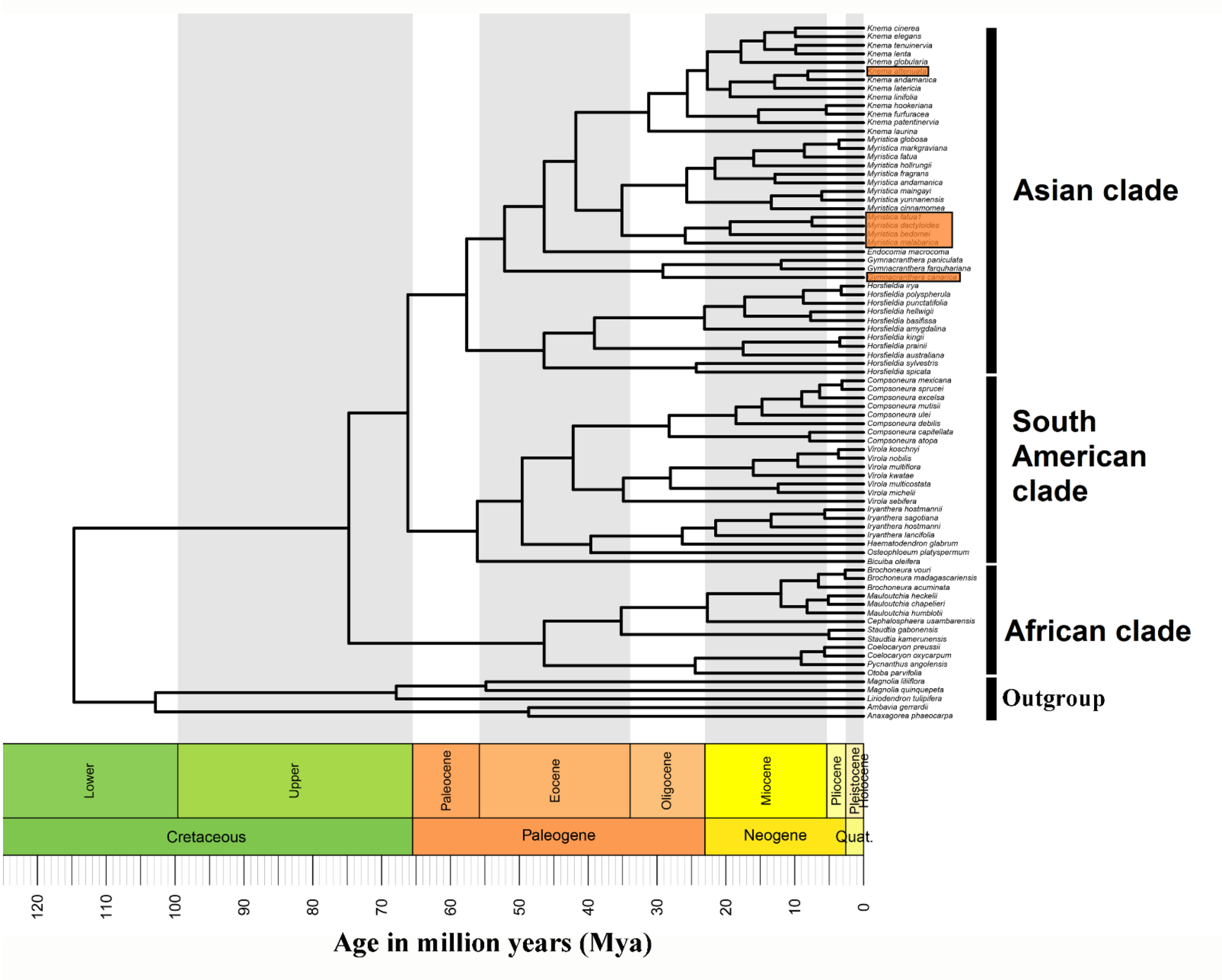
Appendix C9: Density and density ratio of five species of Myristicaceae among contrasting habitat types (seasonally flooded (swamp) and teera-firme (non-swamp) habitat) in Western Ghats, India



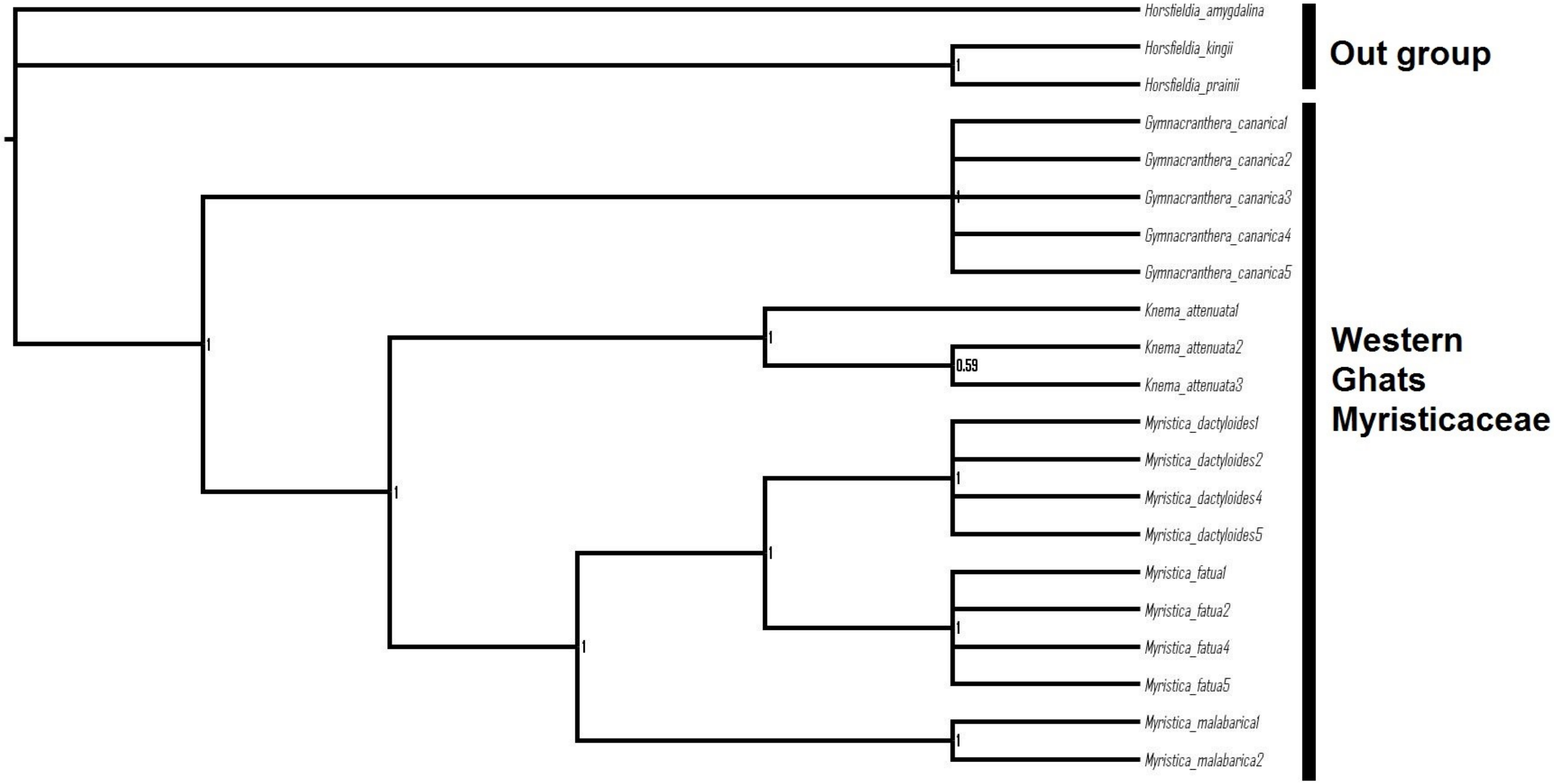
Appendix C10: Summary of plot wise presence of Myristicaceae members among seasonally flooded and terra-firme forest habitat in Western Ghats, India

	No of plots in which species present	
Species	**Seasonally flooded forest (Swamp) (N = 42)**	**Terra firme forest (Non-swamp) (N= 29)**
Gymnacranthera canarica	41 (98%)	0 (0%)
Knema attenuata	9 (21%)	22 (76%)
Myristica malabarica	7 (17%)	15 (52%)
Myristica dactyloides	6 (14%)	14 (48%)
Myristica fatua	27 (64%)	0 (0%)

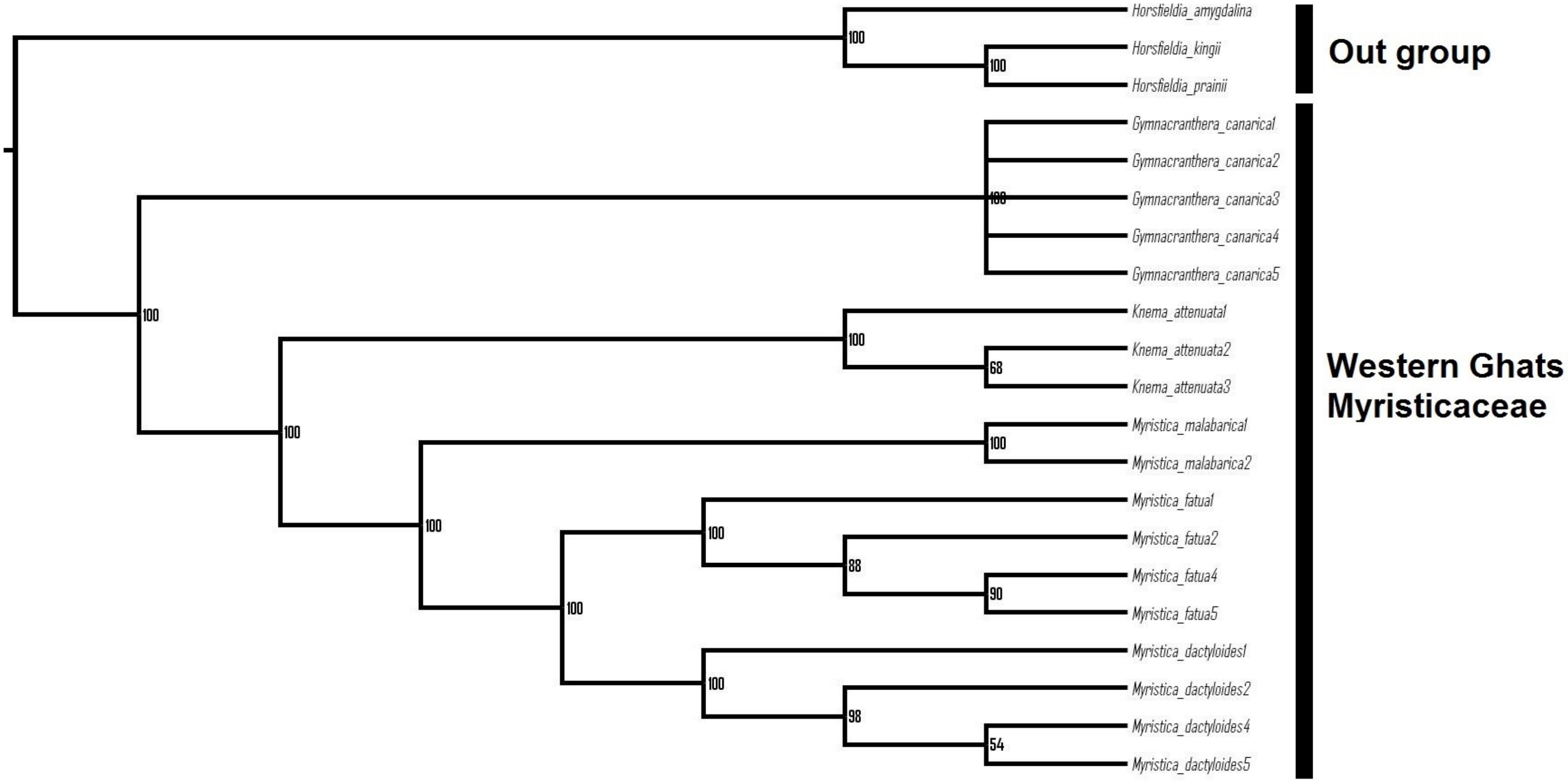
Appendix C11: Dated phylogenetic tree of global Myristicaceae. The Western Ghats endemic Myristicaceae is highlighted in orange color.



Appendix C12: Bayesian phylogenetic tree showing relationship among Western Ghats endemic Myristicaceae members based on combined analysis of matK and psbA-trnH gene. The numbers inside the branches are Bayesian bootstrap support.



Appendix C13: Maximum likelihood (ML) phylogenetic tree showing relationship among Western Ghats endemic Myristicaceae members based on combined analysis of matK and psbA-trnH gene. The numbers inside the branches are Maximum likelihood (ML) bootstrap support.



Appendix C14: Table showing best fit model of ancestral state for habitat affinity and aerial root evolution in global and Western Ghats endemic Myristicaceae based on RJMCMC analysis.

		Harmonic mean	
Traits	**Fixed state at root**	**Global**	**WG endemics**
Habitat affinity	Swampy	**-80.422±0.579**	**-79.422±0.321**
	Non-swampy	-95.672±0.029	-92.370±0.072
Aerial roots	Present	-89.371±0.032	-90.321±0.072
	Absent	**-74.371±0.321**	**-74.321±0,271**

Appendix C15: Matrix showing the minimum and maximum number of changes for habitat affinity (swamp and non-swamp) and adventitious root evolution (present and absent) in global and Western Ghats endemic Myristicaceae based on parsimony analysis.

			To			**To**	
			Swamp	**Non-swamp**		**Adventitious root present**	**Adventitious root absent**
Global	**From**	**Swamp**	0 to 3	0 to 1	**Adventitious root present**	7	1
		Non-swamp	2 to 3	28 to 31	**Adventitious root absent**	4	22
WG endemics	**From**	**Swamp**	0 to 1	0	**Adventitious root present**	6	2
		Non-swamp	1 to 2	5 to 6	**Adventitious root absent**	2	0

Appendix C16: Schoener's D (upper matrix) and Warren et al.'s I (lower matrix) statistic values for Western Ghats Myristicaceae calculated using ENMTools (Warren *et al*. 2008)

	M. malabarica	*G. canarica*	*K. attenuata*	*M. dactyloides*	*M. fatua*
M. malabarica	-	0.665	0.699	0.622	0.587
G. canarica	0.902	-	0.625	0.613	0.630
K. attenuate	0.885	0.868	-	0.682	0.534
M. dactyloides	0.861	0.866	0.905	-	0.529
M. fatua	0.853	0.873	0.810	0.801	-

Appendix C17: Relationship between genetic distance and niche overlap among Western Ghats endemic Myristicaceae a) Schoener's D and b) Warrens's I.