



# Influence of past and present environment on the ecology and biogeography of tree species in the Western Ghats biodiversity hotspot

Ruksan Bose

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## **Influence of past and present environment on the ecology and biogeography of tree species in the Western Ghats biodiversity hotspot**

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## Table of Contents

<b>RESUME DETAILLE EN FRANÇAIS</b>	<b>7</b>
<b>PART I</b>	
<b>GENERAL INTRODUCTION</b>	<b>25</b>
<b>A. BACKGROUND: HISTORICAL PERSPECTIVE</b>	<b>31</b>
1. ECOLOGY AND BIOGEOGRAPHY: 'DUEL' VIEWS	31
2. ECOLOGICAL NICHE, EVOLUTIONARY DYNAMICS	34
<b>B. BACKGROUND: THE REGIONAL SCALE</b>	<b>37</b>
1. MEETING IN THE MIDDLE	37
2. BRIDGING THE GAP: METHODOLOGICAL APPROACHES	40
3. HYPOTHESES AND EXPECTATIONS	44
<b>MATERIAL AND METHODS</b>	<b>46</b>
<b>A. PHYSICAL AND HISTORICAL CONTEXT: WESTERN GHATS OF INDIA</b>	<b>46</b>
1. TOPOGRAPHIC AND HABITAT HETEROGENEITY	47
2. DYNAMIC BIOGEOGRAPHICAL HISTORY	48
3. ENDEMISM AND DIOECY IN THE WESTERN GHATS	51
<b>B. THE DATA</b>	<b>52</b>
1. QUANTIFYING PAST AND PRESENT ENVIRONMENTAL CONDITIONS	52
2. VARIATION IN FLORISTIC COMPOSITION ALONG ENVIRONMENTAL GRADIENTS	57
3. PHYLOGENETIC DATA	62
BIBLIOGRAPHY	63
<b>PART II</b>	
<b>CHAPTER 1</b>	
PAST POTENTIAL HABITATS SHED LIGHT ON THE BIOGEOGRAPHY OF ENDEMIC TREE SPECIES OF THE WESTERN GHATS BIODIVERSITY HOTSPOT, SOUTH INDIA (JOURNAL OF BIOGEOGRAPHY)	71
<b>CHAPTER 2</b>	
PHYLOGENETIC DIVERSITY IN THE WESTERN GHATS BIODIVERSITY HOTSPOT REFLECTS ENVIRONMENTAL FILTERING AND PAST NICHE DIVERSIFICATION OF TREES	93
<b>CHAPTER 3</b>	
ROLE OF DIOECY IN THE ECOLOGICAL AND EVOLUTIONARY DYNAMICS OF TREES IN THE WESTERN GHATS: A LEGACY OF ARIDIFICATION?	117
<b>GENERAL DISCUSSION AND CONCLUSION</b>	<b>143</b>
1. OVERVIEW	144
2. THE STORY THAT CONGENERIC ENDEMICS TOLD: NICHE LABILITY	147
3. CONSERVATION OF ANCESTRAL PREFERENCES IN SOUTHERN REFUGIA	149
4. MACROEVOLUTIONARY CONTINGENCY	150
5. LIMITATIONS OPEN PERSPECTIVES	155
6. IMPLICATION FOR CONSERVATION	159
BIBLIOGRAPHY	161
<b>ANNEXE 1</b>	<b>164</b>
<b>ANNEXE 2</b>	<b>169</b>

## **RESUME DETAILLE EN FRANÇAIS**



## INTRODUCTION

L'organisation de la biodiversité dans l'espace et le temps est déterminée par un mélange complexe de processus écologiques et évolutifs et pourrait refléter l'interaction de l'histoire climatique, biogéographique et géologique (Ricklefs, 2007; Harrison & Noss, 2017). Déchiffrer ces influences entremêlées est essentiel pour comprendre les questions fondamentales concernant la façon dont les espèces sont actuellement distribuées et rassemblées dans les communautés, et comment la biodiversité est produite, maintenue et façonnée dans le temps.

Bien que l'attention des recherches ait été focalisée sur les processus écologiques actuels, des études récentes indiquent l'importance des processus évolutifs pour expliquer les patrons de biodiversité à travers les échelles spatiales. Les théories historiques (Ricklefs, 1987), surtout en ce qui concerne l'histoire du climat (Normand *et al.*, 2011; Svenning *et al.*, 2015), montrent comment les distributions contemporaines reflètent toujours l'héritage des environnements passés. Les processus géologiques et évolutifs tels que les événements de vicariance ou la variation des taux de diversification et d'extinction, ont également des effets durables sur les distributions actuelles d'espèces et leur assemblage dans les communautés (Luebert & Weigend, 2014; Sanín *et al.*, 2016). Synthétiser comment les processus évolutifs, la contingence historique et les facteurs écologiques contemporains façonnent conjointement la répartition et l'accumulation d'espèces au sein des régions est une avenue de recherche émergente (Fine, 2015).

Les progrès dans la modélisation de la distribution des espèces (SDM pour *Species Distribution Model*) ont conduit à étudier les limites historiques des distributions et la dynamique des habitats passés. Par exemple, les SDMs basés sur des occurrences passées et actuelles d'espèces ont été proposés pour obtenir des informations sur les processus biogéographiques tels que la contraction et l'expansion de l'aire de distribution des espèces suite aux changements de l'environnement (Svenning *et al.*, 2011). Deuxièmement, l'analyse de la structure phylogénétique des assemblages d'espèces ajoute la dimension temporelle nécessaire pour aborder l'influence de la dynamique évolutive et biogéographique qui vient s'ajouter aux facteurs contemporains. La distance évolutive séparant les espèces peut être utilisée pour déchiffrer les processus d'assemblage écologique (Webb *et al.*, 2002). Peut-être plus important encore, cette information peut être utilisée pour identifier les particularités macro-évolutives des habitats, les lignées associées à ces habitats, et les communautés créées à partir des lignées existantes (Gerhold *et al.*, 2015). Enfin, le domaine émergent de la modélisation phyloclimatique, combine des SDM et des analyses phylogénétiques pour étudier, par exemple, l'héritabilité des préférences de niche climatique et la reconstruction des niches ancestrales (Yesson & Culham, 2006; Heibl & Calenge, 2013).

Les forêts tropicales ont été la scène de grands événements évolutifs et biogéographiques, et sont parmi les écosystèmes les plus diversifiés et les plus complexes (Gentry, 1992). Ils sont également les plus menacés face à l'altération à grande échelle de l'habitat suite aux changements climatique et anthropique (Asner *et al.*, 2009). Dans ce contexte, la compréhension des processus écologiques et évolutifs qui influencent les patrons de diversité et la coexistence des espèces dans les écosystèmes n'a jamais été aussi pressante pour informer les pratiques de conservation (Rolland *et al.*, 2012; Jezkova & Wiens, 2016). Cependant, dans les forêts tropicales hyper-

diverses, ces études sont souvent entravées par le manque d'échantillonnage floristique à grande échelle et le manque de phylogénies moléculaires. Ainsi, les risques encourus ne sont pas complètement connus. C'est particulièrement le cas dans les forêts des Ghâts occidentaux (WG, pour *Western Ghats*) de l'Inde qui, avec Sri Lanka, forment l'un des originaux 25 points chauds de biodiversité globaux (Myers *et al.*, 2000). Les WG forment un centre important de diversité végétale et d'endémisme (over 56% for evergreen species, Pascal *et al.*, 2004). Malgré un vaste réseau d'aires protégées, c'est aussi l'un des huit points chauds les plus menacés. La composition des forêts des WG, reflète une longue et complexe histoire évolutive et biogéographique. Pourtant, les études sur l'écologie et la biogéographie des forêts des WG à grande échelle spatiale ou sur le long terme manquent. La compréhension des signatures combinées de la dynamique de la biodiversité actuelle et passée est nécessaire pour prévoir les réponses de la région aux changements environnementaux futurs.

La connaissance des patrons de stabilité et de fluctuation climatique dans le temps et l'espace est essentiel pour comprendre les origines et le maintien des refuges et des centres d'endémisme (Harrison & Noss, 2017) tels que les WG. L'influence de la stabilité et du changement varie selon les lignées, au cours du temps géologique et à travers l'espace. Les gradients naturels de l'environnement offrent des occasions de découvrir des liens possibles entre différents aspects de la biodiversité (taxonomique, phylogénétique et trait) et l'hétérogénéité des conditions environnementales dans l'espace et le temps.

#### *Contexte physique et biogéographique : les ghâts occidentaux*

Les WG fournissent un bon cadre pour enquêter sur les patrons à grande échelle étant donné leur répartition sur 10 degrés de latitude. La topographie disséquée des WG impose des variations abruptes des précipitations, de la saisonnalité et de la température. Ces derniers sont les principaux moteurs du renouvellement des espèces et ont servi de base à la caractérisation des forêts du WG en 19 différents types forestières (Pascal, 1988). Par rapport aux autres forêts tropicales en Afrique centrale ou en Amérique du Sud, l'association entre la distribution d'espèces et les variables climatiques était la plus forte dans les WG (Deblauwe *et al.*, 2016).

Plus important encore, les conditions climatiques actuelles sont le produit d'une évolution géomorphologique passée. Après sa séparation du Gondwana, au cours de son long voyage vers le nord passant par l'équateur jusqu'à sa position actuelle, la plaque indienne a rencontré différents paléoclimats qui ont eu un impact sur sa végétation. Durant l'Eocène (45 Mya) les forêts tropicales ont couvert la majeure partie du Deccan (Meher-Homji, 1989) avant la création de l'escarpement des Ghats et la collision subséquente avec la Laurasie. Le soulèvement de l'Himalaya et l'établissement du régime de mousson (11-5 Ma) ont entraîné un changement majeur dans le climat, ainsi que le début de l'aridification dans la majeure partie de la péninsule à la fin du Néogène (Morley, 2000; Guo *et al.*, 2008; Patnaik *et al.*, 2012). Au fur et à mesure que la zone aride s'étendait vers le sud, les forêts sempervirentes humides précédemment répandues étaient progressivement remplacées au nord et à l'est des WG par des forêts décidues. Les précipitations orogènes sur les pentes face aux vents d'ouest ont fourni l'environnement humide nécessaire pour assurer la persistance des forêts sempervirentes humides (e.g. Roelants *et al.*, 2004). Les WG ont donc été isolés d'autres zones humides persistantes et forêts sempervirentes humides qui se trouvent plus au nord-est, en Inde et en Indo- Chine à cette

époque. Au sein des WG, les vents inverses saisonnière de mousson ont induit un gradient de saisonnalité du sud au nord pendant cette époque (Gunnell, 1997; Patnaik *et al.*, 2012; Patnaik & Prasad, 2016). Les forêts moins saisonnières du sud des WG ont servi de refuge récurrent depuis le début de l'Eocène (Prasad *et al.*, 2009), et sont biogéographiquement distincts des forêts plus au nord caractérisées par une plus faible stabilité historique de l'habitat au-dessus de  $\sim 13^{\circ}\text{N}$ .

On s'attend à ce que ces changements environnementaux et la fragmentation des forêts tropicales aient considérablement affecté la migration et la diversification des espèces d'arbres (Gower *et al.*, 2016), d'une façon comparable à l'impact des fluctuations du climat du Pléistocène dans les régions tempérées. Les plus grandes diversité et endémisme attendus dans les zones historiquement stables (Graham *et al.*, 2006; Fine, 2015) est soutenue par le gradient sud-nord de la diversité des espèces et de l'endémisme (Ramesh & Pascal, 1997; Barboni *et al.*, 2003). Les taux d'endémisme diminuent de  $\sim 70\%$  dans la partie la plus méridionale des WG jusqu'à  $<10\%$  dans l'extrême nord (Ramesh, 2001). Bien qu'il n'y ait eu aucune étude reliant spécifiquement la diversification des endémiques et la contraction de la zone humide, les disjonctions observées dans les distributions d'espèces sœurs de certains genres riches en espèces sur les versants orientaux et occidentaux du sud des WG et le long du gradient sud-nord de saisonnalité suggèrent une spéciation allopatrique dans des conditions contrastées (Pascal, 1988; Gimaret-Carpentier *et al.*, 2003). Beaucoup de ces genres comprennent principalement des espèces dioïques. La forte proportion d'espèces dioïques dans les WG (20% des espèces d'arbres, Krishnan & Ramesh, 2005), et le fait qu'elle soit supérieure pour les espèces endémiques, soulève également des questions quant à savoir si les contraintes écologiques ou évolutives sur l'assemblage et la répartition actuelle des espèces peuvent être lié à leurs systèmes de reproduction.

Dans le but de caractériser le rôle des conditions environnementales passées et présentes sur la répartition et la diversification des espèces d'arbres des WG, nous avons intégré des modèles de distribution d'espèces dans des conditions bioclimatiques passées et présentes et une analyse de la variation des caractéristiques phylogénétiques et reproductives à travers les gradients régionaux. Dans les sections suivantes, je présenterai un résumé du contexte et des concepts relatifs aux trois questions abordées dans ce travail, suivi d'un résumé des hypothèses, des attendus et des méthodes utilisées pour y répondre. Je discuterai ensuite les principaux résultats.

## CONTEXTE

### *Niche climatique et réponses des espèces aux changements environnementaux récents*

Pourquoi les espèces sont-elles limitées à certaines conditions environnementales est une question centrale en matière d'écologie, de biogéographie et d'évolution. La niche climatique est à la base de la relation espèces-environnement. Les attributs de niche des espèces leur permettent de maintenir des populations en fonction des conditions environnementales locales données et déterminent ainsi l'étendue et la variation des distributions des espèces dans l'espace et le temps (Hutchinson, 1957; Soberon & Nakamura, 2009). À large échelle spatiale, le climat joue un rôle dominant dans la répartition des espèces (Pearson & Dawson, 2003).

Alors que l'exigence de niche d'une espèce peut se maintenir dans le temps, les conditions climatiques peuvent varier. Lorsque les conditions climatiques changent, selon Jackson et

Overpeck (2000), les espèces doivent soit maintenir une niche fondamentale suffisamment large, soit être capables de changements évolutifs suffisamment rapides pour s'adapter au nouvel espace environnemental. Les espèces ou les populations d'une espèce confrontée à une réduction de l'habitat disponible pourraient répondre en contractant leur distribution et en persistant dans des poches isolées ou des «refuges» d'un environnement encore propice (Holt, 1990), ou dans le cas d'une extension de la zone de conditions propices, élargir leur répartition. Dans le cas d'un changement brusque ou extrême des conditions climatiques, ou le manque de poches de conditions stables, les espèces peuvent échapper à l'extinction en migrant et en suivant l'habitat propice dans l'espace. En raison de la variation des conditions climatiques dans l'espace et dans le temps, on peut observer des espèces dont l'aire s'est réduite à des refuges, en dehors desquelles la fluctuation des conditions signifie qu'une espèce pourrait occuper plus ou moins d'espace selon l'habitat approprié à sa disposition.

Cela nous amène à notre première question, abordée dans le **chapitre 1**, en ce qui concerne la façon dont les patrons actuels pourraient refléter les variations environnementales survenues au fil du temps - par exemple, les récentes fluctuations paléoclimatiques du Quaternaire ont-elles laissé leur empreinte sur les distributions contemporaines des espèces? Comment ont-elles influencé la répartition existante des espèces endémiques dans les WG? Quels ont été les effets de ces variations, ou de l'absence de variation sur les espèces ayant des préférences différentes de niche ?

Bien que les fluctuations climatiques récentes puissent influencer directement la biodiversité par des limites écologiques fixées par le bilan eau-énergie (Francis et Currie, 2003; Hawkins et al., 2003; Currie et al., 2004), des paléoclimats plus anciens peuvent également affecter l'évolution et créer des patterns biogéographiques et macroécologiques (Dynesius & Jansson, 2000; Kissling et al., 2012; Eiserhardt et al., 2015). Les conséquences de la stabilité et du changement ont varié pour différentes lignées au cours du temps géologique et dans l'espace. L'abondance historique des habitats peut être un fort prédicteur de la diversification (Zobel et al., 2011; Jetz & Fine, 2012). La variabilité climatique peut imposer des limites de recolonisation à des lignées particulières et provoquer des extinctions spécifiques au clade (Svenning, 2003). De tels patterns pourraient affecter la structure phylogénétique des assemblages car ils sont façonnés par la dispersion, l'extinction et / ou la spéciation (Jansson & Dynesius, 2002) qui affectent directement le nombre d'espèces dans chaque région.

#### *L'assemblage d'espèces en communautés et le model du filtre*

L'étude de l'assemblage d'espèces considère les mécanismes par lesquels des assemblages ou des communautés sont construits et entretenus par l'arrivée de colons potentiels issus d'un pool d'espèces externe. Le pool d'espèces régional est influencé par des facteurs biorégionaux et évolutifs qui interagissent avec des facteurs locaux et donnent lieu à des processus écologiques complexes tels que la sélection à base de niche, la dérive écologique, la dispersion ou la spéciation (Zobel et al., 2011; Hardy et al., 2012). Le modèle de filtre classique (Zobel, 1997) décrit un pool d'espèces dont les membres des communautés locales sont sélectionnés en passant par une succession de filtres. L'arrivée d'espèces à partir du pool régional est soumise à des contraintes de dispersion, qui constitue un filtre à l'échelle régionale ; suivi par le filtre d'habitat qui exclut les espèces qui ne tolèrent pas les contraintes abiotiques locales et, enfin, le filtre biotique.

Dans l'écologie des communautés végétales, l'accent a été mis sur les caractéristiques des espèces telles que les traits adaptatifs, qui déterminent l'impact de ces filtres sur le devenir d'une espèce. Les mécanismes de l'assemblage des communautés ont été déduits des similitudes et des différences entre espèces co-occurentes. Cependant, quels traits prédominent pour déterminer la niche d'une espèce n'est pas toujours bien connu, et les traits eux-mêmes sont rarement documentés pour toutes les espèces, en particulier dans les régions tropicales.

#### *Phylogénie comme proxy pour les traits de niche*

Les parents proches ont tendance à partager des traits phénotypiques similaires en raison du conservatisme de niche (Wiens & Graham, 2005). Ainsi, les espèces proches parentes devraient être écologiquement plus similaires que celles évolutivement éloignées, car elles partagent une histoire évolutive commune (Freckleton & Jetz, 2009). Selon ce dernier, les relations phylogénétiques – c'est à dire la distance évolutive les séparant - des espèces au sein d'une communauté peuvent être utilisés pour faire des inférences sur les mécanismes d'assemblage des communautés.

Selon le modèle de « phylogeny as proxy » et sous l'hypothèse de la conservation de niche, a) l'assemblage abiotique entraîne la co-occurrence d'espèces phylogénétiquement proches, et cette sous-dispersion ou « clustering » phylogénétique implique un filtrage de l'habitat, et b) l'assemblage biotique entraîne la co-occurrence d'espèces phylogénétiquement éloignées, et la « surdispersion » phylogénétique implique l'exclusion compétitive (Webb *et al.*, 2002). Bien qu'il s'agisse désormais d'une méthode répandue, l'utilisation des patterns phylogénétiques observés comme indicateur des processus d'assemblage de communautés reste controversé (Mayfield & Levine, 2010; Pavoine *et al.*, 2013) en raison, par exemple, la dépendance spatiale et temporelle des patrons phylogénétiques (Cavender-Bares *et al.*, 2006) ou du manque de congruence entre les mesures phylogénétiques et la dispersion des traits (Pavoine & Bonsall, 2011).

En effet, des espèces phylogénétiquement proches ainsi que non apparentées peuvent posséder des traits similaires, en raison de l'adaptation à des conditions climatiques semblables (convergence, Freckleton & Jetz, 2009). Si les niches des espèces ne sont pas conservées phylogénétiquement, les attendus de base ci-dessus seraient contestables. La surdispersion phylogénétique pourrait être la conséquence d'une convergence des niches des espèces éloignées en raison d'un signal plus fort d'adaptation à l'environnement (Cavender-Bares *et al.*, 2004). On pourrait s'attendre à différents niveaux de conservation de niche dans des zones ayant des conditions environnementales différentes (e.g. Khaliq *et al.*, 2015).

Une critique récente de Gerhold *et al.* (2015) suggère donc que, plutôt que d'être simplement un indicateur des mécanismes d'assemblage de la communauté, les patterns phylogénétiques pourraient fournir des informations sur la composante évolutive des processus écologiques. Par ex. Bartish *et al.* (2016) a constaté que les lignées associées à des types d'habitats distincts diffèrent dans leurs antécédents évolutifs; les habitats humides incluant un nombre disproportionné de lignées apparues durant les époques humides et ainsi de suite pour les habitats secs ou froids. L'âge des différents types d'habitat aurait aussi un impact sur les pools de lignées, et par conséquence sur la dispersion phylogénétique (Gerhold *et al.*, 2015).

Plutôt qu'un schéma simpliste sous-dispersion phylogénétique = filtrage de l'habitat et surdispersion phylogénétique = compétition, il est important d'explorer d'autres interprétations et d'examiner la dynamique évolutive et écologique sur plusieurs échelles de temps (Mazel *et al.*, 2015). Huit scénarios et de nombreux processus et interprétations peuvent être envisagés sur la base 1) du scénario écologique, c.-à-d. les filtres abiotiques ou biotiques, 2) de l'existence d'une conservation ou d'une convergence de niche, et 3) de la profondeur phylogénétique, c.-à-d. la dynamique évolutive ancienne ou récente (voir Fig. 1).

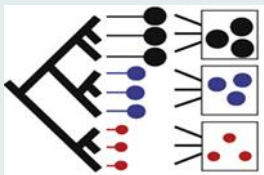
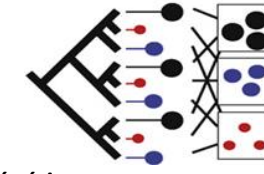
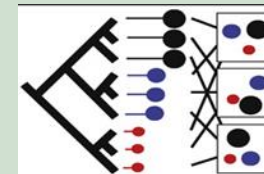
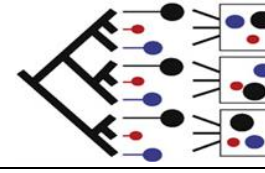
Hypothèses de l'assemblée des communautés	Dynamique évolutive ANCIEN et pattern phylogénétique dans des NCEUDS profondes de la phylogénie	Congruence entre les niches des espèces et leur proximité phylogénétique	Dynamique évolutive RECENTE et pattern phylogénétique dans des NCEUDS terminaux
L'environnement abiotique plus sévère filtre des espèces ayant des niches similaires (EF)	<b>SOUS-dispersion Phylogénétique</b> 	<b>CONSERVATION de niche</b> Les niches écologiques des espèces phylogénétiquement proches sont semblables	<b>Sous-dispersion</b>  Sur-dispersion
	<b>SUR-DISPERSION</b>  Phylogénétique	Niches <b>CONVERGENTES</b> Les niches écologiques dans des clades éloignées sont semblables	<b>Sous-dispersion</b>  Sur-dispersion
Les interactions biotiques filtrent les espèces ayant des niches dissemblables (BF)	<b>SUR-DISPERSION Phylogénétique</b> 	<b>CONSERVATION de niche</b> Les niches écologiques des espèces phylogénétiquement éloignées sont différents	<b>Sous-dispersion (radiation récente)</b>  Sur-dispersion
	<b>SOUS-dispersion Phylogénétique</b> 	Niches <b>DIVERGENTES</b> Les niches écologiques des espèces phylogénétiquement proches sont différents	<b>Sous-dispersion (radiation récente)</b>  Sur-dispersion

Figure 1. Hypothèses et huit scénarios

Notre deuxième question, abordée dans **chapitre 2**, concerne les legs de paléoclimats plus anciens dans la répartition des espèces végétales dans les WG. Comment la structure phylogénétique des assemblages de plantes a-t-elle été influencée par l'héritage des adaptations

aux climats passés et aux filtres environnementaux actuels? Comment distinguer le filtrage actuel de la dynamique évolutive?

#### *Traits reproductifs et évolution*

Des contractions de l'aire de distribution des espèces, des extinctions des lignées et de la diversification des lignées spécifiques dans les zones restreintes a provoqué une restriction spatiale d'espèces uniques ou l'endémisme (Rosauer et al., 2009). Ceci est souvent fortement façonné par la stabilité climatique à long terme (Sandel et al. , 2011; Harrison & Noss, 2017). L'instabilité climatique et les changements à long terme peuvent également contribuer à générer de l'endémisme grâce à une évolution de niche en réponse aux opportunités de spéciation offertes par des environnements novateurs (Särkinen et al., 2012) dépaupérés par des extinctions d'espèces incapables de s'adapter à ce changement (Wellborn & Langerhans, 2014). Selon Jacquemyn *et al.* (2012), les conditions environnementales altérées et la fragmentation de l'habitat peuvent (i) réduire la diversité génétique de la population par la dérive génétique et entraver les réponses adaptatives, par exemple si cette perte concerne les codes pour la variation phénotypique, ou (ii) facilitée par l'absence de flux génétique, la fragmentation peut entraîner des changements adaptatifs dans les traits et augmenter le *fitness* des plantes individuelles. Ceci a été montré par exemple dans l'émergence de l'adaptation au feu suite à la sécheresse climatique à long terme à la fin du Miocène (Simon et al., 2009) et par Barret et al. (2009) pour les systèmes de reproduction (viz. transition d'autogamie à l'allogamie).

Les changements évolutifs dans les systèmes sexuels et les facteurs environnementaux associés à ces changements sont des problèmes centraux de la biologie évolutive, car les traits reproducteurs sont des paramètres clés de l'aptitude physique des organismes (Charlesworth, 2006). En particulier, beaucoup d'efforts ont été consacrés à l'émergence et à la maintenance de la séparation des sexes sur des individus distincts (dioécie). On s'attend à ce que les mécanismes écologiques et génétiques influent sur la réussite reproductive et en conséquence sur l'évolution des systèmes sexuels. En premier lieu, l'allocation différentielle des ressources entre les sexes permet des stratégies sexospécifiques allégeant les compromis entre les fonctions masculines et féminines. En deuxième lieu, l'allogamie limite le coût de la consanguinité mais, en contrepartie, l'autogamie permet de maximiser le transfert de gènes d'un individu à ses descendants.

La littérature rapporte deux conséquences de ces mécanismes : 1) le succès écologique supérieur des espèces dioïques dans certaines conditions environnementales, et 2) la capacité supérieure de colonisation et la diversification subséquentes des espèces dioïques en réponse aux opportunités offertes par les habitats nouveaux. La limitation des ressources ou des pollinisateurs peut modifier les couts relatifs des systèmes sexuels et en conséquence favoriser l'investissement différentiel dans les fonctions masculines et féminines via la séparation des sexes (Bawa, 1980; Burd, 1994; Munoz *et al.*, 2016). Plus précisément, la séparation des sexes a été jugé favorisé par des conditions environnementales stressantes, particulièrement plus sèches (e.g., Costich, 1995; Weller *et al.*, 1995; Case & Barrett, 2004).

Les plantes dioïques sont également plus nombreuses que les autres à coloniser des zones nouvelles ou perturbées dans les communautés forestières de l'Afrique centrale (Réjou-Méchain & Cheptou, 2015). Cette aptitude plus élevée à la colonisation peut être expliquée par leur taux

plus élevé d'hétérozygotie, c'est-à-dire à la diversité génétique plus élevée (Costich & Meagher, 1992). De telles découvertes ainsi que la forte abondance de dioïques dans les îles - suggérant que l'établissement de plantes dioïques par la colonisation peut être plus fréquent qu'attendu - mettent en question les hypothèses traditionnelles telles que la loi de Baker, qui mettent l'accent sur l'avantage sélectif de l'autogamie pour les colonisateurs (Baker, 1955).

La contribution des premiers colons dioïques à la proportion relativement élevée de dioïques sur les îles (Sakai *et al.*, 1995b; Schlessman *et al.*, 2014) a fourni un soutien empirique aux modèles théoriques d'association entre allogamie et dispersion élevée (Cheptou *et al.*, 2009). La survie accrue menant à la spéciation ainsi qu'à l'évolution locale d'autres systèmes sexuels vers la dioécie a aussi contribué à la forte incidence de la dioécie dans les îles (Sakai *et al.*, 1995b; Ito, 1998; Le Péchon *et al.*, 2010). Fait marquant, à Hawaii, le dimorphisme dans la flore globale est associé à des habitats plus humides, mais les espèces dimorphes endémiques sont associées à un déplacement vers des habitats secs (Sakai *et al.*, 1995a; Sakai *et al.*, 2006).

Le rôle des contraintes environnementales sur l'évolution des systèmes sexuels devrait se traduire sur le long terme en modes de diversification reflétant l'influence des environnements passés. La diversité et les adaptations des lignées dioïques existantes peuvent refléter donc la dynamique passée. Notre dernière question, abordée dans le **chapitre 3**, concerne le rôle des systèmes sexuels dans le filtrage environnemental et la dynamique évolutive. La fréquence des systèmes sexuels des arbres des WG varie-t-elle selon des gradients de stress et de limitation des ressources liées à la disponibilité de l'eau et à la stabilité historique de l'habitat ? Existe-t-il une différence entre les espèces endémiques et non endémiques ?

Table 1. Questions principales et objectifs de chaque chapitre

Questions principales	Objectifs
1. Les changements climatiques quaternaires ont-ils affecté les habitats forestiers des WG, et comment ceux-ci ont-t-ils influencés la répartition actuelle des espèces endémiques.	Caractériser l'évolution de la répartition des espèces en réponse aux changements climatique quaternaire.
2. Comment les conditions environnementales actuelles et passées ont-elles influencé la répartition actuelle de diversité phylogénétique dans les assemblages d'arbres des WG., en fonction des contraintes exercées sur les stratégies écologiques au fil du temps et de la conservation de ces stratégies au cours de l'évolution	Quantifier la structure phylogénétique à l'intérieur et entre les ensembles d'espèces d'arbres afin de caractériser l'héritage des adaptations passées et la signature des filtres environnementaux actuels.
3. Comment les variations spatiales du stress, de la limitation des ressources et de la stabilité historique des habitats influencent la fréquence des systèmes sexuels des arbres.	Étudier l'association entre les gradients environnementaux et la fréquence des traits reproductifs des espèces endémiques et non-endémiques.



Les hypothèses et les attendus associées aux questions évoquées ci-dessus, et les méthodes utilisées pour y répondre sont décrites ci-dessous. Chacun des trois aspects sont abordés séparément dans les trois articles mentionnés.

Dans le **chapitre 1**, nous avons évalué l'influence des variations climatiques quaternaires sur la répartition des espèces d'arbres endémiques. Nous avons émis les hypothèses que la dynamique de l'habitat induite par le climat joue un rôle dans le changement de distribution des espèces et la spécialisation des niches écologiques influence leurs réponses. Nous nous attendions à ce qu'il y ait 1) une pression pour un changement dans l'espace écologique (changement de niche) ou géographique (migration) dans le cas d'une inadéquation entre les conditions climatiques du Quaternaire et les préférences d'habitat actuelles des espèces, et 2) la persistance locale dans le cas de chevauchement entre les aires de distribution prédites au cours de ces trois périodes.

Nous avons évalué les préférences bioclimatiques actuelles de 195 espèces endémiques en utilisant l'algorithme de SDM MaxEnt. Les trois premiers axes d'une analyse de composantes principale (ACP) sur les variables environnementales ont fourni des variables synthétiques pour des analyses ultérieures. Les modèles ont été projetés dans les conditions climatiques passées du dernier maximum glaciaire (LGM, ~20 Ma) et le dernier interglaciaire (LIG~120 Ma). Nous avons ensuite évalué l'ampleur des changements dans les distributions prédites de chaque espèce à travers le temps, et testé si les localités actuelles des espèces étaient non-aléatoirement associées aux localités prédites dans le passé. Enfin, nous avons caractérisé les réponses spécifiques des espèces en fonction de scénarios biogéographiques plausibles.

**Bose, R., Munoz, F., Ramesh, B. R. & Pélissier, R. (2016) Past potential habitats shed light on the biogeography of endemic tree species of the Western Ghats biodiversity hotspot, South India, *Journal of Biogeography* 43, 899:910**

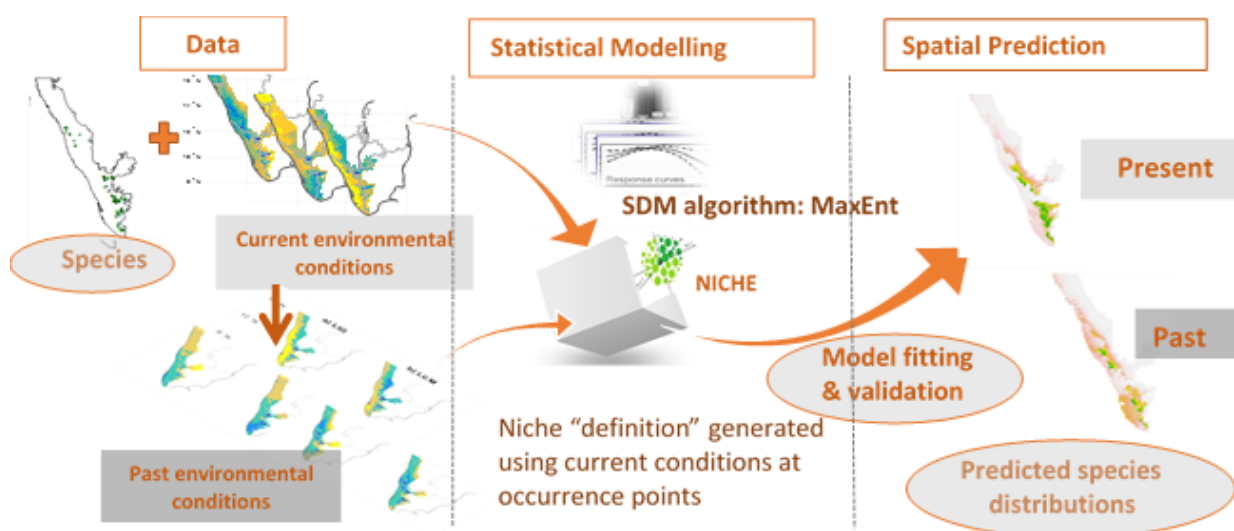


Figure 2. Modélisation de la distribution des espèces en fonction des conditions climatiques du présent et du passé (LGM, LIG)

Dans le **chapitre 2**, nous avons étudié la structure phylogénétique des communautés d'arbres pour caractériser l'héritage des adaptations passées et les signatures des filtres environnementaux actuels. Nous avons testé les hypothèses du gradient de stress (Weiher & Keddy, 1995) et de la stabilité historique (Jablonski *et al.*, 2006; Kissling *et al.*, 2012) avec nos observations de saisonnalité et de stabilité historique de l'habitat. Selon ces hypothèses, nous nous attendions à une sous-dispersion phylogénétique dans des environnements actuellement plus difficiles et dans des régions à climats historiquement moins stables, et à une sur-dispersion phylogénétique dans des conditions opposées. Dans le cadre du filtrage environnemental le long des gradients à large échelle, nous nous attendions à un turnover élevé de la composition phylogénétique, reflétant un changement de lignées adaptés aux différentes conditions environnementales.

Pour tester cela, nous avons caractérisé la structure phylogénétique des communautés des WG par rapport à un modèle nul au sein de et entre 297 parcelles réparties sur 1) des gradients environnementaux actuels représentant différents niveaux de stress abiotique pour les plantes dans les WG, et 2) un gradient historique de stabilité de l'habitat issu d'une étude antérieure (Chapitre 1, Bose *et al.*, 2016). Pour évaluer l'empreinte des contraintes évolutives anciennes et récentes, nous avons calculé respectivement les distances phylogénétiques moyennes (MPD) et les distances entre taxons les plus proches (MNTD), et nous avons rapporté ces indices ainsi que ceux du renouvellement phylogénétique aux variations environnementales. Nous avons également défini des attendus distincts selon le conservatisme de niche ou pas, et testé la congruence entre la convergence phylogénétique et la convergence des niches écologiques.

**Bose, R., Ramesh, B. R., Pélissier, R. & Munoz, F. (in prep.) Phylogenetic diversity in the Western Ghats biodiversity hotspot reflects environmental filtering and past niche diversification of trees.**

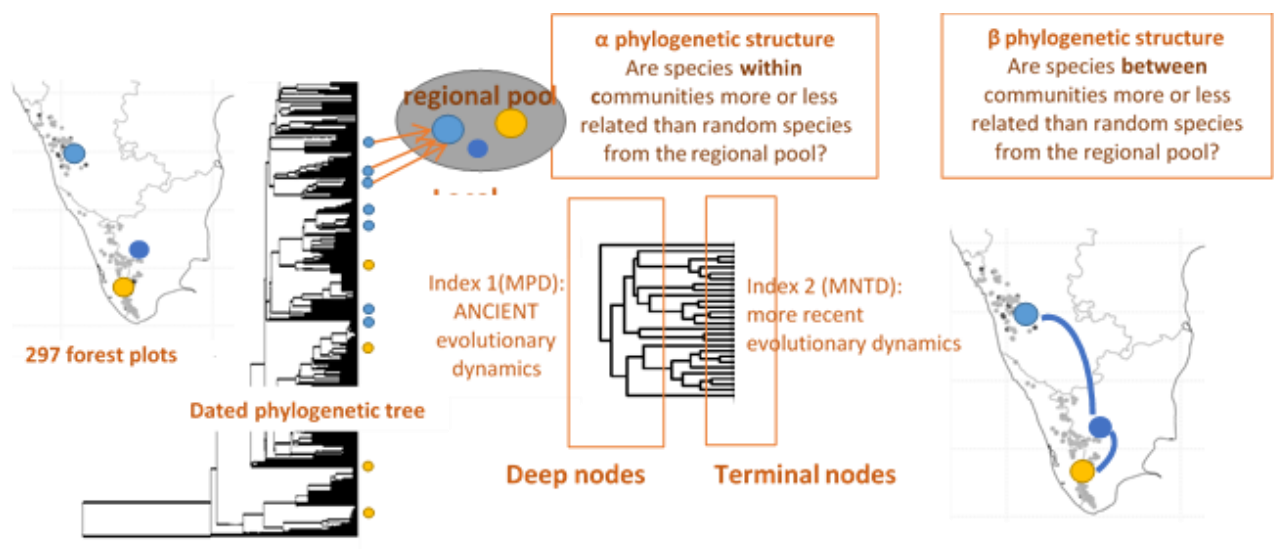


Figure 3. Résumé des méthodes : métriques reflétant la structure phylogénétique à différentes profondeurs de l'arbre phylogénétique ainsi que la structure au sein de (alpha) et entre (beta) les assemblages aident à démêler les influences du le filtrage actuel de la dynamique évolutive

Dans le **chapitre 3**, dans l'objectif de comprendre dans quelles conditions la séparation des sexes (dioécie) a été sélectionnée au cours de l'évolution et dans les écosystèmes existants, nous avons examiné l'association entre la variation du stress et de la stabilité historique des habitats et la fréquence des systèmes sexuelles. Nous avons exploré deux hypothèses non exclusives axées sur le cas particulier des espèces dioïques: 1) la fréquence des espèces dioïques dans les forêts tropicales des WG reflète le filtrage environnemental actuel et 2) les espèces dioïques ont subi une diversification préférentielle dans les WG en relation avec les conditions environnementales passées.

Pour la première hypothèse, nous nous attendions à une relation significative et positive entre la dioécie et le stress environnemental, et aucune différence dans les patterns des espèces dioïques endémiques et non endémiques. Dans la deuxième hypothèse, nous nous attendons à des patrons de diversité en dioïques distincts entre endémiques et non endémiques en raison d'événements de diversification qui ont influencé l'apparition de nouveaux taxons dioïques dans la région. Les lignées plus anciennes pourraient également afficher des associations entre la dioécie et les adaptations aux conditions moins stressantes, dans lesquelles les angiospermes anciennes se sont diversifiées. Sous la deuxième hypothèse, l'on s'attendrait alors à observer cet effet sur les espèces dioïques non endémiques (niches conservées) qui ne seraient pas apparues en conséquence de l'adaptation aux nouvelles conditions plus stressantes locale comme l'ont été les endémiques dioïques (niches divergentes).

Nous avons examiné la relation entre la proportion d'espèces dioïques dans chacune des 297 parcelles et les gradients environnementaux en utilisant un GLM (Generalized Linear Model). Nous avons comparé les patterns des espèces endémiques et non endémiques. Nous avons ensuite caractérisé et testé ces relations en effectuant des analyses de RLQ séparément pour les espèces endémiques et non endémiques, et avons reconnu l'influence des structures phylogénétiques et spatiales en utilisant des analyses RLQ étendues (ESLTP, Pavoine *et al.*, 2011).

L'hypothèse 2 implique que la diversification des espèces dans les WG est liée à la fois au contexte écologique et aux systèmes de reproduction. Nous avons donc étudié le rôle de la différenciation de la niche climatique parmi les endémiques congénères des genres les plus riches en espèces et sa dépendance au système reproductif. Afin de tester l'effet de l'ancienneté des lignées nous avons analysé la variation des âges relatifs (longueurs terminales des branches de la phylogénie) des espèces dioïques endémiques et non endémiques en fonction de leur localisation au long du gradient de la disponibilité saisonnière de l'eau.

***Bose, R., Munoz, F., Ramesh, B. R. & Pélissier, R. (in prep.) Role of dioecy in the ecological and evolutionary dynamics of trees in the Western Ghats biodiversity hotspot: a legacy of aridification?***

- **Les stratégies écologiques des espèces déterminent leurs réponses à la variation du climat quaternaire**

Conformément aux études antérieures sur les WG, nos modèles de distribution d'espèces basées sur les conditions actuelles soutiennent l'importance de la variation de la précipitation annuelle, de la température et de la saisonnalité sur la distribution des arbres endémiques (**Chapitre 1**). Nous n'avons pas trouvé de preuve de refuge quaternaire au sein des WG.

Cependant, en comparant les trajectoires de distribution des espèces modélisés *sur* ~ 150 kyr, nous avons montré que les fluctuations de la mousson et la variation de température ou de la saisonnalité pendant les cycles glaciaire-interglaciaire induisent une dynamique des habitats qui a entraîné des changements des distributions dans le temps, et déterminé les contours actuels des distributions des espèces. Il est important de noter que les réponses des espèces ont varié en fonction de leurs positions respectives le long des gradients environnementaux, à savoir leurs stratégies écologiques. Nous avons identifié trois scénarios de réponses des espèces distincts de stabilité, contraction et migration (Figs. 2-4, Ch. 1) : (i) Les espèces dont les distributions prédites sont les plus stables sont principalement celles des élévations les plus élevées (scénario de stabilité). Les conditions du LGM généralement froides et sèches leur furent moins restrictive que pour les espèces des altitudes moyennes et ceux des basses altitudes du nord (ii) les espèces des altitudes moyennes ont subi une contraction sur les zones climatiques plus stables (scénario de contraction), and (iii) les espèces les plus méridionales nécessitant une saisonnalité minimale ont été limitées par la saisonnalité plus élevée pendant de LIG, et étaient restreintes au Sri Lanka (scénario de shift/migration).

Nos résultats révèlent la persistance locale probable de la plupart des endémiques des WG au cours des 150 derniers kyr, une période relativement récente dans ce refuge de la Paléogène. Le large éventail de préférences bioclimatiques est probablement le résultat d'événements évolutifs antérieurs au Quaternaire.

Sur la base de cette analyse, nous avons pu produire un indice de la stabilité de l'habitat depuis le LIG. Il montre une forte tendance sud-nord de stabilité décroissante. Cet indice représente le nombre d'espèce prédit à toutes les époques dans chaque maille des WG depuis le LIG. Le réseau actuel d'aires protégées dans les WG ne couvre pas les zones stables ayant le plus grand nombre d'espèces.

- **Le climat actuel et sa dynamique quaternaire déterminent la structure phylogénétique actuelle**

Nous avons constaté que les facteurs climatiques actuels, à savoir le stress hydrique en termes de volume de saisonnalité des précipitations, et leur fluctuation depuis le LIG expliquaient conjointement la variation de la structure phylogénétique dans les WG (**Chapitre 2**). Le filtrage par les gradients sud-nord de stabilité et de saisonnalité, et le gradient ouest-est de précipitation annuelle se reflète dans la structure phylogénétique des communautés locales réparties tout au long des WG. Suite à la conservation des niches dans les nœuds plus profonds de la phylogénie, la

plupart des parcelles sous et sur-dispersées phylogénétiquement occupent les extrêmes de ces gradients (Fig. 1, Ch.2).

*...en accord avec les attendus (conservation des niches)*

Les environnements les plus sévères filtrent des espèces plus proches phylogénétiquement (sous-dispersion) dans le nord et les forêts sèches du sud-est (Fig. 4b, Ch. 2). En revanche, dans des habitats moins contraints et plus stables du sud des WG, la surdispersion phylogénétique suggère la différenciation de niche au sein d'espèces plus éloignées. Cette interprétation est confirmée par la faible diversité (convergence) des niches écologiques dans le premier cas et la grande diversité des niches écologiques dans le deuxième.

Notre utilisation de métriques reflétant la structure phylogénétique à différentes profondeurs nous a permis d'examiner la dynamique évolutive et écologique à différentes échelles temporelles. La tendance générale de surdispersion aux échelles phylogénétiques les plus profondes dans le sud contraste avec la tendance générale de sous-dispersion dans les communautés plus au nord. Au sud, le maintien de conditions favorables à travers les époques géologiques est probablement la cause du maintien de lignées plus diverses ici. L'histoire évolutive ancienne sous-tendrait la différenciation des niches (des divisions de lignage plus anciennes qui auraient eu lieu ailleurs, Bartish *et al.*, 2016). Les pools de lignées adaptées à des habitats anciens (comme les forêts tropicales humides) se sont diversifiés pendant de longues périodes, ce qui a entraîné une dispersion phylogénétique plus élevée des pools d'espèces d'angiospermes (Gerhold *et al.* 2015), comme nous l'avons montré pour les WG. D'autre part, les types d'habitats plus jeunes auraient connu des diversifications plus récentes avec une immigration limitée à partir de types d'habitats plus anciens en raison de la prévalence du conservatisme de niche (Prinzing *et al.*, 2001).

*...et contrairement aux attendus de l'hypothèse du gradient de stress*

Contrairement à nos attendus sous l'hypothèse de la conservation des niches, au lieu d'une sous-dispersion phylogénétique augmentant avec le stress le long du gradient d'élévation, nos résultats ont révélé à l'inverse la coexistence d'espèces éloignées (sur-dispersion phylogénétique) dans les communautés de haute altitude. L'évolution convergente vers l'adaptation au froid dans des espèces d'origine tropicale, subtropicale ou tempérée est soutenue par la similitude des traits de niche (basés sur les scores CCA) de ces groupes d'espèces éloignées. La similitude globale des traits de niches est cependant diminuée par la coexistence de deux grands clades d'angiospermes, Magnoliids et Eudicots. Ceci souligne la nécessité de regrouper les espèces qui pourraient être filtrés de différentes manières par la topographie complexe des paysages à haute altitude (Jiménez-Alfaro *et al.*, 2014).

*Signal phylogénétique positive*

Le renouvellement des lignées le long des gradients (turnover phylogénétique) globalement positif correspond aux résultats des études menées à une échelle taxonomique profonde en présence de forts gradients environnementaux (voir Vamosi *et al.*, 2009). Notre étude confirme la corrélation établie entre gradients de précipitation et de saisonnalité d'une part et le turnover

phylogénétique d'autre part, et l'indépendance de l'espace (Swenson, 2011; Hardy *et al.*, 2012). Le renouvellement des lignées à travers l'espace est donc le résultat du filtrage environnemental et non des processus de dispersion. Cependant, notre étude comprend le gradient entier d'élévation dans les WG (> 2000 m) et fournit de nouvelles informations sur les origines biogéographiques et évolutives distinctes des pools d'espèces à faible et à haute altitude. Jusqu'à une différence de 900 à 1000 m (l'étendue d'élévation des parcelles incluse dans les études précédentes), le turnover reste faible entre les parcelles à des élévations contrastées. C'est seulement au-delà, jusqu'à une différence de 1700 m, que le turnover augmente brusquement (Fig. 6c. Ch. 2). Le renouvellement phylogénétique élevé à haute altitude soutient l'existence d'une histoire évolutive distincte des taxons de haute altitude suggérée par les résultats précédents de surdispersion phylogénétique dans les assemblages locaux.

- **Le climat actuel et sa dynamique quaternaire déterminent la structure des traits reproductifs**

Nous avons constaté dans le **chapitre 3** que les variations du stress abiotique de l'habitat influencent la fréquence des systèmes sexuels. Nous avons trouvé des patrons distincts pour les espèces endémiques et non endémiques (Fig. 3, Ch3). Plus précisément, parmi les espèces endémiques, la proportion de dioïques a augmenté de manière significative avec l'augmentation de la saisonnalité dans la partie nord des WG et dans les forêts sèches du sud. Nos résultats ont indiqué un conservatisme le long du gradient de précipitation, les niches des espèces endémiques congénères se chevauchants. Ceci contraste avec la plus grande divergence de niches le long du gradient de saisonnalité (par ex, Fig. 8, Ch.3), montrant la probable divergence écologique et l'adaptation à différentes conditions le long de ce gradient. En revanche, les espèces dioïques non endémiques sont associées à des zones de stabilité dans le sud de les WG.

Les résultats de l'analyse RLQ étendu ont révélé l'association de lignées dioïques particulières qui sont riches en espèces endémiques avec les environnements les moins saisonniers. Au contraire, dans les genres dioïques peu pourvu en endémiques, les espèces non-endémiques étaient associés à la plus grande stabilité historique vers le sud (Fig. 4-5, Ch.3). Ces derniers appartenaient à des lignées qui étaient en moyenne plus anciennes (Fig. 10, ch.3) que celles des espèces dioïques endémiques, y compris Magnoliides, indiquant une adaptation ancestrale à des conditions plus humides.

Ce patron pourrait être attribué à un effet de refuge, où la conservation de niche a conduit des espèces dioïques non-endémiques à persister dans des zones moins saisonnières et historiquement stables, tandis que les opportunités de diversification au sein de et au-delà du refuge du sud ont mené à la spéciation écologique dans d'autres genres dioïques. Différents mécanismes ont donc sélectionné les dioïques dans les WG.

Les trois chapitres de cette thèse sont étroitement liés et se nourrissent à différents niveaux. Je l'illustre ci-dessous avec deux exemples liés aux différents niveaux de conservatisme de niche que nous avons observés le long de différents gradients environnementaux.

- **L'histoire des endémiques congénériques : labilité de la niche**

Des études antérieures sur les WG ont montré que les espèces endémiques de certains genres riches en espèces présentaient des tolérances variables à une saisonnalité croissante, ou une « vicariance écologique » (Pascal, 1988; Gimaret-Carpentier *et al.*, 2003). Dans le **chapitre 1**, nous avons constaté que la réponse de ces espèces endémiques congénériques aux fluctuations quaternaires était dépendante de leurs préférences d'habitat distinctes, et non des affinités phylogénétiques (Bose *et al.*, 2016).

Dans le **chapitre 2**, j'ai suggéré que la tendance à la sous-dispersion dans les nœuds terminaux démontre que les diversifications récentes n'entraînaient pas d'importants changements de niche. Cela peut sembler contredire l'hypothèse de la vicariance écologique évoquée ci-dessus. Cependant, la diversification se réfère à la différenciation locale au sein des communautés alors que la vicariance concerne la variation le long des gradients. Ceci souligne l'importance d'intégrer à la fois les métriques de la dispersion phylogénétique au sein de (alpha) et entre (bêta) communautés. Le signal phylogénétique fort dans les traits de niche liés aux préférences pluviométriques et le taux de renouvellement élevé des lignées le long du gradient de précipitation contraste avec le faible taux de renouvellement le long du gradient saisonnier. Les parents proches occupent des positions différentes le long de ce dernier, ce qui suggère que les traits liés aux préférences de saisonnalité, comme la tolérance ou l'évitement de la sécheresse, peuvent être plus labiles pour certaines lignées que pour d'autres.

Nous avons établi le lien entre le passage à des conditions plus humides et saisonnièrement plus sèches et la dioécie dans le **chapitre 3**. Parmi des genres vicariants en question, plusieurs étaient dioïques ou polygamodioïques. Dans la littérature, les explications de la fréquence élevée de dioïques dans les îles incluaient une évolution autochtone vers la dioécie. Dans certains cas, des espèces dioïques endémiques étaient associées à un déplacement vers des habitats secs, alors que les dioïques non-endémiques sont associées à des habitats plus humides (Sakai *et al.*, 1995b; Sakai *et al.*, 2006). Ces observations suggèrent une acquisition ancienne des dioïques de traits conférant une adaptation à des conditions humides, et une rencontre récente d'habitats plus secs.

Nos analyses constituent une première étape vers la compréhension des mécanismes responsables à la fois de l'incidence élevée de dioïques et de l'endémisme élevé des WG. Nous suggérons que ces mécanismes sont liés au fait que la saisonnalité ne soit devenue contraignante que plus récemment, avec l'établissement du régime de la mousson et l'aridification du Miocène. La littérature suggère que la dispersion vers l'Inde et la diversification ultérieure de certains des clades dioïques en question (e.g. *Garcinia*ae, Ruhfel *et al.*, 2016) coïncide avec cette époque. L'acquisition de phylogénies résolues permettrait de vérifier que la diversification des endémies dioïques coïncide bien avec l'amplification de la saisonnalité. Jusqu'à cela, nous devons nous contenter de fournir des hypothèses qui peuvent être testées à l'avenir et nous soulignons l'importance de prendre en compte le rôle de l'histoire géologique et les tendances paléoclimatiques globales.

- **Conservation des préférences ancestrales dans le refuge du sud**

Les refuges climatiques, ou « musées », dans lesquelles les espèces de lignées anciennes se sont maintenues jusqu'aujourd'hui, sont souvent des zones anciens et historiquement stables. Ils offrent des conditions de haute température et d'humidité qui diminuent la probabilité d'extinction (Rolland *et al.*, 2014; Harrison & Noss, 2017). Une région peut également fonctionner comme un musée parce qu'elle correspond à l'environnement habituellement humide auquel les lignées d'une époque antérieure étaient originaires (Bartish *et al.*, 2016). Nos résultats sont en accord avec les études antérieures basées sur des pollens fossiles et les études phylogénétiques moléculaires de taxons non végétaux pour montrer que le sud des WG représente à la fois un musée évolutif et un berceau de biodiversité. L'histoire évolutive des pools de lignées de l'habitat des forêts tropicales humides a façonné les communautés locales qui en dérivent.

Nos résultats présentés au chapitre 2 montrent que le clade de Magnoliids influence de façon disproportionnée la structure phylogénétique locale. Les espèces de ce clade coexistent avec des lignées distantes d'Eudicot. Toutes deux se sont diversifiées, ont évoluées et ont migrées au fil du temps pour occuper les forêts du sud et à ceux des hautes altitudes, ce qui contribue à la surdispersion phylogénétique basale. La contribution des Magnoliids aux communautés est supérieure à celle attendue s'il ne s'agissait que d'un sous échantillon aléatoire du pool régional. Par contre, ce clade est nettement sous-représenté dans les parcelles de faible altitude plus au nord avec > 6 mois de saison sèche et des niveaux de précipitations annuels plus faibles, ainsi que dans les forêts sèches de versant est dans le sud, ce qui contribue à la sous-dispersion phylogénétique basale.

De telles lignées anciennes conservent des tolérances environnementales et occupent des habitats semblables à travers les continents, bien qu'ils ne partagent pas d'espèces, comme démontré entre le Panama et dans les WG par Hardy *et al.* (2012). Le turnover phylogénétique est attribuable à plusieurs familles, notamment de nombreuses Magnoliid, adaptées aux pluies élevées dans les deux régions. La conservation des niches liées à la pluviométrie est profondément enracinée dans l'origine des clades montrant des tendances adaptatives (Carlucci *et al.*, 2016), plutôt que d'être le résultat de réorganisations d'adaptations des espèces dans des contextes biogéographiques spécifiques (Hardy *et al.*, 2012).

La présence d'espèces dioïques non-endémiques dans le sud des WG renforce l'idée que les zones de forte précipitation et de faible saisonnalité, constituent un refuge pour les lignées plus anciennes (musée). Les endémiques dioïques des genres qui ont affiché une grande labilité de niche se retrouvent également dans les conditions humides et peu saisonnières des WG du Sud, suggérant que la niche originale de ces genres comprenait cet habitat. Les forêts du Sud ont pu constituer un centre de diversification secondaire (berceau) comme cela a été suggéré pour *Diospyros* (De Franceschi, 1993), d'où les espèces se diversifièrent par rayonnement adaptatif et occupèrent différentes positions le long des gradients.

## CONCLUSION

Au cours de ce travail, nous avons tenté de comprendre l'impact des processus écologiques, biogéographiques et évolutifs sur la biodiversité actuelle des espèces des WG. Les processus à l'origine de niveau élevé d'endémisme et de biodiversité procèdent d'interactions complexes



entre l'histoire climatique, biogéographique et géologique (Harrison & Noss, 2017). Dans cet optique, la présente étude à tenter d'évaluer l'impact des conditions environnementales actuelles et passées sur les distributions taxonomiques et les patterns de diversité phylogénétiques et reproductives actuelles des espèces.

Les variations climatiques actuelles et passées sont des facteurs clés de la dynamique écologique et évolutive dans le WG. Ils affectent à la fois la répartition des espèces d'arbres dans l'espace (chapitre 1); leur assemblage dans des communautés existantes et dynamique évolutive à long terme (chapitre 2); et le succès adaptatif des stratégies reproductives. Ils ont également pu jouer un rôle dans la diversification de certains clades à prédominance dimorphique de la flore des WG (chapitre 3). Nous avons trouvé des niveaux variables de conservatisme de niche selon les gradients environnementaux et une variation de la structure phylogénétique entre les sous-types de l'habitat « forêt tropicale humide » dans le WG. Nos résultats contredisent l'idée d'une fracture spatio-temporelle local-régionale et suggèrent l'influence de diversifications macro-évolutionnaires sur les patrons contemporains d'assemblage d'espèces dans les WG.

Le présent travail analyse les patrons écologiques le long des gradients environnementaux majeurs sur 8 degrés de latitude, et cherche ainsi à combler le manque d'analyses des patrons régionaux dans les WG. Il s'agit d'une première tentative d'analyses phylogénétiques des assemblages et des traits reproductifs à large échelle. Cependant, nous avons dû nous contenter d'une compréhension partielle des événements biogéographiques et évolutifs à l'origine de la diversité végétale. En effet, c'est bien la pénurie de données qui limite le plus souvent ce type d'étude, en particulier des données fossiles pour estimer les temps de divergence, les données génétiques ou morphologiques pour reconstituer les phylogénies et les données sur les traits fonctionnels. Nous espérons néanmoins que notre étude ouvrira de nouvelles perspectives en proposant des hypothèses de travail qui motiveront une collecte de données ciblée, des tests d'hypothèses et certainement des découvertes sur l'origine et l'avenir de ce point chaud de biodiversité complexe et fascinant.

Dans une étude récente dans *Science*, parmi les zones protégées du globe, les WG ont été classés deuxième en termes de l'« irremplaçabilité » des multiples taxons menacés et première pour ce qui est des amphibiens (Le Saout *et al.*, 2013). Bien que notre étude soit spécifique aux arbres, les conclusions sont transférables aux autres groupes comme les amphibiens vivant en forêt, et d'autres taxons qui dépendent de ces forêts et assurent des fonctions de pollinisation ou de dispersion. Les animaux, en particulier ceux ayant une relation hôte-plante, peuvent suivre les distributions d'espèces végétales (Condamine *et al.*, 2012) et des études menées dans les WG indiquent la persistance des taxons reliques dans les refuges du sud WG (cf. Joshi & Karanth, 2013), ce qui rend la conservation de ces forêts d'autant plus importante.

## GENERAL INTRODUCTION

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The organisation of biodiversity in space and time is determined by a complex mix of ecological and evolutionary processes, and could reflect interacting aspects of climatic, biogeographic as well as geological history (Leibold *et al.*, 2004; Ricklefs, 2007; Harrison & Noss, 2017). Deciphering these entangled influences is key to understanding fundamental questions relating to how species are currently distributed and assembled into communities, and how biodiversity is produced, maintained and shaped through time.

While much attention has been focussed on current ecological processes, recent research points to the importance of evolutionary processes and historical contingency in explaining patterns of biodiversity across spatial scales. For instance, ecological niche modelling or species distribution modelling (SDM) is primarily used to represent the distribution of species at an equilibrium of population occupancy in suitable habitat conditions. Historical theories (Ricklefs, 1987), especially focusing on climate history (Normand *et al.*, 2011; Svenning *et al.*, 2015), show that recent fluctuations of environment can prevent such equilibrium, and contemporary species distributions still represent a legacy of past environments. Geological and evolutionary processes such as vicariant events (e.g. orogenesis, formation of refugial areas during paleoclimatic fluctuations), or variation in rates of diversification and extinction also have long-lasting effects on present-day species distributions and their assemblage into communities (Luebert & Weigend, 2014; Sanín *et al.*, 2016). Synthesizing how long-term evolutionary dynamics in addition to contemporary ecological factors jointly shape the distribution and accumulation of species within regions is an emerging research avenue (Fine, 2015).

Tropical forests are among the most diverse and complex of ecosystems (Gentry, 1992). They provide a variety of environmental services including climate regulation, but are also the most threatened in the face of large scale habitat alteration of climatic and anthropogenic origin (Asner *et al.*, 2009). Understanding the contribution of both evolutionary and environmental signals to observed patterns of species distributions is important for evaluating species potential responses to global changes (Quintero & Wiens, 2013; Jezkova & Wiens, 2016). Conservation strategies increasingly use information on evolutionary relationships to prioritise decisions on individual species or entire regions (Rolland *et al.*, 2012). Evolutionary insight would also allow assessing species vulnerability to contemporary climate change and responses to habitat fragmentation, depending on their ecological strategies and the conservation of these strategies in the course of evolution. However, in hyper-diverse tropical forests, such studies are often hampered by the lack of large-scale floristic sampling and molecular phylogenies that could represent the large number of species present in these areas. Thus, the implications of threats to the conservation of the evolutionary history of many forest communities are not fully known.

This is particularly the case in the forests of the Western Ghats (WG) of India. Along with Sri Lanka, it forms one of the original 25 global biodiversity hotspots (Myers *et al.*, 2000) and is an important centre of plant diversity and endemism (Ramesh & Pascal, 1997). Despite an extensive network of protected areas, it is also one of the eight hottest of these hotspots. Natural forest vegetation currently represents less than 25% of its original area, notably because of the anthropogenic pressure on cultivable lands and the development of commercial plantations and infrastructure (Davidar *et al.*, 2007; Gunawardene *et al.*, 2007). However, studies on ecology and biogeography at large spatial and temporal scales to inform the conservation of these forests are lacking.

The composition of the forests of the WG reflects a long and complex evolutionary and biogeographical history. India travelled to its current position from Gondwana in the far southern hemisphere carrying with it, like Noah's ark, a diverse array of plant and animals. Yet by the beginning of the Cenozoic, many of them had disappeared, with some reportedly being re-established from refugia at the early Paleogene (Datta-Roy & Praveen Karanth, 2009; Prasad *et al.*, 2009; Joshi & Karanth, 2013). Today, we find a reduced number of these ancient rainforest species, mostly confined to forests of southern WG. Who took their place and what routes did they take to disperse here, what histories did their lineages bring with them in turn?

Indeed, as it moved past the equator to its current position, the Indian plate encountered different paleoclimates, and was briefly connected to neighbouring landmasses, which would have had an impact on its vegetation. From the Palaeocene onwards, it experienced relatively wetter conditions and was covered by humid forests. Three factors are involved in the subsequent onset of drier climates in the peninsular region: i) the northward movement of the plate, ii) global Neogene cooling and drying, iii) the uplift of the WG, and after India's collision with Laurasia, the uplift of the Himalayas and establishment of the monsoon regime. This resulted in the isolation of the WG from other persistent wet-zones, with intervening swathes of drier zones unable to support evergreen forests. Within the WG itself, a south to north gradient of seasonality was established.

These environmental changes and the fragmentation of rainforests can be expected to have substantially impacted the migration and diversification of tree species (Gower *et al.*, 2016; Patnaik & Prasad, 2016). This is visible for instance in the south to north variation in species diversity and endemism (Ramesh & Pascal, 1997; Barboni *et al.*, 2003). While there have been no studies pertaining specifically to the diversification of endemics as a result of wet-zone contraction, the observed disjunction in distributions of sister species of certain genera on eastern vs. western versants of the southern WG are suggestive of allopatric speciation in contrasted climatic conditions (Pascal, 1988; Gimaret-Carpentier *et al.*, 2003).

*Influence of past and present environments*

Indeed, climate and its patterns of stability or change over time and space are key to understanding the origins and maintenance of refugia and centres of endemism (Harrison & Noss, 2017) like the WG. The ecological niche is the basis of the species-environment relationship. Species niche attributes allow populations to be maintained depending on local abiotic and biotic conditions. These, along with their ability to access suitable conditions through dispersal, determine the extent and variation of species distributions in space (Hutchinson, 1957; Soberon & Nakamura, 2009). The variation of climatic conditions in time via periodic transitions from warm to cold phases can also modify the spatial extent of habitat suitable to species. Zones of climate stability can serve as refugia or sites to which biota retreat, persist in and potentially expand from (Keppel *et al.*, 2011). Outside of these, the fluctuation in environmental conditions would mean that a species could occupy more or less space according to the suitable habitat available to it. Our first question therefore relates to how present-day patterns might reflect recent environmental variations in time and space. In particular, *did the climatic fluctuations during the Quaternary leave an imprint on contemporary species distributions in the WG? What were the effects of these variations on species with different niche requirements, and those located in areas with more/less stable climatic conditions?*

While recent climatic fluctuations can directly influence biodiversity via ecological limits set by the water–energy balance (Francis & Currie, 2003; Hawkins *et al.*, 2003; Currie *et al.*, 2004), more ancient paleoclimates can also affect evolution and cause biogeographical and macroecological patterns (Dynesius & Jansson, 2000; Kissling *et al.*, 2012; Eiserhardt *et al.*, 2015a). The consequences of both stability and change may have varied for different lineages in the course of geological time, and across space. Historical habitat abundance can be a strong predictor of diversification (Zobel *et al.*, 2011; Jetz & Fine, 2012) and climate variability can impose recolonization limits to particular lineages and cause clade-specific extinctions (Svenning, 2003). Such patterns could affect phylogenetic assemblage structure as they are shaped by dispersal, extinction and/or speciation (Jansson & Dynesius, 2002) which directly affect the number of species in each region.

Species assemblages are constructed and maintained through the arrival of potential colonists from an external regional species pool. The classic filter model (Zobel, 1997) describes a pool of species from which the members of local communities are selected by passing through a succession of filters – of dispersal, environment and biotic interactions – which each represent barriers to the successful establishment of species in local communities. Our second question therefore is: *how is the phylogenetic structure of plant assemblages in the WG influenced by the*

*legacy of adaptations to past climates and current environmental filters? How can we distinguish current filtering vs. evolutionary dynamics based on the phylogenetic diversity of assemblages?*

A combination of species range contractions, extinctions of lineages, and clade-specific diversification in restricted areas caused spatial confinement of unique species, or endemism (Rosauer *et al.*, 2009), often strongly shaped by long-term climate stability (Sandel *et al.*, 2011; Harrison & Noss, 2017). Climate instability and long-term change may also contribute in generating endemism through niche evolution in response to opportunities for speciation offered by novel environments (Särkinen *et al.*, 2012) depauperized by extinctions of species unable to adapt to this change (Wellborn & Langerhans, 2014). According to Jacquemyn *et al.* (2012) altered environmental conditions and habitat fragmentation may (i) reduce population genetic diversity through genetic drift and hamper adaptive responses, for instance, if this lost genetic variation codes for phenotypic variation, or (ii) facilitated by the absence of gene flow, it could drive adaptive changes in plant traits and increase individual plant fitness. This was shown for instance in the emergence of fire-adaptation (Simon *et al.*, 2009) and by Barret *et al.* (2009) for plant mating systems (viz. selfing, outcrossing).

Reproductive traits are key parameters of the fitness of organisms and thus had an important role in influencing the ecological and evolutionary components of plant populations (Charlesworth, 2006). Plant sexual systems (e.g. hermaphrodite, dioecious, monoecious) play a role in diversification and adaptation to new environments. They may be important in reflecting species ecological strategies related to historical disturbances and stressful environments. Our third question concerns the role of sexual systems in environmental filtering and evolutionary dynamics in the WG. *Does the frequency of tree sexual systems vary along gradients of resource limitation related to water availability and historical habitat stability? Is there a difference between endemic and non-endemic species?*

More intensive data on species distributions over large regions, spatially explicit environmental data, paleoclimatic predictions and methodological advances together allow characterizing biodiversity patterns over a broad range of spatial and evolutionary scales. Advances in species distribution modelling have led to studies examining various aspects of species distributions, including historical limits of distributions and past habitat dynamics. For e.g. SDMs calibrated from both past and current species occurrences have been proposed to gain insights into biogeographical processes such as range contraction and expansion related to past conditions (Svenning *et al.*, 2011). Secondly, the incorporation of evolution and historical contingency into the ecological research agenda has been favoured by the increasing availability of phylogenetic information and the development of community phylogenetics and formed the basis for the discipline of Ecophylogenetics, an emerging fusion of ecology, biogeography and macroevolution

(Webb *et al.*, 2002; Mouquet *et al.*, 2012). Information on the evolutionary relatedness among species can be used decipher ecological assembly processes (Webb *et al.*, 2002) and, this information may be applied to identify macroevolutionary particularities of habitats, their associated lineage-pools and hence the communities sampled from these pools (Gerhold *et al.*, 2015). Lastly, the emerging field of phyoclimatic modelling, combines SDM and phylogenetic analyses to investigate for e.g. the heritability of climatic preferences and reconstruct ancestral niches (Yesson & Culham, 2006; Heibl & Calenge, 2013).

Natural environmental gradients provide opportunities to discover possible links between different aspects of biodiversity (taxonomic, phylogenetic and trait) and the heterogeneity of environmental conditions in both space and time. Being one of the few examples of a belt of tropical evergreen forests spread over 10 degrees of latitude outside of the equatorial zone, characterised by strong bioclimatic gradients that are heterogeneous in space and time, with high rates of endemism (Ramesh & Pascal, 1997) and dioecy (Krishnan & Ramesh, 2005), the WG provides an good setting for investigating broad-scale patterns. In the present work, I propose to address the following three research questions with regard to the impact of ecological, biogeographical and evolutionary processes on current biodiversity in the WG:

- 1) Whether and how Quaternary climatic changes affected the habitats that support tree species in this biodiversity hotspot, and how this influenced the extant distribution of endemic species**
- 2) How current and past environmental conditions influenced current patterns of phylogenetic diversity in tropical tree assemblages, depending on constraints exerted on ecological strategies over time and the conservation of these strategies in the course of evolution**
- 3) Whether and how the variation along gradients of stress and resource limitation related to water availability and historical habitat stability influences the frequency of tree mating systems**

#### *Organisation of the thesis*

This thesis is organized in two parts. In the first section of Part I, I begin by outlining a few concepts as a background to some of the issues examined; I go on to develop the relevance of addressing our research questions at the regional scale and methods we propose to employ, culminating with a laying out of the main hypotheses and expectations that will be explored in subsequent chapters. The second section of Part I comprises an overview of salient characteristics of the WG relevant to this work and a presentation of the climatic and floristic data used in this thesis. This includes results of preliminary analyses on which the articles that follow are based.

Part II consists of the manuscripts of the three articles which form the core of this work, followed by a general discussion.

## A. BACKGROUND: HISTORICAL PERSPECTIVE

The two disciplines of ecology and biogeography represent recently imbricating ends of a spatiotemporal gradient within which this thesis is situated. As this touches on issues and concepts that provide the theoretical context to the present work, I first present the divide that existed between ecology and biogeography and the need for, and recent push to integrate them in order to refine our view of how contemporary and historical processes both govern the distribution of biodiversity. Bridges in terms of concepts and analytical approaches exist and those that I propose to employ in the present work will be the subject of next section.

### 1. ECOLOGY AND BIOGEOGRAPHY: 'DUEL' VIEWS

Biological systems are characterized by (i) *general properties* arising from universal processes with usually deterministic outcomes and (ii) *special properties* reflecting the unique history and current circumstances of every species and location (Ricklefs, 2006). Ecologists have traditionally been concerned with the former, while the latter forms the foundation of fields such as biogeography. High rates of diversification in a biodiversity hotspot, driven by certain ecological conditions such as temperature, would be a general process; whereas if it depended instead on unique geomorphology, it is a special process. The extensive extinction of flora and fauna in India triggered by flood basalt outpourings of the late Cretaceous volcanism (Samant & Mohabey, 2009; Schoene *et al.*, 2014) is an example of a special process; as is the more recent pauperisation of European tree flora as a result of differential extinction of species of tropical and subtropical lineages due to the Quaternary glacial cycles (Svenning, 2003).

In general terms, ecology and biogeography, while having common roots, have for historical reasons come to focus on different spatial (local to regional vs. regional to global) and temporal (geologically instantaneous vs. centuries to aeons) scales. While the one focussed on the composition and functioning of ecological communities using ideas of population processes, and abiotic conditions and species interactions to explain coexistence of species in local areas, the other addresses evolutionary, climatic and geological processes to reconstruct the history of areas and their biotas (Chiarucci *et al.*, 2011; Jenkins & Ricklefs, 2011; Peterson *et al.*, 2011).

### *Scope for integration*

The two disciplines have much to offer to each other, as highlighted by Wiens and Donoghue (2004) and others, and an integration within a common analytical framework would help to resolve enmeshed and interactive effects of both ecological and evolutionary processes affecting observed patterns (Ricklefs, 2007). Whether past or present conditions, evolutionary history or current environment, best explain large-scale diversity gradients has been hotly debated over the years on either side of the intellectual divide (see summary in Hawkins *et al.*, 2011). Typical



ecological explanations focused on the strong correlations between species richness and environmental predictors (e.g. Francis & Currie, 1998; Francis & Currie, 2003; Hawkins *et al.*, 2003). Ricklefs (1987) and others pointed out however that correlation is not causation, and environmental variables cannot increase or decrease local or regional diversity: only processes such as dispersal, speciation or extinction can. Ecologically mediated selection has since been recognised as an important driver of speciation ('ecological speciation', Schluter, 2001); and for populations undergoing reproductive isolation (allopatric, parapatric or sympatric), some isolation mechanisms can be directly linked to ecology (Mittelbach *et al.*, 2007). In fact interactions are bidirectional; ecology and climate are important, but they must act on these evolutionary and biogeographical processes to determine patterns of species diversity, especially at larger scales (Wiens *et al.*, 2007).

Views regarding large-scale top-down vs. bottom-up scaling can be contrasted; in the first case "static" regional pools resulting from long-term dynamics determine local dynamics; in the second case, local ecological dynamics cumulate to give rise to emergent properties at regional scale (Chave, 2013). The hierarchical relationship between regional and local diversity (Ricklefs, 1987; Webb *et al.*, 2002; Ricklefs, 2004) is a fundamental insight of recent years. Local process-based hypotheses were based on the idea of species saturation in sites due to competition for limited resources, limited niche space and limiting similarity. In other words, ecological interactions in local assemblages may constrain the number of species that can coexist. On the other hand, differences in diversity of similar habitats in different regions ('diversity anomalies', Qian & Ricklefs, 2000) suggested that this limit is not fixed. Observations that local sites do not appear to be saturated (Ricklefs, 1987; Stohlgren *et al.*, 2008), which continue to be confirmed (e.g. Pinto-Sánchez *et al.*, 2014), then led to the alternative explanation that local species diversity is limited by the availability of species that could colonize a site from a regional pool of species (Harrison & Cornell, 2008). Therefore, the composition of local-scale communities should depend on the regional species pool, the composition of which depends on large-scale biogeographic processes (Webb *et al.*, 2002). The observation that a species does not occur in all regions where its suitable habitat is available, could mean that it is not only habitat that determines its distribution. Patterns of biodiversity within and among local communities are thus expected to depend on influences of evolutionary and/or biogeographical history, dispersal limitation and colonization dynamics at regional scales (White & Hurlbert, 2010).

Biogeographers tended to neglect the influence of assembly rules at local scales, and ecologists often tended to ignore biogeography (Wiens, 2011). In community ecology, the composition of local-scale communities was long seen as being disconnected from regional effects since the species pool was considered to be static at time scales over which ecological communities were

established (Emerson *et al.*, 2011), ignoring the dynamic nature of the species pool, and not recognizing that processes operating over a range of spatiotemporal scales are involved in community assembly (Mittelbach & Schemske, 2015). Patterns studied by ecologists may originate through processes that historical biogeographers focus on and vice versa (Stephens & Wiens, 2009), making the dichotomy between historical and ecological explanations artificial according to Wiens and Donoghue (2004).

### *Spatiotemporal convergence*

The convergence on common topics and spatiotemporal scales relevant to both ecology and biogeography in recent years has been aided by the opportunities provided by shared technologies and analytical approaches. This was partly pushed by perceived threats to biodiversity in the context of climate change which created interest in making observations and predictions at larger scales. Ecology witnessed a shift towards spatial and temporal scales beyond local habitats, an outcome of a paradigm shift away from locally based equilibrium viewpoints towards a dynamic mixture of local and regional mechanisms as drivers of species distributions (Jenkins & Ricklefs, 2011). Recent years have seen the emergence of more regional perspectives with the development of disciplines like macroecology (Brown, 1995) and landscape ecology, and concepts of metapopulations and metacommunities (Leibold *et al.*, 2004). These depict local and regional scales as interdependent through frequent dispersal among localities and source-sink dynamics (Pulliam, 2000), especially in relation to expansion and contraction of species ranges during climate fluctuations (e.g. Taberlet & Cheddadi, 2002), providing a mesoscale bridge between ecology and biogeography (Jenkins & Ricklefs, 2011).

Regional scales correspond to intermediate timescales relevant to both (Chiarucci *et al.*, 2011): patterns at this scale reflect balance between regional processes of species production, extinction and dispersal and within-region species sorting according to adaptations to environmental conditions and competition (Ricklefs & He, 2016). To return to the idea of 'diversity anomalies' (i.e. differences in diversity in similar habitats located distinct regions), local processes cannot fully explain biodiversity patterns in different regions having similar environments (Latham & Ricklefs, 1993) and the potential effects of regional processes and species pools (Wang *et al.*, 2012; Ricklefs & He, 2016) is now increasingly recognised.

In the context of contemporary changes of anthropogenic or climatic origin and subsequent threats to biodiversity (Newbold *et al.*, 2015), the importance of striking a balance between ecology and biogeography to understand and predict the effects of habitat fragmentation due to local land-use and global processes has created a fertile scientific ground. An increasing number of studies now incorporate the joint influence of historical, evolutionary and biogeographic

factors in addition to contemporary and local climates (e.g. Svenning & Skov, 2005; Sandel *et al.*, 2011; Svenning *et al.*, 2015).

Biogeography and community ecology are increasingly integrated into a cross-disciplinary framework for understanding the distribution of diversity. A central concept underpinning this framework is the species ecological niche (Chase & Leibold, 2003; Wiens & Graham, 2005) and its evolutionary dynamics, which will be the subject of the next section.

## 2. ECOLOGICAL NICHE, EVOLUTIONARY DYNAMICS

From its foundations early in the last century (Grinnell, 1917; Elton, 1927) and its decline in the 70's and early 80's after having become too closely aligned with competition (Wiens *et al.*, 2009), the niche concept has since been resurrected as its potential relevance to predicting ecological responses to global climate change and biodiversity loss has become apparent (Holt, 2009). Specifically, seeking detailed answers to the questions of how species distributions change through time and how species evolve in different habitats in this context provoked a renewed interest in the ecological niche (Soberón, 2007; Schoener, 2009).

Hutchinson (1957) defined the ecological niche of a species as a part of a multi-dimensional environmental hyperspace in which the species can potentially survive and maintain a positive rate of population growth. Hutchinson distinguished the realised niche from the fundamental niche, of which it is a subset to which a species is constrained by dispersal and interactions with other species (Wiens *et al.*, 2009). The ecological niche of a species determines its responses to environmental conditions, and hence its distribution in space and time. There is widespread support for the idea that (i) abiotic constraints on species establishment and survival (fundamental niche) limit species distributions, and (ii) positive and negative interactions with other species (realised niche) further restrict population occurrences within these limits (Soberon & Nakamura, 2009).

While ecological niches influence the distribution limits of species, these aggregated limits create biogeographic patterns of biodiversity. A species cannot spread beyond its specific ecological niche which defines habitats suitable to it; in this context geographic barriers like mountains, rivers or oceans are unsuitable habitats and what is considered unsuitable is organism-specific (Wiens, 2011). Distribution limits are not only set by unsuitable abiotic or biotic conditions at the margins of distributions (Louthan *et al.*, 2015) but (iii) limitation in dispersal and colonisation abilities restricting species spatial occupancy (Soberón, 2007) or metapopulation dynamics (Holt & Keitt, 2000), (iv) historical pathways of contraction and expansion related to past conditions and incomplete remigration also influence species distributions and hence biogeographic patterns (Normand *et al.*, 2011). Lastly species distribution limits are also shaped by (v) the

failure to adapt unsuitable conditions encountered, which would otherwise allow them to continue expanding (Wiens, 2011).

#### *Evolutionary heritage of the niche*

A species niche is determined by traits that allow it to acquire resources, evade enemies and other factors that influences its survival (Chase & Leibold, 2003). Species' traits are shaped by the process of evolution. As the niche depends on traits, it must also depend on evolution. However, species traits and thus their ecological niche, depend not only on convergent adaptations of species to their current and past habitats but also on the legacy of species' ancestors (Prinzing *et al.*, 2001). Evolutionary heritage reflects how lineages can retain the ecological characters of their ancestors over millions of years (niche conservatism, Wiens & Graham, 2005).

Niche conservatism is implied in tracking of suitable climates in periods of environmental change (Ackerly, 2003). In this regard, rather than its ability to evolve and thus adapt to new biomes, the evolutionary success of plants may be partly due to the expansion of biomes as climates changed (Crisp *et al.*, 2009). This also implies a failure of species to adapt to changing environmental conditions or expand to new habitats (Wiens *et al.*, 2010), affecting evolutionary dynamics. The niche thus represents the interface between ecological and evolutionary processes that shape a species distribution.

The concept of niche conservatism, in the sense that it may be "easier to move than to evolve" (Donoghue, 2008), offers a bridge between evolutionary and biogeographic processes by accounting for evolutionary heritage (Wiens & Graham, 2005). Phylogenetic niche conservatism (PNC, Harvey & Pagel, 1991) is an evolutionary pattern according to which descendant species tend to share, by common descent, a substantial proportion of the biological and physiological characteristics that determine their fundamental ecological niches (Rangel *et al.*, 2007). It follows that descendant species tend to retain the adaptations of a common ancestor to the particular environmental conditions of its origin, with little adaptive modification.

Qian and Ricklefs (2004) made the proposition that climate influences diversity through the tropical origin of angiosperms and evolution of freezing tolerance. The tropical conservatism hypothesis (TCH) posits that many clades originated in the warm and wet tropics, which historically covered a larger geographic area and experienced greater environmental stability than extra-tropical climates; and that dispersal and diversification into cold and dry climatic regions have been both recent and evolutionarily challenging (Wiens & Donoghue, 2004; Zanne *et al.*, 2014). As such, clades will be richer in climates that are most similar to where they originated. This is because PNC would limit the number of subclades that can move into new environments, and because they have had more time to speciate (Stephens & Wiens, 2009) and a

higher net diversification rate in the tropics (Ricklefs, 1987; Donoghue, 2008). This would result in the tropics being both the 'cradle' and 'museum' of species diversity (Jablonski *et al.*, 2006). As pointed out by Wiens and Graham (2005) the TCH reconciles both ecological (e.g. high richness associated with high temperatures and rainfall) and evolutionary (this pattern is linked to processes like dispersal and speciation that directly affect the number of species in each region) perspectives.

In this regard, climate plays a crucial role in species distribution dynamics at multiple scales. When climatic conditions change, according to Jackson and Overpeck (2000) species must either maintain a sufficiently broad fundamental niche or be capable of evolutionary changes that are wide and rapid enough to adapt to the new environmental space. If not, species can escape extinction by migrating and tracking suitable habitat through space, or persisting in isolated pockets or "refugia" of still suitable environment (Holt, 1990). The lability of the climatic niche in the context of global change is of fundamental importance as it influences the need for species to track climate change in geographical space (range shift) or take recourse to adaptive evolution to rescue them (niche shift). The latter situation refers to a change in niche-related traits during or following speciation events, allowing descendants to adapt to novel environmental conditions (Rangel *et al.*, 2007). The interplay between processes leading to niche conservatism or not thus has an impact on large scale patterns of species distributions and their historical biogeography (Wiens & Donoghue, 2004).

#### *Multidimensional, dynamic niche*

Species are predicted to track environmental factors for which they exhibit narrow tolerances, and have an evolutionary adaptive response along the niche axis for which they exhibit greater niche breadth (Ackerly, 2003). Holt's (1990) reformulation of Hutchinson's niche is the mapping of population dynamics onto a multidimensional abstract space, defined by environmental axes that affect an organism's fitness. This allows for a representation of the niche as a dynamic space, within which change or stasis can occur along different axes. Selective pressure along a particular axis can lead to evolutionary responses to the environment in the course of time. Silvertown *et al.* (2006) proposed that traits related to habitat preferences (beta niche traits) may be more phylogenetically conserved than those involved in local co-existence within communities (alpha niche traits), i.e. whether traits and thus niches are evolutionary labile or conserved may be scale-dependent. Thus, one or the other niche axis in a multidimensional niche space may have different breadths (e.g. Gómez-Rodríguez *et al.*, 2014) and levels of conservatism and lability (e.g. Losos *et al.*, 2003; Hu *et al.*, 2015) and this could vary with scale.

## B. BACKGROUND: THE REGIONAL SCALE

In this section, I highlight the relevance of the regional scale for formulating hypotheses and addressing our research questions which deal with broad-scale gradients in the WG, followed by an outline of methods we propose to employ for doing this.

### 1. MEETING IN THE MIDDLE

Bioregions, defined as biomes within continents or realms (Jetz & Fine, 2012; Fine, 2015) are a useful construct, as they could help reconcile ecological and evolutionary perspectives at the regional scale. Such bioregions are "delineated by biologically meaningful boundaries that correspond with the physiological and biotically enforced thresholds that enforce concordant geographic range limits for regional species assemblages" (Fine, 2015), and these boundaries result from processes affecting dispersal, survival, or gene flow (Donoghue & Edwards, 2014).

The eco-region or bioregion is interesting because it captures the entire gradient of abiotic variation within a region, and taxa within it share a common biogeographic history. Bioregions could also include relatively high degrees of environmental heterogeneity and be under "geomorphographic control" (Guitet *et al.*, 2015). Mountainous regions are often hotspots of biodiversity given their topographical complexity (Dobrowski, 2011; Graham *et al.*, 2014), and regions that have experienced orogeneis also present more opportunities to promote speciation given their diversity of habitats and natural barriers. For instance, in the Andes it is now being recognised that the timing of diversification of many montane and lowland lineages coincided with the uplift of these mountains (Luebert & Weigend, 2014; Sanín *et al.*, 2016).

It is common to find gradients in diversity at the regional scale, and hypotheses that explain the contemporary large-scale/global latitudinal diversity gradients involving drivers such as abiotic gradients, biotic interactions, resource availability and climate stability could also be relevant to bioregions. For instance many variables relating to temperature change in similar ways along both the elevation (Sanders *et al.*, 2007) and latitudinal gradients (Mittelbach *et al.*, 2007). A regional elevation gradient may present advantages over the latitudinal one since the temperature gradient is much steeper - an increase of 100m in elevation being comparable to a poleward shift of 100km in temperate zones (Jump *et al.*, 2009). Orographic rainfall could have a similar effect. Regional elevation gradients thus provide higher variation in climate within dispersal distances of many species than do latitudinal gradients (Graham *et al.*, 2014) making them ideal for studying the role of temperature and other gradients such as orographic rainfall as an environmental filter structuring species assemblages (e.g. Qian *et al.*, 2014). Lastly, apart from being more manageable in terms of scale compared to global gradients, a region would also present a more limited species pool that is the source of locally co-existing species, whereas larger

scale or global latitudinal gradients could include sites with species from numerous distinct species pools and evolutionary histories making it more difficult to disentangle ecological and evolutionary factors at play (Graham *et al.*, 2014).

#### *Phylogenetic diversity and past and present environmental dynamics*

The environmental axes that define a species ecological niche can be used to envision a gradient of these factors at the regional scale (Chase & Leibold, 2003). The hypothesis of PNC predicts an increasing trend of phylogenetic relatedness among species within assemblages along a latitudinal stress gradient from the equator to the poles, with closely-related species co-occurring at higher more stressful latitudes (Qian *et al.*, 2013). Such phylogenetic diversity patterns are best studied across space as a function of broad environmental gradients as they can include a range of conditions along a continuous spatial scale (Graham & Fine, 2008) potentially with different areas in the region displaying relatively greater influence of environmental filtering or biotic filtering due to species interactions like competition. In this context, stress gradient hypothesis (Weiher & Keddy, 1995) predicts a shift in the relative importance of environmental filtering and competition along a gradient of abiotic stress related to moisture, temperature or resource availability.

In addition, different environmental gradients present in a bioregion could display a variation in niche conservatism among extant species, possibly reflecting the environmental opportunities of their ancestors during diversification. Prinzing *et al.* (2001) proposed that environmental changes between geological epochs may explain this variation, as different environmental gradients dominated the plants' environment during different epochs. In a similar vein, recent work has shown that the evolutionary heritage of a lineage depends on the abiotic conditions of the epoch in which a lineage diversified, since present-day climatic conditions control the diversity of lineages dating back to a given geological epoch (Bartish *et al.*, 2016).

The tropical conservatism hypothesis (Wiens & Donoghue, 2004) and time-integrated area hypothesis (Fine & Ree, 2006) also involve historical factors. For instance, differences in ages and sizes of areas could promote greater opportunities or not for speciation, leading to the idea that tropical zones are more diverse than temperate ones as they covered larger areas over the past 100 My resulting in longer time to speciate and spread. This idea can also be translated to the regional scale as there could be habitat types in a region that were once widespread but subsequently contracted as a result of global climatic changes (e.g. Neogene aridification, Patnaik & Prasad, 2016), or tectonic events changing regional climate systems (e.g. Himalayan orogeny and the onset of the Indian monsoon, Patnaik *et al.*, 2012). This would have led to habitat types within regions that are more or less ancient and covered more or less large areas in the geological past.

Local diversity patterns are also dependent on the size of available species pools, which are expected to be large when the particular habitat type has been evolutionary more abundant (Zobel *et al.*, 2011). For instance, Bartish *et al.* (2016) found that lineages associated with different habitat types differ in their evolutionary histories, with communities in wet habitats disproportionately including lineages from wet epochs and similar for dry, warm or cold habitats. The age of different habitat types would have an impact on the lineages pools, with the result that phylogenetic dispersion may be much higher in local communities of evolutionary older habitat types than in younger ones (Gerhold *et al.*, 2015). Certain communities may thus function as museums harbouring a diversity of particular and ancient clades. Further, wet habitats appear to function as museums containing older lineages and dry habitats as cradles containing younger ones, although a habitat could be both a museum and a cradle, containing both older and younger lineages (Bartish *et al.*, 2016).

#### *Historical habitat or climate stability gradients*

Zones of climate stability can serve as refugia or sites to which biota retreat, persist in and potentially expand from under changing environmental conditions (Keppel *et al.*, 2011).

According to the historical climate stability hypothesis, given ecological tolerances and their conservation over time, species are differentially excluded from areas experiencing greater historical climate fluctuation, while climate stability enhances persistence and ecological diversification over geological time-scales (Jablonski *et al.*, 2006; Svenning *et al.*, 2015).

Historically stable climatic zones could constitute both 'museums' where older lineages persist through evolutionary time (paleoendemism), and 'cradles' where new species continue to be generated (neoendemism) (Fjeldsa° & Lovett, 1997; Verboom *et al.*, 2009).

Past climate fluctuations have continuously modified the spatial habitat suitable to species (Bush *et al.*, 2011). The intensity of climatic changes may vary in space at global scales (viz. Quaternary glaciations affected temperate zones more than tropical ones in the recent past) as well as within regions. This would create a gradient of historical climate stability, another important driver of the latitudinal diversity gradient which can be mirrored at the regional level. The influence of both climate stability and change may have varied for different lineages, in the course of geological time, and across space.

While early emphasis was put on Quaternary refugia (Hewitt, 2000; Jansson, 2003), in zones that were protected from the effects of earlier climatic cycles such as post-Eocene cooling and Neogene aridification, refugia with high levels of paleoendemism have since been identified (e.g. Linder, 2008). They are especially present in the tropics that were less affected by glacial cycles. Neo-endemism can be linked to stable historical climates in association with factors such as insularity or geographical isolation and topographical heterogeneity that could have provoked



species to differentiate and ultimately diversify (Jetz *et al.*, 2004). The incidence of habitat specialization should be more common in climatically stable tropical bioregions, leading to greater frequency of parapatric and sympatric speciation (Moritz *et al.*, 2000; Beheregaray *et al.*, 2015). On the other hand, climate instability and long-term change may also have generated new species through niche evolution (Wellborn & Langerhans, 2014). If niche conservatism is stronger than niche evolution, this could also lead to diversification. A fluctuating environment could create shifting patterns of fragmentation of a species suitable habitat, as it fails to adapt in some portions of its initial distribution. Populations that are thus isolated geographically undergo reproductive isolation in time to create new species through allopatric speciation (Kozak & Wiens, 2006).

## 2. BRIDGING THE GAP: METHODOLOGICAL APPROACHES

More intensive data on species distributions over large regions, spatially explicit environmental data, paleoclimatic predictions and more comprehensive molecular phylogenies, together allow characterizing biodiversity patterns over a broad range of spatial and evolutionary scales. Here, I focus on two approaches that I propose to employ in subsequent chapters: species distribution modelling based on both past and present environmental conditions, and ecophylogenetics.

Niche-based dynamics influence species distributions given both evolutionary dynamics and current environment, and the associated theories provide expected patterns at the equilibrium of these dynamics. Advances in SDM have led to studies examining various aspects of species distributions (e.g. interaction of biotic factors and processes in SDM, Morin *et al.*, 2007; Godsoe & Harmon, 2012; Wisz *et al.*, 2012), including historical limits of these distributions. Recently, an alternative has been proposed for gaining insights into biogeographical processes underlying current species distributions (Nogués-Bravo, 2009; Varela *et al.*, 2009; Graham *et al.*, 2010; Keppel *et al.*, 2011; Svenning *et al.*, 2011). This approach compares current (based on present climates) and past (based on paleo-climates) species niches and discusses how the distributions of different species could overlap in the past versus in the present. Linkages between spatial distributions and the macroecology of a species offers the possibility of inferring the main ecological and historical factors that shape such distributions (Fattorini, 2013).

That paleoclimate-based modelling can generate predictions about stable or unstable areas in a biodiverse region with complex topography and steep environmental gradients, was shown in the case of the Australian Wet Tropics (Hugall *et al.*, 2002) and in Brazil (Carnaval & Moritz, 2008). SDM reconstructions of refugia during the Last Glacial Maximum (LGM) were found to be a useful complement to palaeoecological (Alba-Sánchez *et al.*, 2010; Svenning *et al.*, 2011), and molecular (Waltari *et al.*, 2007; Poncet *et al.*, 2013) studies. The approach has been validated in

the tropics through pollen records and in congruence with phylogeographical data (Hugall *et al.*, 2002; Carnaval & Moritz, 2008).

A contributing factor to the basic separation of ecology and biogeography may have been the paucity of analytical approaches that bridge the gap between large-scale/ long-term patterns that concern historical biogeography and the shorter-term/ local-scale processes that were the focus of for instance community ecology (Stephens & Wiens, 2009). Analysing the phylogenetic structure of species assemblages adds the temporal dimension needed to address the influence of evolutionary and biogeographic dynamics in addition to contemporary factors. The latter hypothesized that community structure should vary depending on both the ecological mechanisms (e.g. competitive exclusion, environmental filtering) and the distribution of species characteristics within the phylogeny (evolutionary history),

#### *Phylogeny as proxy for niche traits*

In plant community ecology, the focus has been on species characteristics such as adaptive species traits that would determine the impact of these filters on the fate of a species. Mechanisms contributing to community assembly were inferred from observed patterns of species occurrences, i.e. similarities and differences of co-occurring species. However, which traits predominate to determine a species niche is not always well known, and species traits are rarely known for all species, especially in the tropics. In many plant groups, close relatives tend to share similar phenotypic traits due to niche conservatism (Wiens & Graham, 2005). Thus closely related species are expected to be ecologically more similar than distantly related ones they share a common evolutionary history (Freckleton & Jetz, 2009). Thus, patterns of phylogenetic relatedness within a community can also be used to make inferences about community assembly mechanisms.

The increasing availability of phylogenetic data and computing tools lead to the widespread integration of phylogenetic information as a proxy for difficult to measure traits. According to the ‘phylogeny as proxy’ model, assuming that niche traits are conserved, a) abiotic assembly results in the co-occurrence of closely related species or “phylogenetic clustering” implies habitat filtering, and b) biotic assembly results in the co-occurrence of distantly related species or “phylogenetic overdispersion” which implies competitive exclusion (Webb *et al.*, 2002). However, the rapid increase in the use of observed phylogenetic patterns as proxies of the process of community assembly has also lead to an increase in critiques (Mayfield & Levine, 2010; Pavoine *et al.*, 2013) regarding for instance the spatial and temporal scale dependency of phylogenetic patterns (Cavender-Bares *et al.*, 2006) or lack of congruence between phylogenetic and trait dispersion measures (Pavoine & Bonsall, 2011).

Indeed, similar traits in related or unrelated/distantly related species can also arise from living in and adaptation to similar climatic conditions (convergence, Freckleton & Jetz, 2009). If species niches are not phylogenetically conserved, the basic expectations above may be challenged. We may find for e.g. overdispersion under more stressful conditions through convergent evolution in distantly-related species due to a stronger signal of adaptation to the environment and low phylogenetic conservatism (Cavender-Bares *et al.*, 2004). Different levels of niche conservatism may be expected in areas with different environmental conditions (e.g. Khaliq *et al.*, 2015).

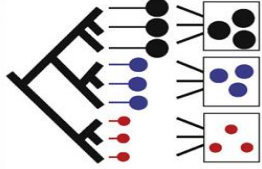
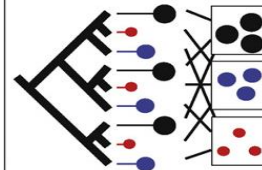
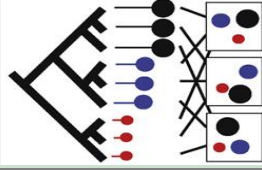
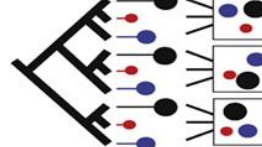
Paleoclimatic changes can also leave a long-term impact on phylogenetic diversity and clustering patterns (Kissling *et al.*, 2012; Eiserhardt *et al.*, 2015b). Local diversity patterns are also dependent on the size of available species pools, which are expected to be large when the particular habitat type has been evolutionary more abundant (Zobel *et al.*, 2011). A recent critique by Gerhold *et al.* (2015) thus suggests that rather than being simply proxies of community assembly mechanisms, phylogenetic patterns could provide underappreciated information. Importantly, the diversification and adaptation of lineages in the past, which would be different for different lineages, are also expected to be reflected in the changing phylogenetic composition with changing environments (Gerhold *et al.*, 2015). The phylogeny could thus be used to address other, perhaps more interesting questions and provide insight into the evolutionary component of ecological processes like environmental filtering. For instance, Bartish *et al.* (2016) found that lineages associated with different habitat types differ in their evolutionary histories, with communities in wet habitats disproportionately including lineages from wet epochs and similar for dry, warm or cold habitats. The age of different habitat types would have an impact on the lineages pools, with the result that phylogenetic dispersion may be much higher in local communities of evolutionary older habitat types than in younger ones (Gerhold *et al.*, 2015).

Rather than a simplistic phylogenetic clustering = habitat filtering and phylogenetic overdispersion = competition therefore, it is important to explore alternative explanations and examine different timescales of evolutionary and ecological dynamics (Mazel *et al.*, 2015). Eight possible scenarios and many possible processes and interpretations can be envisaged based on 1) ecological scenarios i.e. abiotic or biotic filters, 2) niche conservatism vs niche convergence, and finally, 3) timing or phylogenetic depth i.e. ancient vs. recent evolutionary dynamics (see table 1)

With the aid of phylogenies, niche modelling has also recently been incorporated into evolutionary and ecological studies to gain insight into processes such as niche diversification, mechanisms of speciation and ecological evolution. The trend of integrating both historical and ecological inferences has led to the emerging field of phyloclimatic modelling, which combines

SDM and phylogenetic analyses to investigate for instance. the heritability of climatic preferences and reconstruct ancestral niches (Yesson & Culham, 2006; Heibl & Calenge, 2013).

**Table 1 Hypotheses on species assembly and eight associated scenarios**

Hypothesis on community assembly	ANCIENT evolutionary dynamics & phylogenetic pattern in DEEP NODES	Congruence between species niches and phylogenetic relatedness	RECENT evolutionary dynamics & phylogenetic pattern in TERMINAL NODES
Harsher abiotic environment filters species with similar niches (EF)	Phylogenetic <b>CLUSTERING</b> 	Niches are <b>conserved</b> Ecological niches of co-occurring closely related species are similar	Clustering Overdispersion
	Phylogenetic <b>OVERDISPERSION</b> 	Niches are <b>convergent</b> niches of co-occurring distantly related species are similar	Clustering Overdispersion
Biotic interactions filter species with dissimilar niches (BF)	Phylogenetic <b>OVERDISPERSION</b> 	Niches are <b>conserved</b> niches of co-occurring distantly related species are dissimilar	Clustering (recent radiation) Overdispersion
	Phylogenetic <b>CLUSTERING</b> 	Niches are <b>divergent</b> Niches of closely related species are dissimilar	Clustering (recent radiation) Overdispersion

### 3. HYPOTHESES AND EXPECTATIONS

With the basic objective of characterizing the role of past and present environmental conditions on the distribution and diversification of WG tree species, we integrated tree species distribution models under past and present bioclimatic conditions and an analysis of phylogenetic and reproductive trait variation across regional gradients. The hypotheses and expectations associated with our research questions specified previously are outlined below and were separately addressed in the three articles listed.

In **Chapter 1** we evaluated the possible influence of Quaternary climatic variations on the distribution of endemic species. We hypothesised that climate-induced habitat dynamics plays a role in species' distributional change (Normand *et al.*, 2011; Svenning *et al.*, 2015), and ecological niche specialisation would affect species-specific responses to this (Graham *et al.*, 1996; Moussalli *et al.*, 2009). We expected that there would be pressure for a shift in either ecological (niche shift) or geographical (range shift) space in the case of a mismatch between climatic conditions in the Quaternary and species' current habitat preferences, and local persistence in the case of broad overlap between predicted models of species' distributions over these three periods.

**Bose, R., Munoz, F., Ramesh, B. R. & Pélissier, R. (2016) Past potential habitats shed light on the biogeography of endemic tree species of the Western Ghats biodiversity hotspot, South India, *Journal of Biogeography* 43, 899:910**

In **Chapter 2** we investigated the phylogenetic structure of tree communities to characterize the legacy of past adaptations and the signatures of current environmental filters along gradients. For this we tested the stress gradient (Weiher & Keddy, 1995) and historical stability (Jablonski *et al.*, 2006; Kissling *et al.*, 2012) hypotheses to study the role of the variability of seasonal water availability and historical habitat stability on extant patterns of phylogenetic dispersion within and between communities. According to these hypotheses, we expected phylogenetic clustering in both currently harsher environments and in areas with historically less stable climates, and overdispersion in opposite conditions. Under environmental filtering along broad-scale gradients we expected high turnover in phylogenetic composition, reflecting a change of lineages adapted to different environmental conditions.

**Bose, R., Ramesh, B. R., Pélissier, R. & Munoz, F. (*in prep.*) Phylogenetic diversity in the Western Ghats biodiversity hotspot reflects environmental filtering and past niche diversification of trees.**

Finally, in **Chapter 3**, with the objective of understanding in what conditions separation of sexes (dioecy) has been selected for in the course of evolution and in extant ecosystems, we addressed whether and how the variation of abiotic stress and resource limitation related to

water availability and historical habitat stability influences the frequency of mating systems along these gradients. We explored two non-exclusive hypotheses focussed on the particular case of dioecious species: 1) the frequency of dioecious species in WG rainforests reflects current environmental filtering, and 2) dioecious species underwent preferential diversification in the WG related to past environmental conditions. Accordingly, under the first scenario, we expected a significant and positive relationship between dioecy and environmental stress, and no difference in patterns for endemic and non-endemic dioecious species. In the second, dioecious endemic and non-endemic species should display differential patterns, due to specific diversification events having influenced the emergence of new dioecious taxa in the area.

**Bose, R., Munoz, F., Ramesh, B. R. & Pélissier, R. (*in prep.*) Role of dioecy in the ecological and evolutionary dynamics of trees in the Western Ghats biodiversity hotspot: a legacy of aridification?**

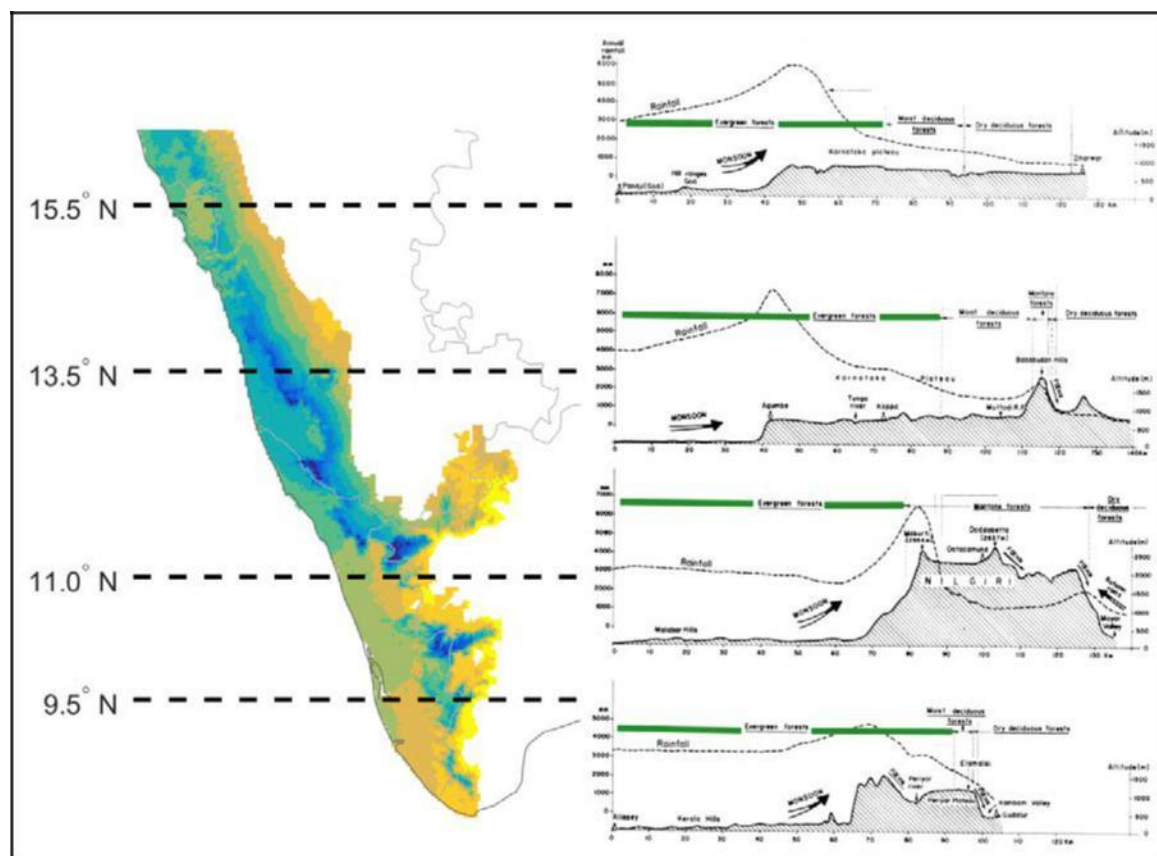
In general, the basic underlying hypotheses are common to all, viz. the historical climate stability hypothesis, and the stress gradient hypothesis, specifically the abiotic stress gradient related to water and resource availability. Our formulation of these hypotheses was based on the potentially key role of environmental gradients in the organisation of WG biota that is indicated in the literature, which also points to important climatic changes that mark the biogeographic history of this region. An overview of salient characteristics of the WG relevant to this work and on which our hypotheses are founded will be the subject of the following section.

## MATERIAL AND METHODS

The aim of this section is to highlight characteristics of the study region, the Western Ghats of India (WG) that point to the key role of climate both present and past in this region. It is followed by a presentation of the climatic and floristic data used in the present work, including preliminary analyses of this data. Methodological details for each chapter are detailed in within each chapter/article.

### A. PHYSICAL AND HISTORICAL CONTEXT: WESTERN GHATS OF INDIA

The escarpment of the WG represents the elevated rim of the Deccan plateau running along India's south-western coast ( $8^{\circ}$ - $20^{\circ}$ N) at elevations *c.*1200m (highest peak 2,695m). The chain of mountains mediates the rainfall regime of peninsular India by intercepting the heavy south-western monsoon rainfall favourable to the establishment of evergreen forests. The humid forests of the WG are isolated from other evergreen forests of north-east India and Indochina peninsula. This is because, apart from a narrow belt in the south, the rapid decline in rainfall on eastern leeward slopes makes them unable to support wet evergreen forests (Figure 1), and to the north, deciduous formations replace the evergreen with increasing dry season lengths.



**Figure 1** The annual rainfall gradient in the Western Ghats (left) with rainfall transects for different latitudes (right). Evergreen forest limits are shown in green correspond to the zones with highest rainfall (dotted line)

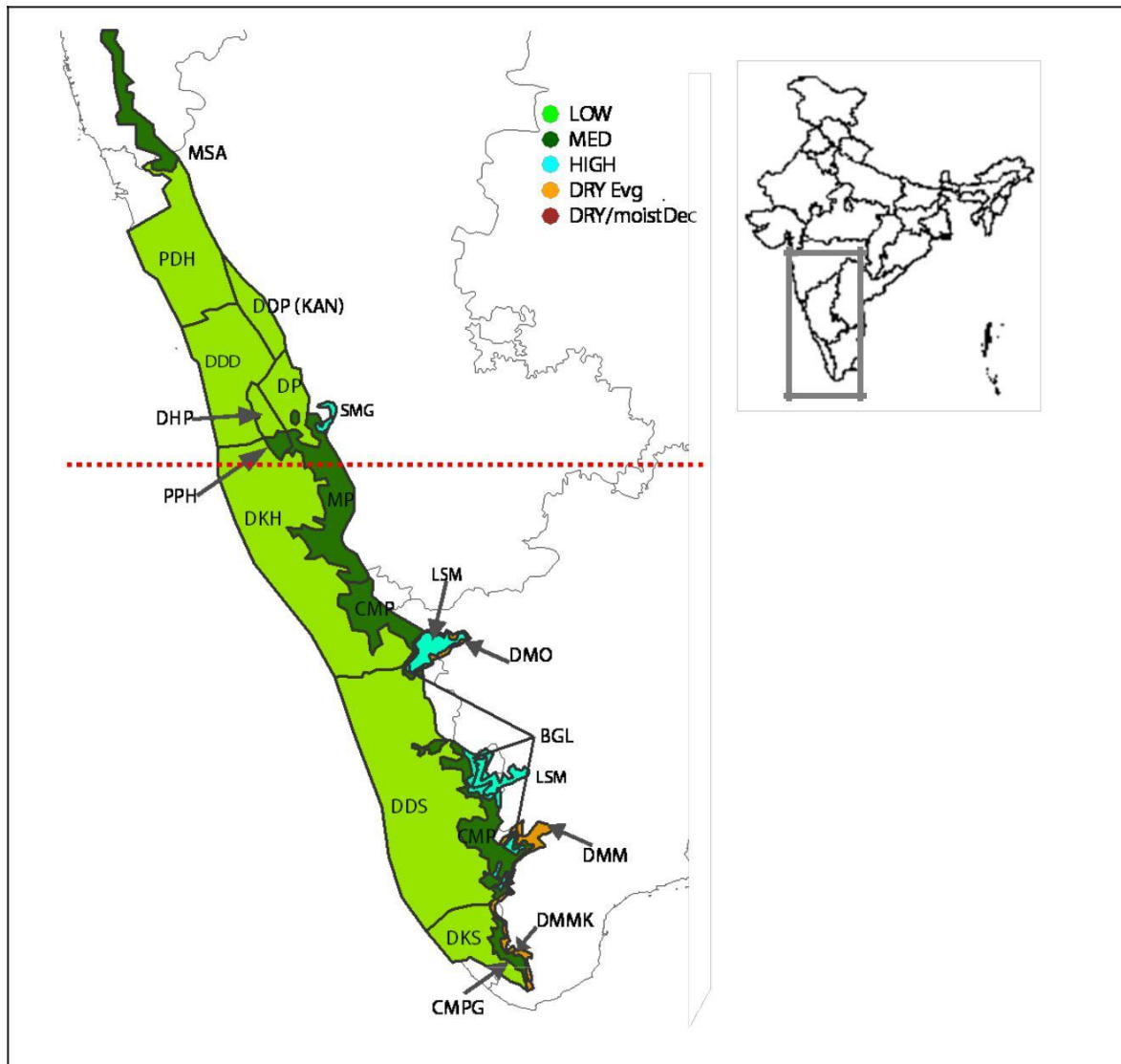
## 1. TOPOGRAPHIC AND HABITAT HETEROGENEITY

The heterogeneity associated with the deeply dissected topography has engendered the creation of multiple environmental conditions with drastic changes in bioclimatic conditions over space and time. The WG comprise a variety of vegetation types, from scrub forests in low-laying rain shadow areas of the plains, to deciduous and tropical wet forests up to about 1500m, and a unique mosaic of montane forests and grasslands above that.

The interaction of the summer monsoon winds with the relief results in a strong west to east rainfall gradient with high precipitation on windward slopes (2000 to >5000mm) that diminishes towards the interior (2000 to 900mm). A marked difference in precipitation seasonality correlates with the sharp decrease in rainfall beyond the crest of the WG, increasing from two dry months on the windward slopes to up to 6 months on leeward slopes in the south. Since the monsoon arrives from the south and retreats in the opposite direction, this creates another strong gradient in dry season length from two dry months in the south to up to eight in the north. An additional effect of topography is the fall in temperature with altitude: at elevations > 800m between the coast and the crest of the WG, mean temperature of the coldest month temperature is about 23°C, whereas it varies between 16-23°C at medium elevations (800-1400m), and 13.5-16°C at the highest elevations (Ramesh *et al.*, 2010a).

These basic gradients in rainfall, temperature and seasonality are major drivers of species turnover (Pascal, 1988; Bonnefille *et al.*, 1999; Barboni *et al.*, 2003; Ramesh *et al.*, 2010a). A critical threshold in terms of vegetation differentiation is the transition from 4 to 5 dry months that separates the humid regions of evergreen forest from those that include deciduous elements (Gunnell, 1997). Previous work in the WG also underlined major ecological differentiation of forest types related to drought stress along the latitudinal gradient, with a transition zone between 13-14°N. Modern pollen analyses points to the dominance of *Dipterocarps* characterising the evergreen belt up to 14°N after which it is replaced by species of *Diospyros* in the semi-evergreen forests (Pascal, 1986; Barboni *et al.*, 2003). From these bioclimatic characteristics, Pascal (1988) defined four main domains of potential forest vegetation in the WG region: wet evergreen dry evergreen, moist deciduous and dry deciduous, within which 19 floristic types are delineated (Figure 2 see details in Table 2).





**Figure 2** Floristic types in the Western Ghats showing low, medium and high wet evergreen, dry evergreen forest types in different colours

## 2. DYNAMIC BIOGEOGRAPHICAL HISTORY

The vegetation of India is unique in that it was shaped by changing conditions as it crossed various paleoclimatic belts between the time of its breakup from Gondwana in the far southern hemisphere in the early Cretaceous (~130Ma), and subsequent collision with Eurasia (~50Ma) (Briggs, 2003). The separation, latitudinal displacement and collision of the Indian plate led to large-scale continental plant re-organisation, palaeoceanographic and paleoclimatic changes, and the accompanying evolution and dispersal of flora (Bajpai *et al.*, 2012). Being embedded in the peninsular, the geological and climatic history of the WG is closely tied to that of India. Two points can be highlighted in relation to India's complex biogeographical history: 1) rather than being isolated during its long northward drift, current studies indicate that the Indian plate would have had occasional biological contacts with other continents, resulting in the extant flora being a mix

of Laurasian and Gondwanan as well as Indo-Malaysian affinity, and 2) the present-day climate is a product of geomorphological evolution.

### *Diverse biogeographical origins*

It is now believed that, rather than the "biotic ferry" or Noah's ark model (Hedges, 2003), the Indian plate was less isolated from neighbouring landmasses during its long northward drift than previously thought (Briggs, 2003; Ali & Aitchison, 2008). While there is agreement that there were prolonged periods of isolation to which we can attribute unique assemblages of ancient plant and animal taxa (Biju & Bossuyt, 2003; Roelants *et al.*, 2004; Van Bocxlaer *et al.*, 2012), and phylogenetic relationships show that a number of taxa in India are basal to south-east Asian lineages in support of their Gondwanan origin and the "out of India hypothesis" (Conti *et al.*, 2002; Karanth, 2006), mixing did take place with tropical flora and fauna of neighbouring landmasses (Rust *et al.*, 2010).

In terms of Gondwanan ancestry, the Gondwanan vicariance hypothesis postulates that a subset of such lineages was already present on the Indian plate since mid to late Cretaceous. Competing hypotheses propose their arrival through alternative routes during the Tertiary: migration from Africa to Asia facilitated by a northern mid-latitude corridor of frost-free climates during the Eocene (~40 Ma, boreotropical migration hypothesis); overland dispersal across Arabia at the Miocene Climatic Optimum (18-16 Mya, Miocene geodispersal hypothesis); and transoceanic dispersal aided by the 'stepping stone' effect of islands in the Indian Ocean (Thomas *et al.*, 2015). The biota is thought to have been assembled through multiple colonisation events of lineages of Gondwanan and other ancestry from Africa, Eurasia and south-east Asia, especially as new areas would have opened up with the extinction of many existing Gondwanan elements triggered by late Cretaceous (~65Ma) flood basalt volcanism after the Indian plate crossed the Reunion mantle plume (Samant & Mohabey, 2009).

Knowledge of the origin and epoch of diversification of lineages is important because species are best adapted to abiotic conditions under which their lineages originated (Ricklefs, 2006; Bartish *et al.*, 2016). In the WG, monospecific families with Laurasian affinities (e.g. *Magnoliaceae*, *Ericaceae*, *Myrsinaceae*) are mostly found at medium to higher elevations whereas monospecific families of Gondwanan affinity are characteristic of low to medium elevations subject to short dry seasons (Gimaret-Carpentier *et al.*, 2003). Carlucci *et al.*, (2016) found that Magnoliids, which generally show conserved preferences for Gondwana-like montane or moist and shady habitats, tracked these conditions in the Andean forests. Along the same vein, species of different lineages might vary in their responses to climate-induced habitat change, depending on their evolutionary heritage. For e.g. lineages that diversified in a warmer epoch might still carry adaptations to such

a warmer climates while others might be more sensitive to climate change as suggested by Bartish *et al.*, (2016).

Lastly, mounting molecular evidence that ancient Gondwanan lineages from the Cretaceous survived in WG despite dramatic climatic changes and volcanism, points to the existence of refugial conditions here. Joshi and Karanth (2013) show evidence of relict humid forest-dwelling taxa in southern WG refugia having diversified and dispersed into other parts of the WG under favourable conditions commencing in the Palaeocene. Indeed, recent pollen analyses from western and northern India indicate the re-establishment of wet evergreen forests in the late Palaeocene after the extensive volcanic activity (Prasad *et al.*, 2009). This study revealed the striking similarity of extant pollen flora of WG endemic plants with 28 most common fossil pollen taxa of the early Palaeogene (~50-55 Mya). The southern WG is thus thought to have served as refugia for wet evergreen species that were widely distributed prior to the volcanic period as well as a centre of origin for others. The high diversity is a legacy of the globally warm interval of this period, when the Indian plate experienced long periods of high precipitation and low seasonality in the low latitude equatorial region. These conditions were key factors in the widespread distribution of the tropical rain forest community in the Indian subcontinent (Bajpai *et al.*, 2012).

#### *Rainforest dynamics after the Miocene*

The present-day climate in the WG is a product of geomorphological evolution. In the Eocene (45 Mya) tropical forests covered most of the Deccan plate (Meher-Homji, 1989) before the creation of the WG escarpment and the subsequent collision with Laurasia. The upliftment of the Himalayas and subsequent establishment of the monsoon regime brought about a major shift in climate, with the onset of aridification in large parts of the Indian peninsula after the mid-Miocene (Morley, 2000; Guo *et al.*, 2008; Patnaik *et al.*, 2012). As the arid zone spread southwards, previously widespread wet evergreen forests were largely replaced by deciduous forests to the north and east of the WG (Meher-Homji, 1983; Patnaik & Prasad, 2016). Orographic rainfall provided the necessary humid environment and habitat conditions to ensure the persistence of wet evergreen forests on the western slopes of the WG (e.g. Roelants *et al.*, 2004). The WG was thus isolated from other persistent wet zones and evergreen forests in North-east India and Indo-China at this point. Within the WG itself, the seasonal reversing monsoon winds introduced a south to north gradient of seasonality during this period (Gunnell, 1997; Patnaik *et al.*, 2012; Patnaik & Prasad, 2016).

### 3. ENDEMISM AND DIOECY IN THE WESTERN GHATS

The distribution and high rates of endemism (over 56% for evergreen species, Pascal *et al.*, 2004) in the WG raise questions regarding the past history and origin of the flora and their possible evolution from the time that the WG was isolated from other evergreen formations in India. The high rates of endemism are comparable to that of oceanic islands, where endemism may be due to the fact that, fortified by its insularity the flora underwent an evolution giving rise to endemic species (cradle); or, protected by a (sea) barrier, might have escaped the onslaught of unfavourable climatic fluctuations/ biological instabilities which affect larger landmasses, thus serving as a refugia for relict flora (museum).

Two points are of particular interest: Firstly, species richness and endemism are not uniformly distributed along the WG. The southernmost regions that have the most favourable conditions with high (but not excessive) annual rainfall and low seasonality are the richest in species (Ramesh & Pascal, 1997; Barboni *et al.*, 2003; Davidar *et al.*, 2005). The rate of endemism among evergreen trees decreases from ~70% in the southernmost WG to ~60-65% up to about 12°N, followed by a drastic decline from 38% to 25% up to about 14-15°N. In the extreme northern WG it is less than 10% (Ramesh, 2001). Additionally, birds, amphibians, and fishes also exhibit similar patterns of decreasing diversity and endemism towards the north (Dahanukar *et al.* 2004; Aravind and Gururaja, 2010 in Joshi and Karanth, 2013). Most of these studies have identified contemporary ecological factors like seasonality, productivity, climate, and low seasonality to explain these patterns. However, speciation and biogeographic processes are poorly understood for the WG biota (Joshi & Karanth, 2013)

To summarise what the literature in the previous section points to: within the WG, the southern forests have been least affected by past climatic changes and studies show that they have served as recurrent refugia since the early Eocene. This stretch of forests (8°-13°N) is biogeographically delineated from forests further north that experienced lower historical climate and habitat stability, having experienced multiple alternations in climate and alterations in habitat - with accompanying cycles of contraction and colonisation of species distributions - dating from the early Palaeocene flood basalt volcanism, to the Miocene aridity, and the more recent Quaternary climate fluctuations that the southern forests were spared from. The northern forests are both at the limit of the Deccan traps (lava deposits from Cretaceous volcanism) and have been subject to greater seasonality since the mid-Miocene. The effect of more recent climate fluctuations, especially reduced rainfall in Quaternary, was also stronger in northern WG according to global circulation models (GCM).

Secondly, the presence of co-generic wet evergreen species belonging to species-rich genera in habitats that are environmentally distinct has led previous work to allude to 'ecological

vicariance' along a south-north gradient and between western windward and eastern leeward slopes, based on a capacity to tolerate lengthening dry seasons (Pascal, 1988; Gimaret-Carpentier *et al.*, 2003). Many of these genera comprise predominantly dioecious species. The high proportion of dioecious species overall in the WG (20% of tree species, Krishnan & Ramesh, 2005), which increases slightly for endemic species, thus also raises questions regarding whether there were ecological or evolutionary constraints on the assemblage and current distribution of species that may be linked to their reproductive systems.

## B. THE DATA

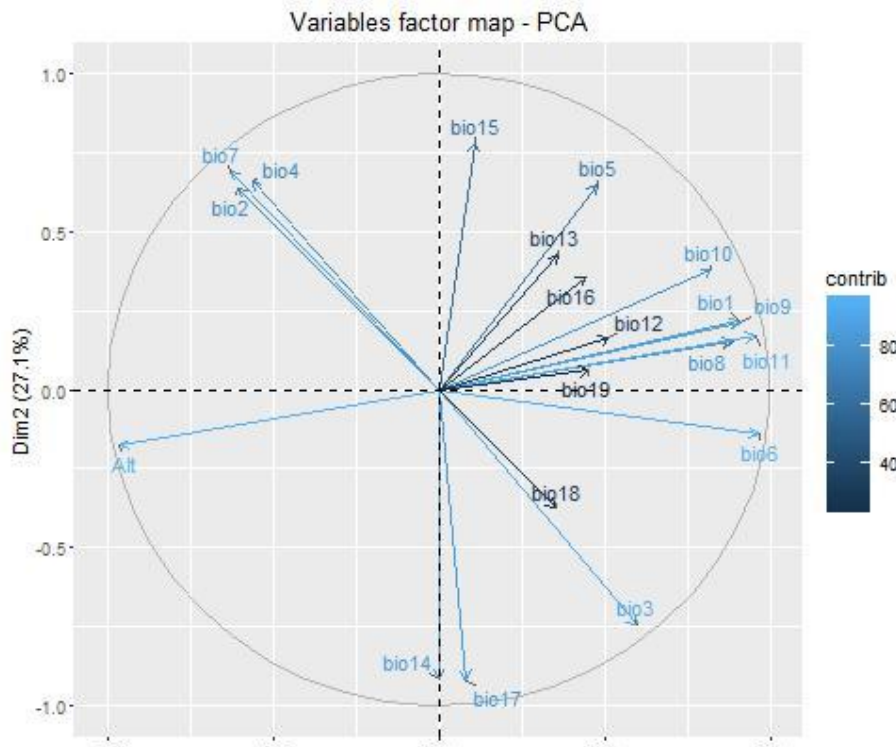
The objective of this section is to present the floristic and climatic data as well as results of preliminary analyses of this data that are applied in subsequent chapters. We thus detail 1) how we quantified past and present environmental conditions to create synthetic variables that we used to model species distributions in the past as well as the present (Chapter 1) and for phylogenetic and reproductive trait analyses (Chapter 2 & 3), and 2) canonical correspondence analysis (CCA, ter Braak, 1986) to assess species responses to the abiotic gradients, the results of which are also used in subsequent chapters.

### 1. QUANTIFYING PAST AND PRESENT ENVIRONMENTAL CONDITIONS

For a synthetic climatic characterisation, we performed a Principal Component Analysis (PCA) of the 19 bioclimatic variables as well as elevation at a resolution of 5 arc-minutes (~10 km<sup>2</sup>) obtained from WorldClim database (Hijmans *et al.*, 2005) covering the study area. The three first axes explained 90.42% of the overall bioclimatic variability and yielded synthetic variables for subsequent analyses. Variables relating to temperature (bio 1-11) and elevation (Alt) contribute strongly to PCA Axis 1 (Figure 3); Precipitation seasonality and precipitation of the driest month/quarter (bio 15 and bio 14/17) contribute to PCA Axis 2 and lastly, other precipitation variables such as annual rainfall contribute most strongly to PCA Axis 3. See Table S1 in Annexe 1 for details on the bioclimatic variables from WorldClim.

These variables, devoid of the co-linearity effects among the initial variables, thus summarized the main environmental gradients present in the WG (Figure 4c), namely, (i) the temperature-elevation gradient (range of mean temperature of the coldest month: 3-22°C); (ii) the N-S precipitation seasonality (duration of dry season) gradient (range of months with rainfall < 100 mm: 3-8) and (iii) the rainfall gradient (annual precipitation: 484 to 6032mm). These three primary components are consistent with the three main climatic drivers of vegetation change formerly identified in the WG (Pascal, 1988; Bonnefille *et al.*, 1999; Barboni *et al.*, 2003). We also considered past environmental conditions of the Last Glacial Maximum (LGM; ~21 kyr BP) and the Last Inter-Glacial (LIG; ~ 120-140 kyr BP) to investigate the possible scenarios of species

distribution changes. These periods represent important climatic extremes in the last 150 kyr. The same 19 bioclimatic variables, as described above, downscaled from Global Circulation Models (GCM) output, were retrieved for the LGM from the WorldClim server.

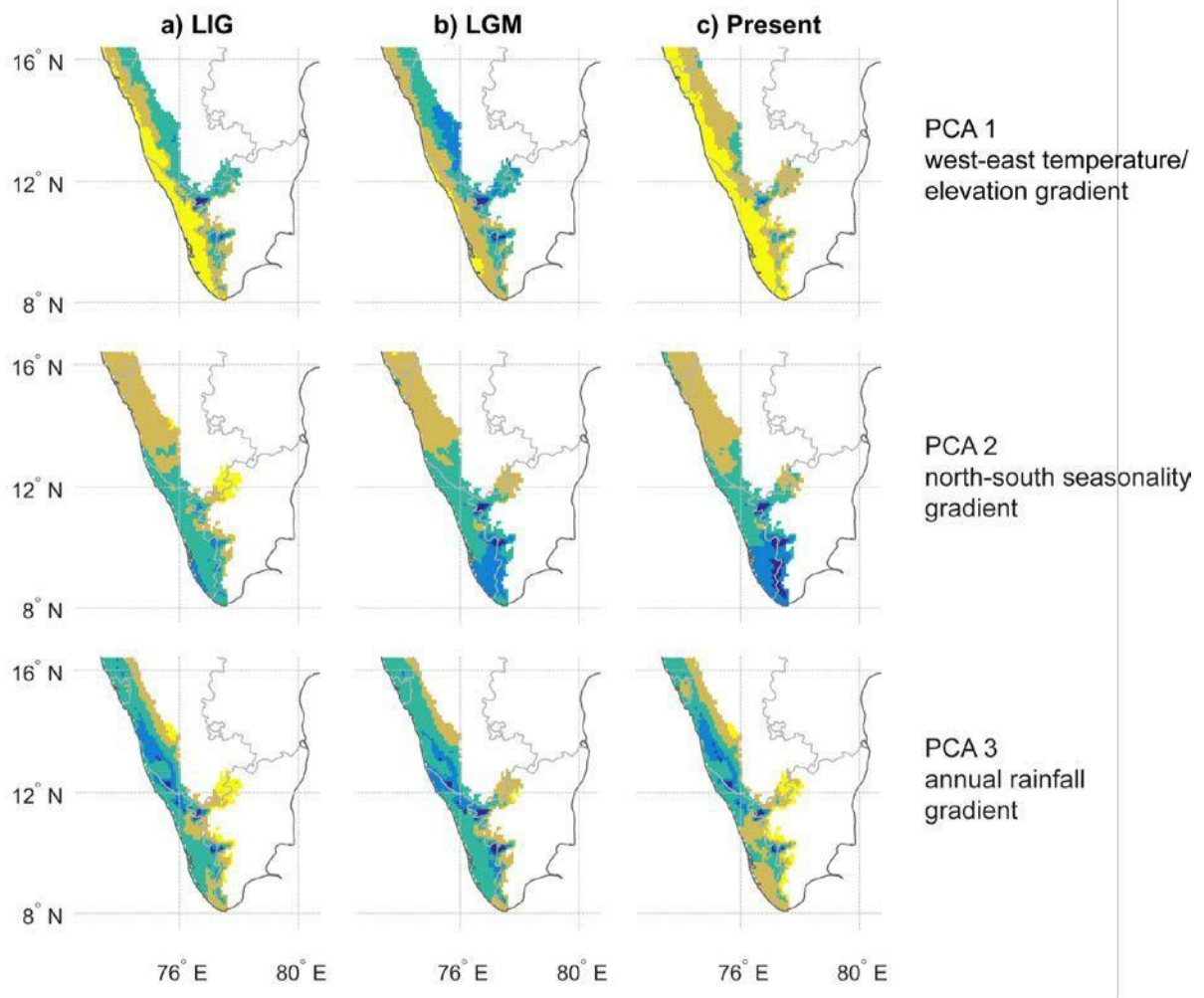


**Figure 3** Plot of the first two PCA axes of 19 variables (BIO1–BIO19) and elevation extracted from WorldClim database for the Western Ghats area in India. Lighter colours indicate stronger contribution to the axes by the variables. Bio 1-11 are variables pertaining temperature, with bio 2,3,4 and 7 dealing with ranges and seasonality of temperature. Bio 12-19 are precipitation related variables

The choice of GCM is a major source of uncertainty in SDM projection (Beaumont *et al.*, 2008; Diniz-Filho *et al.*, 2009; Buisson *et al.*, 2010) as GCMs vary in the way they model the climate system, and so produce different projections for the past climates. In addition, there is uncertainty in simulations of paleoclimates and statistical downscaling of those simulations to fine-scale topography (Gavin *et al.*, 2014). Our choice of climate model is supported by a review of the literature on climatic conditions during the LGM in India. Upon a comparison of LGM climatic models based on the GCMs CCSM4, MIROC and MPI from the PMIP3/CMIP5 project available in the WorldClim database we found that for the WG, the simulation for LGM conditions based on CCSM4 was the most consistent with terrestrial and marine paleo-proxy reconstructions for the region. These reconstructions describe cooler and arid (up to 20% decrease in rainfall) conditions in the LGM, attributed to a stronger winter monsoon and a weakened summer monsoon (Fortugne & Duplessy, 1986; Van Campo, 1986; Sukumar *et al.*, 1995; Rostek *et al.*, 1997; Prabhu *et al.*, 2004; Farooqui *et al.*, 2010; Tiwari *et al.*, 2011; Agrawal *et al.*, 2012).

A comparison of the annual precipitation variable across models for example highlights inconsistencies in the other GCMs. Like the previous CCSM version, CCSM3, which has been much improved upon in CCSM4 (Meehl *et al.*, 2012), the other climate models also display equivalent or higher annual precipitation in the WG for the LGM (MIROC range 490–6550 mm and MPI 456–6034 mm/year) than at present (484–6032 mm/yr), especially in the area which receives the most rainfall during the summer monsoon. While some authors argue for substantial precipitation during the LGM, pointing out that LGM climate in the Asian monsoon region was more variable than assumed (Chabangborn *et al.*, 2014), and studies on India show that the period was punctuated by short wet intervals (Rashid *et al.*, 2007; Govil & Naidu, 2011; Mahesh *et al.*, 2011), this pertains to areas over the Bay of Bengal, Sumatra, the South China Sea and others, but not to the WG / Arabian sea region. We thus used the climate predictors based on the GCM model CCSM4 (annual precipitation range 425–4922 mm/year) from WorldClim for the LGM at a resolution of 5 arc-minutes. For the sake of consistency with present and LIG climatic layers from the same source, we ruled out using comparable predictors available from other sources.

The LIG data (Worldclim, source Otto-Bliesner *et al.*, 2006) were aggregated (mean) at a 5 arc-minute resolution. Values of the bioclimatic variables for these two periods over the WG and Sri Lanka were then introduced as supplementary observations in the above PCA to obtain the projected bioclimatic maps at LIG and LGM (Figure 4 a-b).



**Figure 4** Main climatic gradients in the Western Ghats biodiversity hotspot, South India, as depicted by the first three PCA axes based on 20 climatic variables. These variables are mapped at Last Inter Glacial (LIG), 120-140 kyr BP (a), at Last Glacial Maximum (LGM), 21 kyr BP (b), and at present (c). The blue to yellow colour gradient indicates low to high temperature, seasonality and monsoon rainfall.

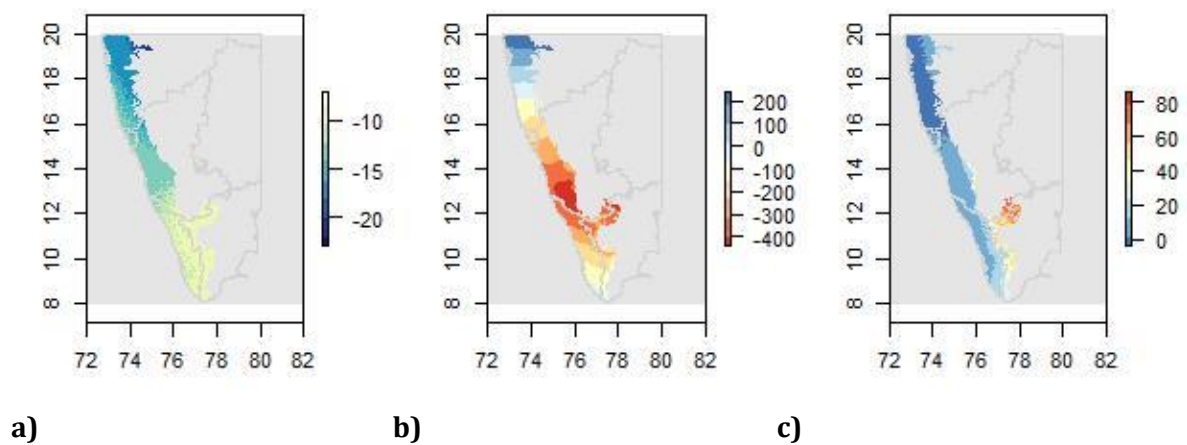
To assess the differences between present WG climate and GCM simulated paleoclimates, we used the package *raster* in R to subtract values of representative variables for temperature and precipitation: annual mean temperature (WorldClim Bio1), mean annual precipitation (Worldclim Bio12) and precipitation seasonality (Worldclim Bio15) for each gridcell in each GCM model of past conditions from present climatic values. A new raster map was produced by the subtraction, where positive values indicate a past climate that was hotter/wetter and negative values indicate a past that was colder/drier than present climate (Figure 5 & Figure 6).

In the LIG, temperatures were lower than in the present, and this difference is more pronounced above 12°N and especially in extreme northern WG; annual rainfall was higher in the extreme north and reduced elsewhere - by 200-400mm between 10-15°N and not much less than at

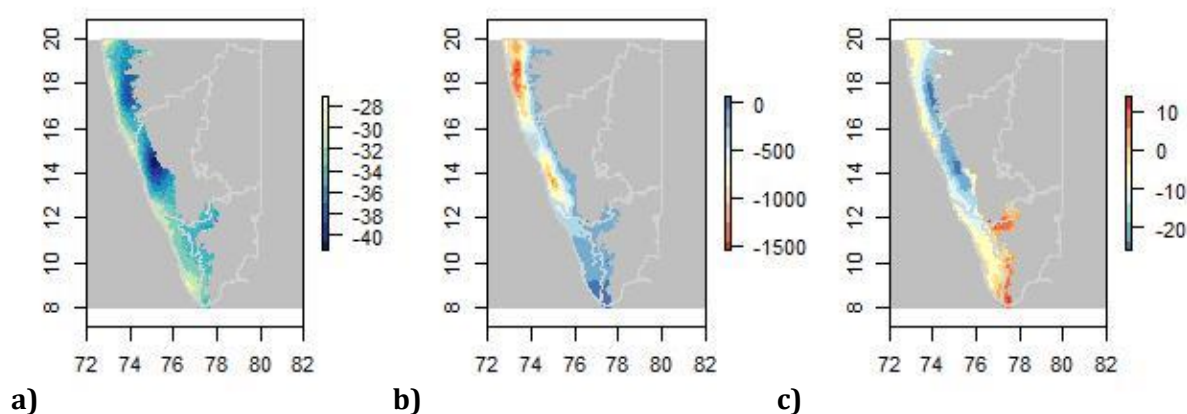


present below 10°N; and precipitation seasonality was higher than present during the LIG and more so below 12°N, especially for the eastern areas of WG (Figure 5 a-c).

According to the GCM models of the LGM, temperatures were lower than the present by 2-4°C all over the WG especially above 12°N and coolest towards the interior. The GCM hindcasts and the literature indicate a lower mean annual precipitation at the LGM (a reduction of 500-1500mm in the LGM compared to the present) than in the LIG and the present, especially in areas that receive most of their rain during the summer monsoon (12-15°N). In contrast, probably due to the dominance of the winter monsoon during the LGM (Sarkar *et al.*, 1990), areas south of 12°N experienced higher or no change in rainfall, barring local variations. However, precipitation seasonality was higher below 12°N, especially eastern areas of the WG (Figure 6 a-c)



**Figure 5** Difference between LIG and present conditions for a) annual mean temperature ( $^{\circ}\text{C} \times 10$ ), b) annual precipitation (mm) and c) precipitation seasonality. Positive values indicate a past climate that was hotter/wetter/more seasonal and negative values indicate a past climate that was colder/drier than present climate



**Figure 6** Difference between LGM and present conditions for a) annual mean temperature ( $^{\circ}\text{T}$ ), b) annual precipitation (mm) and c) precipitation seasonality. Positive values indicate a past climate that was hotter/wetter/more seasonal and negative values indicate a past climate that was colder/drier than present climate.

## 2. VARIATION IN FLORISTIC COMPOSITION ALONG ENVIRONMENTAL GRADIENTS

### ***Floristic data***

The French Institute of Pondicherry (FIP), is practically the sole repository of plant species data covering the entire WG, as a result of extensive field missions undertaken for vegetation mapping projects. Our floristic dataset consisted of 1) 9,649 occurrences from FIP 's Atlas of endemic tree species of the WG (Ramesh & Pascal, 1997), updated with additional observations from the FIP herbarium and 2) 297 ~1ha plots including 459 species, both endemic and non-endemic, from fieldwork conducted in the 1990s. Each of these plots were characterised by its location in one of 19 discrete floristic types delineated by Pascal (1988).

### *Occurrence records*

The atlas of endemic tree species of the WG (Ramesh & Pascal, 1997), reported species occurrences in this area based on three sources: 1) herbaria specimens; 2) data published in the literature; 3) results of intensive field surveys by the botanists of the French Institute of Pondicherry (FIP), mostly in the 1970's to 1990's. We updated these data with additional occurrence data collected at the FIP herbarium (HFIP; <http://ifp.plantnet-project.org/>) since 1997. We selected the taxa that were represented by at least 10 occurrences, obtaining 9,649 occurrences corresponding to 195 taxa. To match the resolution of the climatic layers used (5 arc-minutes or 10 km<sup>2</sup>), this resulted in 640 pixels having one occurrence/pixel. The occurrence data was used to model past and present potential species distributions detailed in Chapter 1.

### *Sample plots*

For the analyses of phylogenetic diversity (Chapter 2) and reproductive trait distribution (Chapter 3) we used a presence/absence dataset of 297 plots including 459 species, comprising a) 189 plots located in wet or dry evergreen forests between 8°5' et 11°5'N (Gimaret Carpentier, 1999; Pascal et al., 2004), b) 96 plots covering a wide array of habitats between 13°30'-15°N in north-central WG (Ramesh et al., 2010b), and c) 12 plots between 10-12°5'N from Chandrashekara (2004). Species names were checked and updated with The Plant List (2013) and a recent WG flora (Nayar et al., 2014).

### *Floristic Types*

The relationships between the vegetation types, the species and their natural environmental conditions are depicted in vegetation maps produced by the FIP in collaboration with the forest departments of the Indian states across which the WG are located. 19 discrete floristic types were delineated by Pascal (1988). Of these, 16 floristic types were classified according to elevation: wet evergreen forest types classified according to low (0-800m), medium (800-

1400m) and high elevation (>1400m). Dry evergreen forests found on the eastern slope of the WG, south of Palghat gap (~11°N), account for the other three floristic types. These types are named after the species selected for their abundance, or characteristic value, or both (Ramesh & Pascal, 1997) as detailed in Figure 2 and Table 2.

Table 2

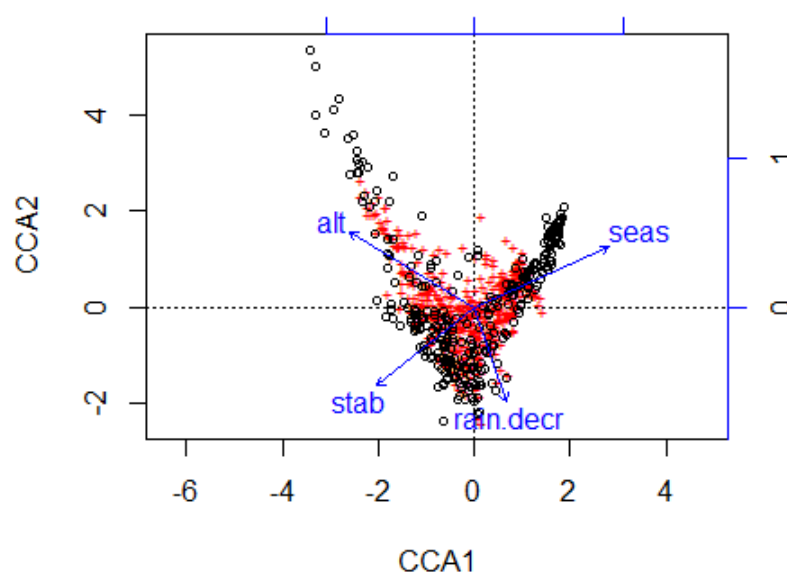
Forest Type	Rainfall (mm)	Dry (mo)	T(C)	Latitudes
<b>Wet Evergreen: plains and low elevation types</b>				
<b>DKS</b> = <i>Dipterocarpus indicus</i> - <i>Kingiodendron pinnatum</i> - <i>Strombosia ceylanica</i>	2000-5000	2-3	>23	8°-9°N
<b>DDS</b> = <i>Dipterocarpus indicus</i> - <i>Dipterocarpusbourdillonii</i> - <i>Strombosia ceylanica</i>	2000-5000	2-3	>20	9°-11°N
<b>DKH</b> = <i>Dipterocarpus indicus</i> - <i>Kingiodendron pinnatum</i> - <i>Humboldtia brunonis</i>	2000-6000	4-5	>20	11°-13°N
<b>DHP</b> = <i>Dipterocarpus indicus</i> - <i>Humboldtia brunonis</i> - <i>Poeciloneuron indicum</i>	5000-8000	4.4-5.5	>20	13°-13°5N
<b>DP</b> = <i>Dipterocarpus indicus</i> - <i>Persea macrantha</i>	>2000	5-6	>20	13°-14°N
<b>DDD</b> = <i>Dipterocarpus indicus</i> - <i>Diospyros candolleana</i> - <i>Diospyros oocarpa</i>	3500-7000	5-6	>20	13°-14°4N
<b>DDD+P</b> = <i>Poeciloneuron indicum</i> facies of DDD				
<b>PDH</b> = <i>Persea macrantha</i> - <i>Diospyros spp.</i> - <i>Holigarna spp.</i>	2000-6000	6-7	>23	14°4-15°5N
<b>DDP</b> = <i>Diospyros spp.</i> - <i>Dysoxylum malabaricum</i> - <i>Persea macrantha</i> (KAN)	1500-2000	6-7	23-24.5	14-15°N
<b>Wet Evergreen: medium elevation types</b>				
<b>CMPG</b> = <i>Cullenia exarillata</i> - <i>Mesua ferrea</i> - <i>Palaquium ellipticum</i> - <i>Gluta travencorica</i>	2000-5000	2-3	16-23	8°-9°N
<b>CMP</b> = <i>Cullenia exarillata</i> - <i>Mesua ferrea</i> - <i>Palaquium ellipticum</i>	2000-5000	2-4	16-23	9°-12°N
<b>MP*</b> = <i>Mesua ferrea</i> - <i>Palaquium ellipticum</i>	2000-5000	4-5	17-22	12-13°5N
<b>PPH</b> = <i>Palaquium ellipticum</i> - <i>Poeciloneuron indicum</i> - <i>Hopea ponga</i>	5000-7000	4-5	18-20	13°-13°5N
<b>MSA *</b> = <i>Memecylon umbellatum</i> – <i>Syzygium cumini</i> – <i>Actinodaphne angustifolia</i>	5000-6500	5-7	17-23	15°5-20°N
<b>Wet Evergreen: high elevation types</b>				
<b>BGL</b> = <i>Bhesa indica</i> - <i>Gomphandra tentandra</i> - <i>Litsea spp</i>	3000-5000	2-3	13.5-16	9°-11°5N
<b>SMG*</b> <i>Schefflera spp</i> - <i>Meliosma arnottiana</i> - <i>Gordonia obtusa</i>	>2000	3-6	13.5-17	13°-13°5N
<b>LSM</b> = <i>Litsea spp</i> - <i>Syzygium spp</i> - <i>Microtropis spp.</i>	900-6000	0-4	<13.5	10°-11°5N
<b>Dry Evergreen forest types</b>				
<b>DMMK</b> = <i>Diospyros foliosa</i> - <i>Mitrephora heyneana</i> - <i>Miliusa spp.</i> - <i>Kingiodendron pinnatum</i>	1200-1500	4-6	>23	8°-9°N
<b>DMM</b> = <i>Diospyros foliosa</i> - <i>Mitrephora heyneana</i> - <i>Miliusa spp.</i>	1200-1500	4-5	>23	9°-10°N
<b>DMO</b> = <i>Diospyros ovalifolia</i> - <i>Memecylon lushingtonii</i> - <i>Olea gladulifera</i>	1200-1500	4-6	16-23	11°-11°5N
<b>Plots in transition zone between evergreen and deciduous domains (21 plots in Moist and 8 in Dry Deciduous)</b>				
<b>LTD</b> (Moist deciduous) <i>Lagerstroemia microcarpa</i> - <i>Tectona grandis</i> - <i>Dillenia pentagyna</i>	1500-2000	4-7	25-31	
<b>ATT</b> (Dry deciduous) <i>Anogeissus latifolia</i> - <i>Tectona grandis</i> - <i>Terminalia tomentosa</i>	<1500	7-8	25-31	

### Variation in floristic composition along environmental gradients

We performed a canonical correspondence analysis (CCA, ter Braak, 1986) using the vegan package in R to assess species responses to the abiotic gradients based on the presence/absence data of the sample plots. The CCA analysis produces axes representing variables that maximise species niche separation and thus represented the main changes in community composition along the environmental gradients.

In addition to the three synthetic variables detailed in section B1 and shown in Figure 4c), we included an index of habitat suitability over the last 150 kyr. Species distribution models on which this was based are detailed in Chapter 1. For each 5 arc-min grid cell in the WG, binary maps of potential habitat models were calculated for each species at three periods, namely, present, Last Glacial Maximum (LGM; ~21 kyr bp) and LIG. In each grid cell, we then calculated the number of species potentially occurring at all the three epochs. The higher this number, the greater the number of species that could persist locally over time, thus providing an index of habitat stability.

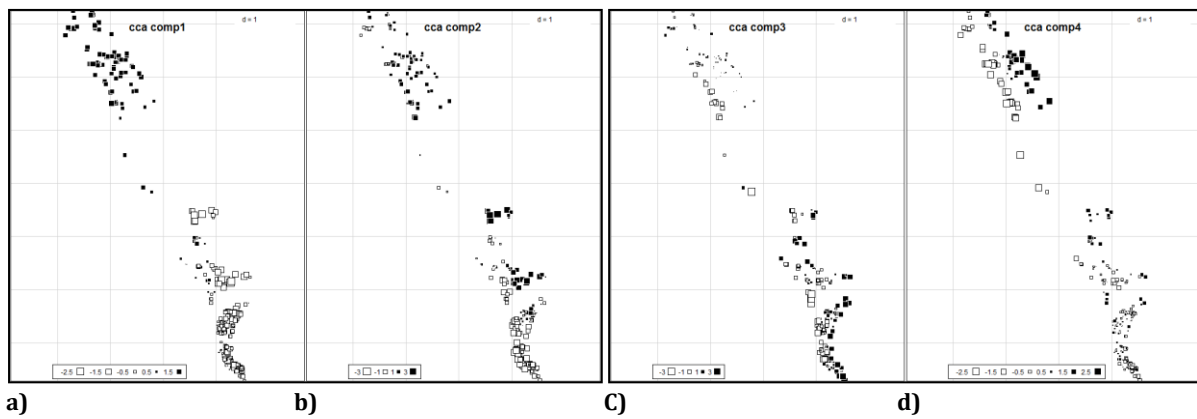
Seasonality, elevation and habitat stability all contributed strongly to CCA axis1 (50% of variance explained), and rainfall to CCA axis2 (30%), and were thus major drivers of both changing community composition (Figure 7). We can see a few well-defined groups of plots linked for e.g. to higher seasonality (positive Axis1), and higher elevations (positive Axis2).



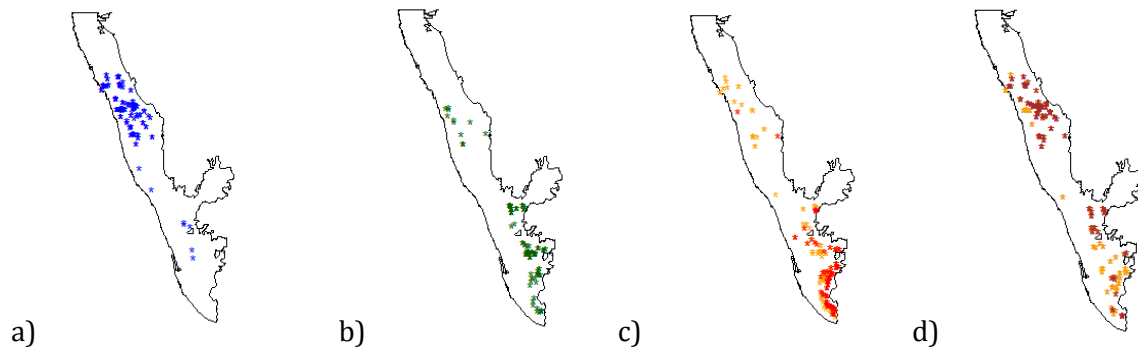
**Figure 7** CCA biplot of axes 1-2 representing main changes in community composition along the environmental gradients. Weighted averages of species scores are shown in black and site in red.

Plots are separated along the increasing seasonality axis (**Error! Reference source not found.a**). Plots located in the northern lowland part of our study area characterised by higher seasonality

and lower historical climate stability (positive CCA axis 1) are contrasted to plots in habitats characterised by low seasonality in southern areas (negative CCA axis 1). This corresponds to the location of species with positive (Figure 8 a) scores along CCA Axis1. Species with a preference for higher rainfall (negative CCA Axis2) conditions exemplified by plots at high elevations on either side of the Palghat gap (Figure 8 b) are located in southern WG (Figure 9b). Historical habitat stability and rainfall contribute most strongly to CCA axis 3 and 4 and plots characterising these gradients are located in areas of low stability (Figure 8c) and low rainfall (Figure 8 d) on the leeward slopes of the southern and northern regions of the study area (Figure 9c-d).

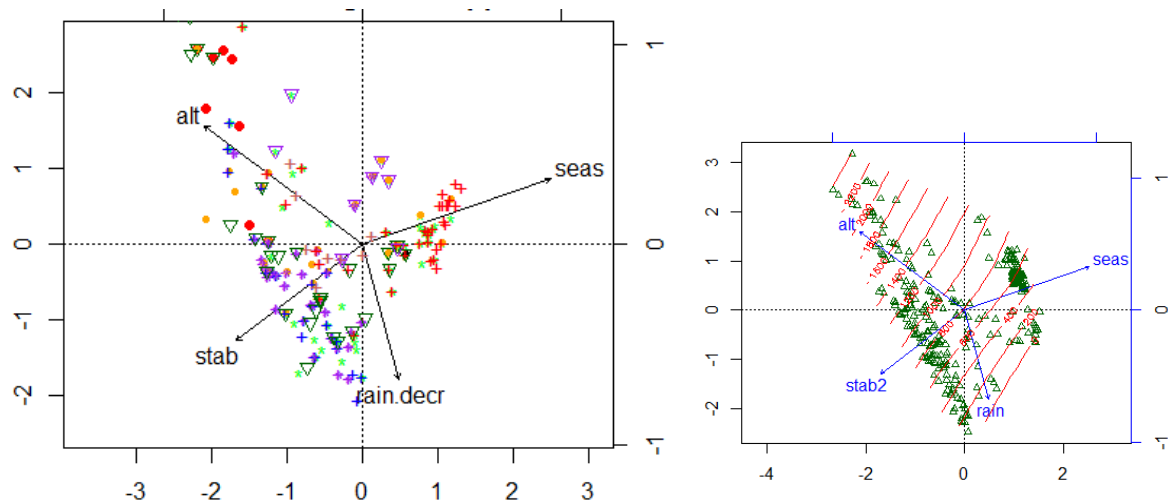


**Figure 8** CCA scores plotted on a map of the Western Ghats showing the location of plots with positive (black) and negative (white) scores along a) CCA Axis 1 and b) CCA Axis 2.

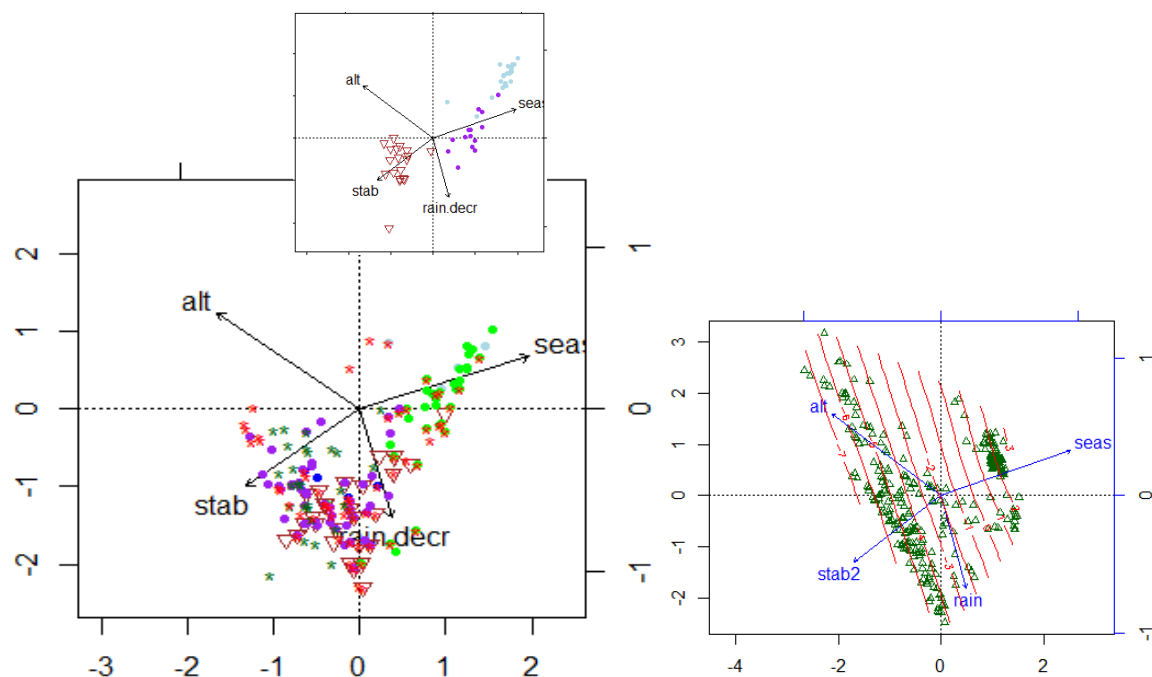


**Figure 9** Maps of the Western Ghats showing plots locations where species with positive scores along the a) CCA Axis 1, b) Axis 2, c) Axis 3, and d) Axis 4 are present.

Interestingly, species niche separation along the gradients depicted in the CCA biplot also occurs within genera. For instance, niches of endemics of certain species-rich genera such as *Litsea* and *Diospyros* are separated along the elevation and seasonality gradients (Figure 10 and Figure 11). A smooth response surface of values of the environmental variables fitted over the limits of the biplot using the function *ordisurf* of the *vegan* package in R shows the direction and linearity of the increase in environmental variable values.



**Figure 10** Niches of endemic species of a) the genus *Litsea* are separated along the elevation gradient. Points of different colours or shapes represent different species positions. In b) a smooth response surface of values of elevation shows that elevation increases linearly from 100m to 2200m in the direction perpendicular to the biplot arrow "alt" denoting elevation.

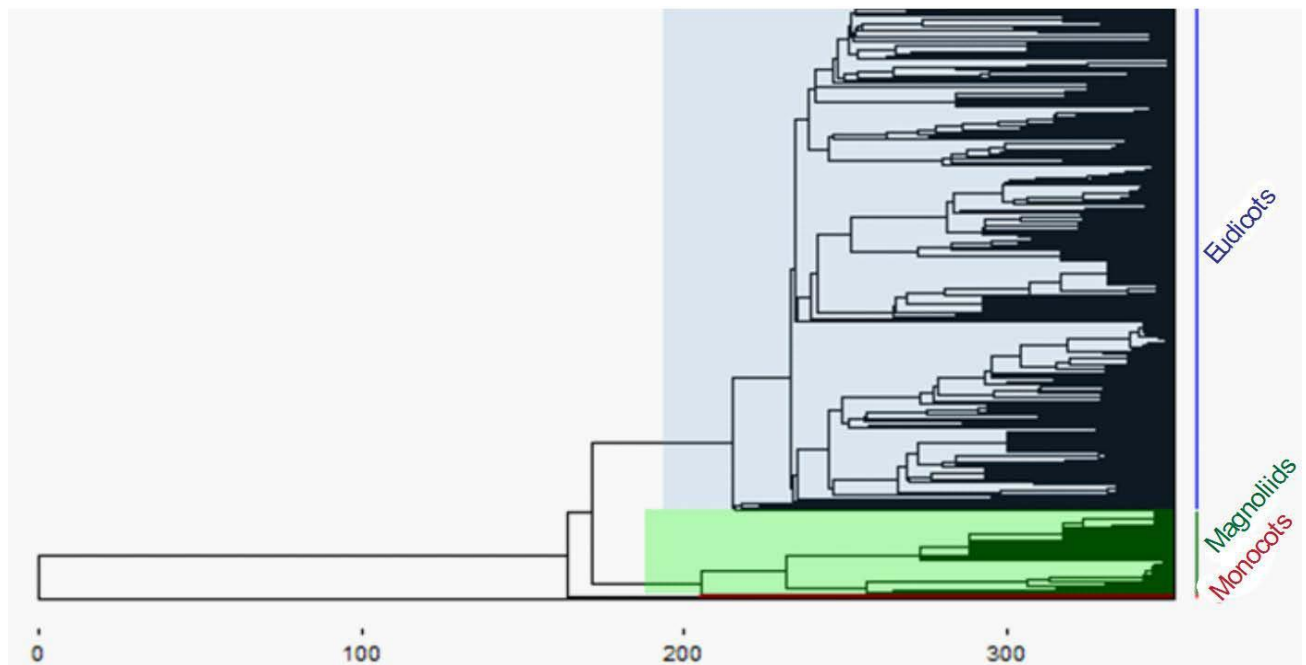


**Figure 11** Niches of endemic species of the genus a) *Diospyros* are separated along the seasonality gradient at lower elevations. Points of different colours or shapes represent different species positions with inset showing three representative species. In b) the smooth response surface of values of seasonality in the sample plots shows that this variable increases linearly in the direction perpendicular to the biplot arrow "seas" denoting seasonality.

### 3. PHYLOGENETIC DATA

To integrate phylogenetic information into studies of community ecology, a dated family-level phylogeny (Davies *et al.*, 2004) or undated ones archived at PHYLOMATIC v3. (Webb *et al.*, 2008) are commonly used. While the problem with the former is that it predates APG III, the latter necessitates assigning branch lengths which require assumptions for e.g. using BLADJ (Webb *et al.*, 2008) where branch lengths between two dated nodes are evenly divided among the nodes separating the dates. Furthermore, the commonly used plant clade age estimates provided by Wikström *et al.* (2001) are for only 176 internal nodes, including less than 30% of APG III families. Since almost all phylogenetic indices are based on branch length, using this method which has not been critically evaluated according to Beaulieu *et al.*, (2012), may bias the results (Gastauer & Meira-Neto, 2013; Qian & Jin, 2015).

We therefore used an up-to-date time-calibrated version of a comprehensive species-level phylogeny constructed by Zanne *et al.*, (2014) and updated by Qian and Jin (2015), based on gene sequences available in GenBank for land plants. It includes 98.6% of all extant seed-plant families and 51.6% of genera. Our tree (Figure 12) of the regional pool of 678 WG species were extracted from the supertree using PHYLOMATIC v.3. Of the three approaches proposed by Qian and Jin (2015) for adding the genera and species of the WG that are absent from the megaphylogeny, we opted for the approach implemented in PHYLOMATIC.



**Figure 12** Dated phylogenetic tree of Western ghats tree species showing the major clades and timescale in Myr since the root of the tree (i.e. 300 Myr since the root is ~ 50 Myr BP, 200 Myr would be 150 Myr BP and so on). It includes Eudicots 610 species (85.43%); Magnoliidae 98 species (13.73%); Monocots 5 species (0.7%); and 1 gymnosperm *Nageia Wallichiana*, which was not included in the analysis.



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PAST POTENTIAL HABITATS SHED LIGHT ON THE BIOGEOGRAPHY OF ENDEMIC TREE SPECIES OF THE WESTERN GHATS BIODIVERSITY HOTSPOT, SOUTH INDIA (JOURNAL OF BIOGEOGRAPHY)



**ABSTRACT**

**Aim** To investigate whether and how Quaternary climatic changes affected the habitats that support endemic tree species distributions in a tropical rain forest. Based on past and present predicted species distributions, we assessed (1) whether climatic conditions may have supported species survival in the same area over the studied period, (2) the effect of ecological niche specialisation on species-specific responses, and (3) the persistence of current populations in areas that were more climatically stable over time.

**Location** Western Ghats, Western Ghats-Sri Lanka Biodiversity Hotspot, India.

**Methods** We assessed species' current bio-climatic preferences based on their occurrence data using MaxEnt distribution modelling. The models were projected into past climatic conditions of the Last Glacial Maximum (LGM) and the Last Inter-Glacial (LIG) to assess the extent of changes in species' predicted distributions through time. Further, we tested whether species' current occurrences were located non-randomly in pixels predicted to have been suitable in the past. Finally, we characterized species-specific responses in relationship to plausible biogeographical scenarios.

**Results** We identified three distinct scenarios of species responses to past climate changes - stability, contraction, and shift - depending on their bioclimatic preferences. For high elevation species, the cool-dry LGM was less restrictive than for medium elevation and northern lowland species. Southern-most species requiring minimal seasonality were restricted by higher LIG seasonality, and only predicted to have been present in Sri Lanka at the time. Barring these southern-most narrow endemics, past suitable habitat, within which observed current occurrences are located, were predicted for most species.

**Main conclusions** Palaeoclimate modelling reveals the likely local persistence of most Western Ghats endemics over the last 150 kyr, a relatively recent period in this Paleogene refugium. The large spectrum of bioclimatic preferences probably arose as a result of evolutionary events prior to the Quaternary. Our results highlight the need for further studies based on molecular phylogenetics in this relatively poorly-studied biodiversity hotspot.

**Keywords** biodiversity hotspot, biogeography, endemic flora, India, palaeoclimate, rain forest refugia, species distribution modelling

## INTRODUCTION

Understanding the drivers of species distributions is a major goal in biogeography. Much attention has been focused on investigating the effect of contemporary ecological processes on species distributions (Guisan & Thuiller, 2005; Elith & Leathwick, 2009). However, historical events are increasingly recognized as strong determinants of current large-scale biodiversity patterns (Jansson, 2003; Ricklefs, 2004).

In particular, fossil, palaeoecological and phylogeographical evidence point to dramatic effects of Quaternary fluctuations on the distribution of some organisms (Taberlet *et al.*, 1988; Jansson & Dynesius, 2002; Moussalli *et al.*, 2009). In the tropics, varied rainfall regimes affected the distribution of rainforests (Anhuf *et al.*, 2006). However, direct information on past occurrences from fossil data is often scarce or missing in these regions. A major challenge is therefore to investigate the fingerprint of biogeographical processes on current species distributions, such as range contraction and expansion related to past conditions, and species diversification generated by past environment (Glor & Warren, 2011).

Recently, Species Distribution Models (SDM) calibrated from both past and current species occurrences have been proposed to gain insights into past habitat dynamics (see Svenning *et al.*, 2011). SDM reconstructions of refugia during the Last Glacial Maximum (LGM) were found to be a useful complement to palaeoecological (Alba-Sánchez *et al.*, 2010; Svenning *et al.*, 2011) and molecular studies (Waltari *et al.*, 2007; Poncet *et al.*, 2013). The SDM approach has been validated in the tropics through pollen records and in congruence with phylogeographical data (Hugall *et al.*, 2002; Carnaval & Moritz, 2008).

SDM representing current suitable habitats can be projected onto past climatic conditions to predict the changes in potential distributions under the assumption of niche conservatism, as defined by Wiens *et al.* (2010), over the period under study. This predicts the areas where past climatic conditions were compatible or not with the current species habitat preferences. Spatial mismatch of the past and present predicted areas could indicate whether pressure for shift over the period was likely, either in ecological (niche shift) or geographical (range shift) space. It can also support hypotheses on cryptic refugia based on environmental effects not acknowledged in the SDM. Conversely, when the predicted distributions broadly overlapped over time, under the assumption of niche conservatism, no selective pressure should have exerted either for dispersal or niche change, and the species could have persisted locally in the same geographic area.

Our aim here is to examine the effect of biogeographical processes on evergreen endemic tree species in the Western Ghats (WG) of India, based on the analysis of climatic changes in the area over a period covering the last major glacial cycle. The WG form part of the Western Ghats-Sri

Lanka Biodiversity Hotspot (Myers *et al.*, 2000), and its evergreen tree flora displays a high (63%) level of endemism (Ramesh & Pascal, 1997). Strikingly, data are missing on the biogeographical context of the WG, and molecular phylogenetic studies are mainly focussed on herpetofauna (Joshi & Karanth, 2013 and references therein). We therefore performed SDM reconstructions in the past and present for 195 tree species endemic to the WG to assess the environmental changes experienced by these species. Our first objective was to ascertain whether their survival was possible in the same area during the last 150 kyr.

The Pleistocene was characterised by a complex mix of warm and cold periods, and major variations in the intensity of the monsoon (Fontugne & Duplessy, 1986; Van Campo, 1986). The proportion of wet evergreen vs. deciduous and savanna elements of the WG flora varied accordingly, as documented from Arabian Sea sediment cores (Prabhu *et al.*, 2004) and Nilgiri basin peats (Sukumar *et al.*, 1995). The regional context of the climatically and topographically heterogeneous WG is especially relevant to address the effects of biogeographical processes over this period, because the niches of the selected endemics are highly variable according to the orographic monsoon regime, and cover a broad range of environmental conditions from low elevation to middle and high elevation evergreen forests (Pascal, 1988). In this regard, cooler and relatively humid mountain valleys and coastal areas could have served as refugia for wet-zone species during the cool-arid LGM, while lowlands could have experienced re-colonization during wetter inter-glacial periods (Moussalli *et al.*, 2009; Migliore *et al.*, 2013). Specifically, with the weakening of the summer monsoon in the LGM, we would expect contraction in the distributions of species depending on these seasonal rains. On the other hand, more southern species requiring year-round rainfall may have benefited from the winter monsoon dominance. Indeed, in a given biome, organisms can vary in their responses to a common history, resulting in complex and changing community compositions and a diversity of biogeographical scenarios (Graham *et al.*, 1996; Moussalli *et al.*, 2009). In this context, our second objective was to address whether the diversity of ecological niches among the WG endemic tree species allows detecting possible refugia or range change scenarios during the Quaternary.

Many refugia in non-glaciated regions are associated with complex topography such as mountain ranges (Keppel *et al.*, 2012), to which studies on the WG allude. To further address the latter using SDM, our third objective was to assess whether current populations are more often located in areas predicted suitable in the past - as opposed to areas that were unsuitable or became suitable recently. If yes, it supports the hypothesis of persistence of populations in areas where conditions have been more stable over time.

Lastly, the proximity and floristic similarity of the wet forests of the Eastern Ghats and southern Sri Lanka to the WG (Gunatilleke & Gunatilleke, 1990), the latter separated from India only by the

Palk Straits, suggest regular regional exchanges over time, which are expected to have influenced range shifts and speciation events among the endemics. We thereby discuss plausible ecological drivers of the biogeographical scenarios and their relation to species climatic preferences, the presence of putative refugia as well as the nature of floristic affinities with adjoining regions.

## **MATERIALS AND METHODS**

### **Study area and endemic tree species distributions**

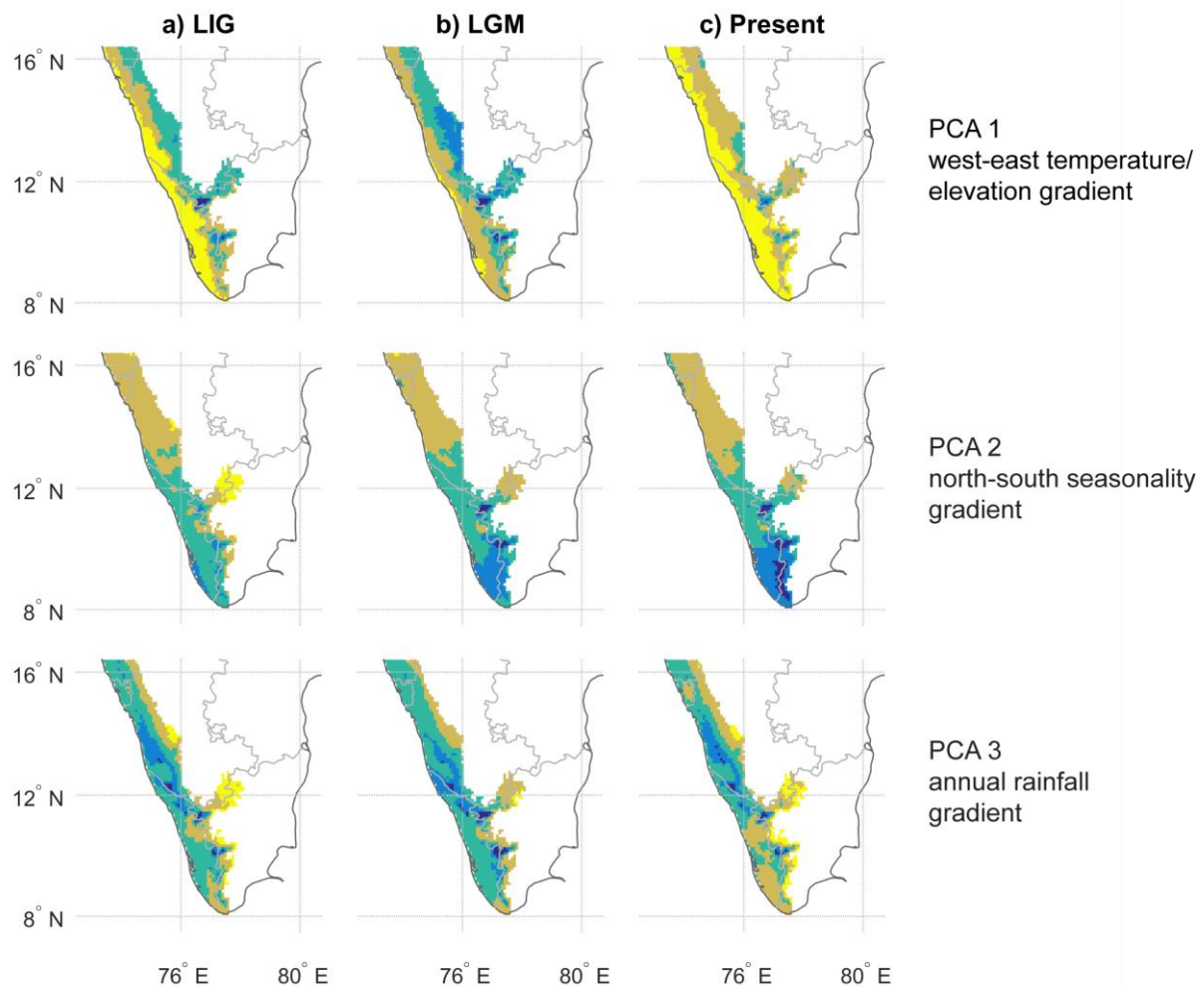
The Western Ghats (WG) form a 1600 km escarpment at elevation c. 1200 m (highest peak 2,695 m) along India's south-western coast, broken only by the Palghat Gap. The area between 8° to 16.4°N covers the biogeographical domain of a major part of the wet evergreen forests of the region, and receive the bulk of the south-west summer monsoon rains (Pascal 1988). These forests are isolated from the evergreen forests of north-east India and the Indochina peninsula by the rapid decline in rainfall towards the leeward east and the north.

The atlas of endemic tree species of the WG (Ramesh & Pascal, 1997) reported species occurrences based on three sources: 1) herbarium specimens; 2) published data; and 3) results of intensive field surveys conducted in 1970-1990 by French Institute of Pondicherry (FIP) botanists. We included additional observations from the FIP herbarium (<http://ifp.plantnet-project.org/>). Our dataset comprised 9,649 occurrences corresponding to 195 taxa with at least 10 occurrences each. A grid of 5 arc-minute pixels was laid on the study area.

### **Climatic data**

For a synthetic climatic characterisation of the region, we performed a Principal Component Analysis (PCA) of the 19 bio-climatically significant variables and elevation obtained from the WorldClim database (Hijmans *et al.*, 2005) at a resolution of 5 arc-minutes. The first three axes explain 90.4% of the overall climatic variation and yielded synthetic variables devoid of co-linearity (see Appendix S1 in Supporting Information).

These three synthetic variables summarize the three main environmental gradients formerly identified as major drivers of vegetation change in the WG (Pascal, 1988; Bonnefille *et al.*, 1999; Barboni *et al.*, 2003): (i) the temperature-elevation gradient (mean temperature of the coldest month from 3 to 22°C); (ii) the south to north increase in seasonality (from 3 to 8 months of dry season, with rainfall < 100 mm) and (iii) the west-east decreasing rainfall gradient (annual precipitation from 484 to 6032 mm) (Fig. 1c).



**Figure 1.** Main climatic gradients in the Western Ghats biodiversity hotspot, South India, as depicted by the first three PCA axes based on 20 climatic variables (see Appendix S1). These variables are mapped at Last Inter Glacial (LIG), 120–140 kyr BP (a), at Last Glacial Maximum (LGM), 21 kyr BP (b), and at present (c). The blue to yellow colour gradient indicates low to high temperature, seasonality and monsoon rainfall.

To investigate possible scenarios of species distribution changes, we considered past climates at the Last Glacial Maximum (LGM; ~21 kyr BP) and the Last Inter-Glacial (LIG; ~120–140 kyr BP), representing important climatic extremes during the last 150 kyr. The same 19 bioclimatic variables, downscaled from Global Circulation Models (GCM), were retrieved for the LGM from WorldClim. The choice of GCM is a major source of uncertainty in SDM projection (Beaumont *et al.*, 2008; Buisson *et al.*, 2010). We compared climatic projections based on GCMs CCSM4, MIROC and MPI models from the PMIP3 / CMIP5 project available from WorldClim. CCSM4 was the most consistent with terrestrial and marine palae-proxy reconstructions for the region, which describe cooler and more arid LGM conditions, attributed to a weakened summer monsoon and a stronger

winter monsoon (e.g. Van Campo, 1986; Tiwari *et al.*, 2011). The LIG data (Worldclim, source Otto-Bliesner *et al.*, 2006) were aggregated (mean) at a 5 arc-minute resolution. Values of the climatic variables for these two periods for the WG were introduced as supplementary observations in the above PCA to obtain projected maps of the 3 synthetic climatic variables at LIG and LGM (**Fig. 1a-b**).

### Species distribution modelling

SDMs characterize species environmental requirements by a statistical comparison of species occurrences with environmental layers. They predict areas where a species is likely to be present based on local climatic information (Elith & Leathwick, 2009). The prediction can concern a period distinct from that used for model calibration, allowing investigations into past or future distribution change. Here the sampling of tree species occurrences is spatially comprehensive since our database provides a complete picture of endemic species distributions; it consists, however, of presence-only data. In this regard, we applied the MaxEnt algorithm (v.3.3.3), proven to perform well when sampling coverage is neither biased nor deficient (Phillips *et al.*, 2006). The model was trained on present climatic conditions synthesized in the 3 PCA axes presented above.

A random set of 90% of occurrence localities was used to train the model and 10% for testing. We performed 10 replicate runs as recommended by Nogués-Bravo (2009), with distinct sets of 10% pixels for testing so as to avoid statistical bias due to spatial autocorrelation (Friedlaender *et al.*, 2011). One thousand random background points of putative absences were drawn from the study area. To assess SDM performance, we estimated for each replicate model, the area under the curve (AUC) of both training and test data. Lastly, we designed a null model to test whether our species were more related to the climatic factors considered than random occurrence points of equal prevalence (Raes & ter Steege, 2007). AUC scores from observed data were compared to 999 null AUC values generated with this procedure. The null hypothesis was rejected whenever the observed AUC fell outside the 95% confidence interval of null values.

We derived a binary map of predicted presence/absence from the SDM of each species using a threshold maximizing the sum of sensitivity and specificity, as recommended by Liu *et al.* (2013) for presence-only SDM. We also considered an alternative lower threshold with zero omission of training and test data to compare between liberal and conservative predictions.

The MaxEnt model for each species was projected into past climatic conditions to characterize its past predicted distribution. We obtained binary maps of past predicted presence-absence using the same threshold as for the current predictions for each species (Fig.2). To test the hypothesis that they could have served as a refuge for WG endemic species, we included the Eastern Ghats and Sri Lanka for projections into the past.

### Changes in predicted distributions: LIG to the present

From predicted presence-absence maps at the three epochs in the WG, we could classify any pixel into categories representing whether a given species was predicted present (1) or absent (0) under LIG, LGM and current climatic conditions, respectively. We thus obtained for each pixel a triplet code denoted 100, 010, 001, 110, 101, 011 or 111, with for instance, 100 meaning that a species predicted present in the LIG in a given pixel was predicted absent from that pixel in the LGM and the present.

We then assembled a single contingency table giving, for each species, the total number of pixels in each of the seven situations above, which we submitted to Correspondence Analysis (CA) to compare the patterns of change over time across species. The prominent CA axes synthesised the variation of biogeographical histories among species (Fig. 3). We mapped the spatial signatures of these histories across the WG range by summing the current binary distribution maps of each species, weighted by their respective scores on the CA axes (Fig. 4).

### Effect of species climatic preferences

We characterized the climatic niche preferences related to these biogeographical histories by a multiple regression of the species scores on the CA axes according to their average environmental preferences on the three synthetic climatic variables, including quadratic predictor terms to acknowledge non-linear effects. The most important predictors were selected through a stepwise procedure based on AIC comparison of the models with sequential addition and dropping of predictors.

### Relationship between current occurrences and past predictions

We addressed whether species current (observed) occurrences were located in areas that were stable over time according to the models, to test the hypothesis of long-term persistence in more stable areas. We performed a multinomial test of the distribution of current observations in each of the seven pixel categories, relative to a random draw over its current predicted distribution (Read & Cressie, 1998). The null hypothesis was that the current observations of a species could be found in any pixel of its current predicted distribution, independently of past predicted habitat history. More specifically, we tested (i) whether populations currently located in suitable habitats (categories 001, 011, 101 and 111) were distributed randomly with regard to past habitats, and (ii) whether populations located in currently unsuitable habitats (categories 010, 100 and 110) were the relicts of a habitat that was suitable in the past. In both cases, a multiple-comparison correction was applied for controlling the false discovery rate of the multinomial tests (Benjamini & Hochberg, 1995).

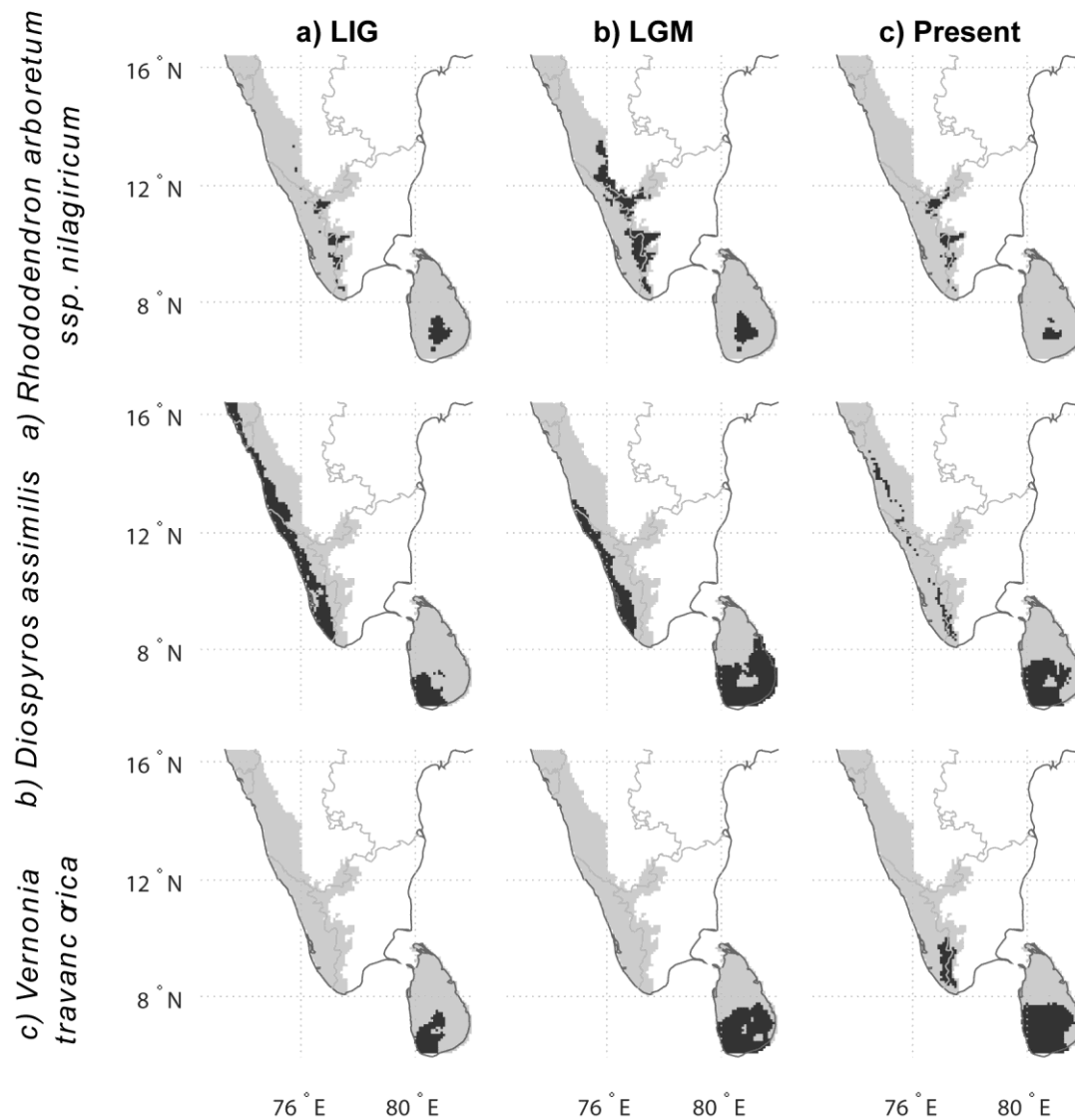
## RESULTS

Based on the 195 models of species distributions, we found a significant influence of climatic variables for over 96% of species (null model based  $p < 0.05$ ). All the models displayed moderate to high predictive power: average of 0.903 training AUC (SD=0.061) and 0.871 test AUC (SD=0.081) over ten replicate models. **Fig. 2** shows the SDM projections into LIG and LGM climates for three representative species. Almost all the species had suitable habitat predicted in Sri Lanka at the LIG, while very few had suitable habitat in the Eastern Ghats over the 3 periods. Three main groupings of species emerge from the analysis: (i) high elevation species; (ii) species of mid-elevations and northern lowlands, and (iii) species restricted to the extreme southern WG ( $<9^\circ\text{N}$ ); the results are presented and discussed following this logic.

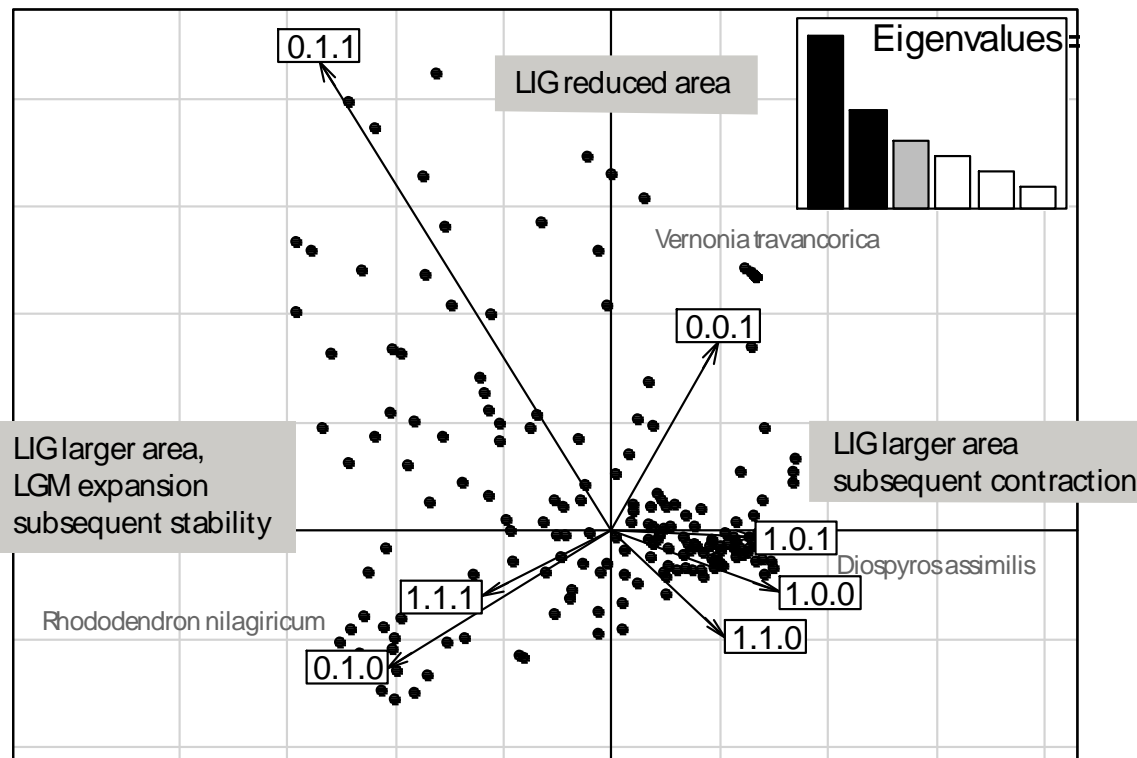
### Changes in predicted distributions: LIG to the present

We performed the Correspondence Analysis of the contingency table giving the total number of pixels for each of the seven possible trajectories from the LIG to the present for each species. The first two CA axes explained over 50% of the overall variance (**Fig. 3**), and thereby represented contrasting biogeographical scenarios: (i) predominant stability since the LIG (higher frequency of 111 pixels), including cases of transient increase during the LGM (010), exemplified by *Rhododendron arboreum* Smith ssp. *nilagiricum* (Zenk.) Tagg in **Fig. 2a**; (ii) contraction/fragmentation of predicted distribution since the LIG with a majority of pixels in 100, 110 and 101 categories, a case exemplified by *Diospyros assimilis* Bedd. in **Fig. 2b**; and (iii) expansion since the LIG with a majority of pixels in 011 and 001 categories, exemplified by *Vernonia travancorica* J.Hk. in **Fig. 2c**. Noticeably, the latter group of species comprised largely of endemics of southern WG which were devoid of suitable habitat in the WG at the LIG, and for 23 southern-most of these species, at both LIG and LGM (001). However, they all display suitable habitat in Sri Lanka at these epochs (e.g., **Fig. 2c**). Using the more liberal threshold (zero omission), only five of these were predicted to have suitable habitat at the LIG, whereas all but three did so in the LGM in the WG. Therefore, in either case most of the southern-most endemics did not have suitable habitat predicted in the WG between the LIG and LGM.





**Figure 2.** Three cases illustrating the basic scenarios of predicted distribution change from Late Inter Glacial (LIG, 120–140 kyr BP) to Late Glacial Maximum (LGM, 21 kyr BP) and present of species. a) *Rhododendron arboreum* displays a relatively stable area of predicted suitable habitat from the LIG through to the present; b) the area predicted suitable for *Diospyros assimilis* in the LIG was larger than in the LGM and was further reduced in the present; and lastly c) *Vernonia travancorica* had no area predicted suitable in the WG in the LIG and LGM (0 pixels) compared to the present, whereas it is predicted present in Sri Lanka.



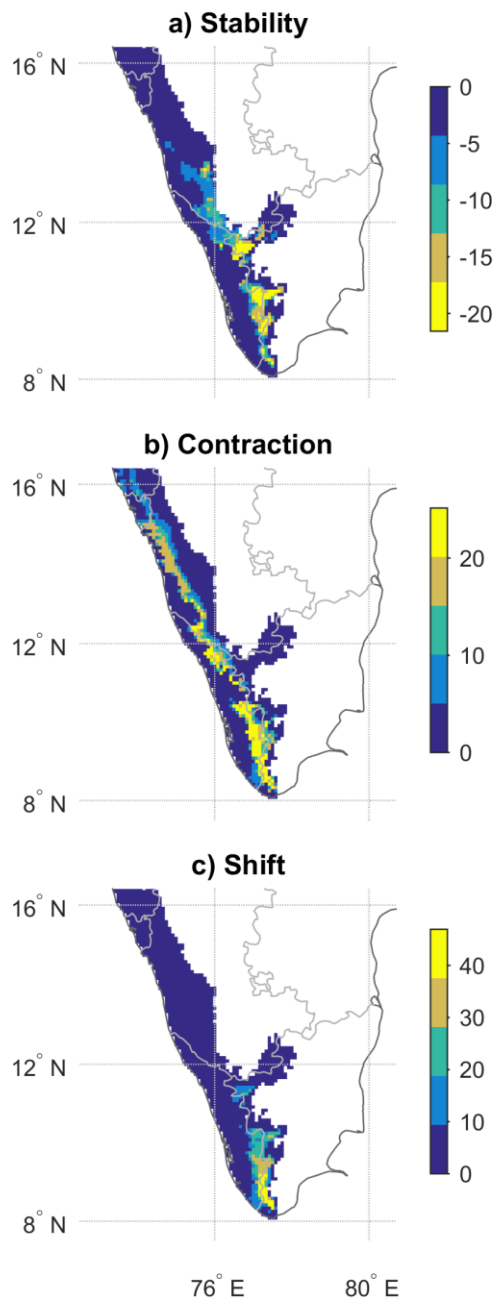
**Figure 3.** Scatter plot of the Correspondence Analysis representing the changes in predicted distributions for each species at the three epochs. The pixels of the predicted distribution maps are coded in 7 classes representing combinations of predicted presence-absence at the three epochs: the first binary number of the index represents Late Inter Glacial conditions (LIG, 120–140 kyr BP), the second the Last Glacial Maximum conditions (LGM, 21 kyr BP) and the third number represents present conditions. The relative frequency of these classes for each species determines scenarios of: area contraction (larger suitable area at LIG than at LGM and/or present); area expansion scenario (reduced predicted habitat area at LIG as compared to LGM and/or present); area stability (similar areas in the LIG, present and/or LGM). A representative species in each scenario is highlighted (see also Fig. 2).

### Biogeographic scenarios and species climatic preferences

The synthetic maps of **Fig. 4** represent the spatial signature of these main biogeographic scenarios. They highlight areas where the endemic species that more frequently underwent stability, contraction or shift are currently located, according to their scores on the CA axes. Species scores on CA axis 1 increased with their mean temperature and seasonality preferences (multiple regression  $R^2 = 0.48$ , Fisher  $p < 0.001$ ; Table S2 in Appendix S2). This model thereby pointed to the persistence of suitable habitat from the LIG (negative CA axis 1) for species that currently occur at higher elevations and montane forests below 12°N, i.e. which prefer lower temperatures and lower seasonality (see **Fig. 4a**). At the other end of the spectrum (positive CA axis 1) are species associated with lower elevations and higher seasonality, for which predicted

distribution contracted after the LIG. They are found at the ridge of the Ghats, exposed to high rainfall due to monsoon convection, and in the drier northern WG (**Fig. 4b**).

Conversely, the fit was less good but still significant and temperature preference increased whereas seasonality decreased along CA axis 2 ( $R^2 = 0.29$ , Fisher  $p < 0.00$ ; Table S3 in Appendix S2). The relationship with seasonality was consistent with the extreme negative scores of southern-most species, in a region where seasonality is minimal (see **Fig. 4c**).



**Figure 4.** Mapping of the biogeographic expansion, stability and contraction scenarios of Fig. 3, based on the sum of current binary species predicted distributions weighted by their scores along CA axis 1 and 2.

### Imprint of past predicted distributions on current populations

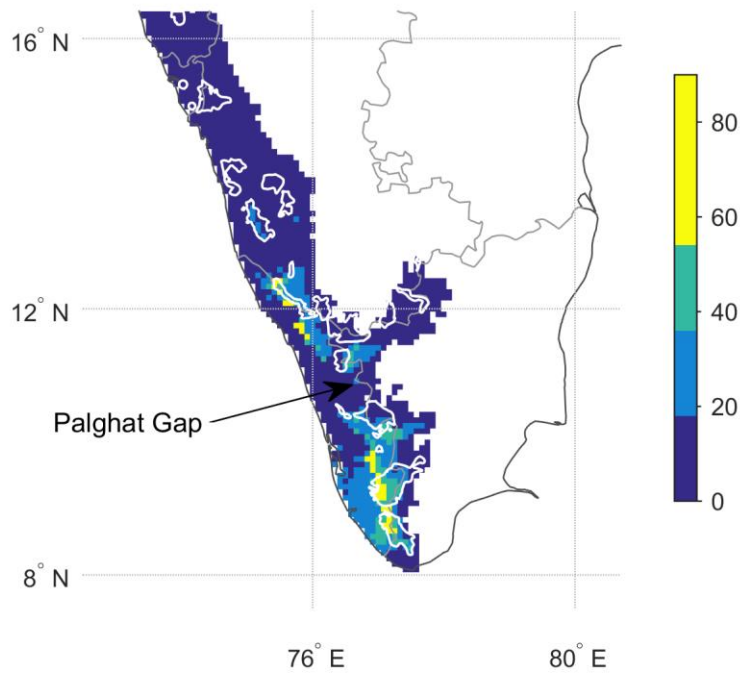
From the multinomial test of the distribution of observed current occurrences in each of the 7 pixel categories, we found that populations located in currently suitable habitats of almost a quarter of the species (44) were not randomly distributed with regard to past predicted distributions (adjusted  $p < 0.05$ , Appendix S3).

Of the species with negative scores on the first CA axis, 16 species displayed more current observations in category 111 than expected by chance, suggesting that these populations could have persisted in the same area since the LIG (scenario of stability). These include species  $<12^{\circ}\text{N}$  and montane species spanning the Palghat Gap according to **Fig. 4a**.

Of the species having contracted in area since the LIG (more frequent 100, 101, 110 pixels, positive CA axis 1), 17 species have more current observations in category 111 (pointing to contraction to stable areas) and five species in 011 (shift, expansion since LIG to areas suitable since LGM) than expected by chance. A number of these species are today distributed predominantly at mid-elevations along the ridge of the WG and the northern lowlands (**Fig. 4b**). In addition, some species displayed significantly more occurrences than random in the category 101, reflecting possible survival at the LGM despite a transient reduction in favourable habitat. The multinomial test results for species with reduced or null distribution at the LIG, like those restricted to the southern WG (**Fig. 4c**), were not meaningful as the species are not predicted present in most of the 4 pixel categories.

One species, *Glycosmis macrocarpa* was significant when testing whether populations currently located in unsuitable habitats were over-represented at LIG and/or LGM (situations 010 and 110), i.e. a possible relict of a habitat that was suitable in the past.

Areas in the WG that were predicted suitable throughout the period studied summed over all the species are shown on **Fig. 5**, in which pixel colour scales with the number of species having a suitable habitat predicted there across the three epochs (111 category).



**Figure 5.** Synthetic map highlighting the putative stable zones from Late Inter Glacial (LIG, 120-140 kyr BP) to present in the Western Ghats. The grey colour scale represents the number of species for which a given pixel was predicted suitable at the three epochs i.e. LIG, LGM (Last Glacial Maximum, 21 kyr BP) and present. The high elevation forests span the 30km-wide Palghat Gap, which otherwise forms a geographical barrier to dispersal of species restricted to the southern WG. Protected areas (source: IUCN and UNEP-WCMC, 2014, [www.protectedplanet.net](http://www.protectedplanet.net)) in the WG are superimposed in white outline. The present network of protected areas in the WG does not cover the areas with the highest number of species in stable zones.

## DISCUSSION

### *No evidence of Quaternary refugia within WG*

Jackson and Overpeck (2000) suggested that to avoid extinction, a species must either maintain a sufficiently broad fundamental niche or be capable of evolutionary changes rapid enough to track the realised environmental space. Our analysis of past predicted species distributions provided evidence for the likely persistence of most of the studied endemic species in the WG over the last 150 kyr. Over this period, extensive suitable habitats remained in this topographically contrasted region. Our results, based on the assumption of niche conservatism, indicate that many species are currently found in habitats that were suitable in the past, suggesting the absence of strong selective pressure for niche change over this period. We suggest that no significant climatic fluctuation should have influenced biodiversity dynamics after the Cenozoic, implying that the high biodiversity of WG is mainly rooted in evolutionary processes before the Quaternary (Fjeldsa & Lovett, 1997).

Our results highlight zones that are more climatically stable than others, yet did not reveal restricted late-Pleistocene refuges in the WG. Over larger temporal and spatial scales, however, pollen analyses, studies on climate stability and the persistence of other humid forest-restricted relict taxa (Joshi & Karanth, 2013) support the hypothesis that areas of the WG and Sri Lanka served as refugia at the sub-continental level since much earlier, dating to the late Palaeocene–Early Eocene (Prasad *et al.*, 2009).

### *Scenarios of distributional changes relate to climate-induced habitat dynamics*

The comparison of the species trajectories, however, provided evidence of distinct biogeographical scenarios driving distributional changes within the WG over time and determining the current distributions, namely, (i) that species with most stable predicted distributions are mainly those that occur at higher elevations (stability scenario), (ii) that mid-elevation species along the ridge of the Ghats underwent a predicted reduction to more stable climatic areas (contraction scenario), and (iii) that no suitable habitat existed at the LIG for southern-most species occurring in least seasonal areas, implying recent range shift (shift scenario).

Spatial variation in rainfall regimes partly explains the origin of these contrasting scenarios. The CCSM4 GCM hindcasts and the literature indicate a lower mean annual precipitation at the LGM than in the LIG and the present, especially in areas that receive most of their rain during the summer monsoon (12–15°N). In contrast, probably due to the dominance of the winter monsoon during the LGM (Sarkar *et al.*, 1990), areas south of 12°N experienced higher or no change in rainfall, barring local variations. Here, fall in temperature probably played a relatively important role. The

stability scenario (i) concerned montane forests spanning the Palghat Gap as well as species with large altitudinal amplitudes mostly occurring below 12°N, and a few widespread species. The transient predicted expansion in the LGM of the latter two types with broader fundamental niches to lower elevations is consistent with the cooler conditions. The stability predicted over time of upper montane species appear to contrast with previous findings based on stable-isotope analysis of peat cores in the Nilgiri hills: that forest elements ceded to savanna at the LGM (e.g. Sukumar *et al.* 1995). However the latter findings were generalised for all the southern montane forests whereas neither climatic nor vegetation changes were uniform across them (Caner *et al.*, 2007). In the Nilgiri basin alone, the studied peat bogs were located in valleys in the west or centre where forests are restricted by strong south-west winds or low rainfall to sheltered valleys, and cooling due to temperature inversion here would have been more pronounced during the LGM. By contrast, the eastern Nilgiris, receiving winter rains and less sensitive to south-west monsoon fluctuations, support larger forest patches not confined to valleys according to Caner *et al.* (2007). Further, floristic composition across montane forests is not homogenous in terms of dispersal abilities or physiognomy, ranging from frost-tolerant temperate shrubs like *Rhododendron* to tropical elements. This opens up a host of possibilities for species-specific responses to environmental fluctuations. Many of the montane species currently have relatively wide altitudinal amplitudes, possibly reflecting their expansion to lower montane forests and transition zones and/or the occurrence of populations there since before the LGM.

The contraction scenario (ii) concerned species with larger latitudinal amplitudes having distributions extending to the drier north, and mid-elevation species occurring mostly between 12-15°N and above. The contraction can be explained by the weakened summer monsoon, reducing annual rainfall by up to 15% during the LGM in this area. The distribution of a species that was widespread earlier may thus have become fragmented. This is the case for *D. assimilis* and other species, which, having contracted to climatically stable areas after the LIG, currently have observations located in the category 111 (stable across the 3 periods), 011 (stable since LGM) or, for those with northern distributions, 101 (transient reduction in suitable habitat during the LGM). The topographic complexity of the middle elevation reliefs of the Ghats could have favoured species survival (e.g., Fjeldsa & Lovett, 1997), whereas the lowland northern species could have expanded to suitable habitat along the coastline exposed by the sea-level lowstand during the LGM (Farooqui *et al.*, 2014).

The third, shift scenario (iii) concerned 23 southern-most endemics (< 9°N), specialized to very short dry seasons (< 2-3 months). They all occur in the ecologically diverse Agasthyamalai Biosphere Reserve, a recognised centre of micro-endemism with zones of active speciation (Nayar, 1996). These species were predicted present in Sri Lanka but not in the WG at the LIG or

LGM. Using a lower threshold, most of these species were predicted present in the WG at the LGM, pointing to possible sub-optimal habitats and cryptic refuges in which populations of these endemics - over half being understorey species - survived. But at the LIG, seasonality, a major predictor for these species, was much higher and southern WG diverged from LGM and current conditions. This could suggest a more recent appearance in the zone for some of these specialized endemics. 15 of the 17 species-rich genera in question include species common to both WG and Sri Lanka, as well as endemic to each region. Close phylogenetic relatedness to extant Sri Lankan endemics (e.g., *Garcinia thwaitesii*), on which more study is needed, could mean that the ancestors of some of these taxa migrated to the WG between the LIG and the LGM and underwent parapatric speciation. In fact the two regions, together forming the Deccan plate, were bridged at several instances of lowered sea-levels over the past 500kyr (Rohling *et al.*, 1998) and the only other place 30% of Sri Lanka's non-endemic tree species are found is the WG (Gunatilleke & Gunatilleke, 1990). On the other hand, other affinities to more broadly distributed WG endemics are known (e.g., *Poeciloneuron pauciflorum* Bedd., a narrow southern endemic of a genus endemic to WG), suggesting possible ecological diversification from ancestors present in other parts of the WG. Therefore, our results support the idea that southern WG is a major evolutionary melting pot where particular conditions have favoured ecological and geographic speciation events, possibly even in recent times. Recent studies support Fjeldsa and Lovett's (1997) theory: stability permitted the survival of relictual lineages and explains the general lack of diversification in East African forests during the Pleistocene, yet does not preclude some cases of speciation on the periphery of stable areas (Dimitrov *et al.*, 2012).

An important issue is whether the three biogeographic scenarios can be attached to distinct lineages, which could reveal other underlying evolutionary forces acting in the Quaternary. Notably, the WG endemic flora is characterized by a number of species-rich genera, like *Diospyros*, *Garcinia*, *Humboldtia* and *Litsea*, the species of which occupy a broad range of distinct niches across the WG (Pascal 1988). In our analysis, species within these genera displayed diverse biogeographic scenarios during the Quaternary, related to the diversity of their abiotic habitat dynamics. Most had rather stable predicted distributions with no strong selective pressure for climatically-mediated diversification over the period. The diversity of endemic niches at fine taxonomic scales thus likely reflects evolutionary events preceding the last glacial cycle, with the possible exception of the above-mentioned southern-most endemics.

We further note that few species were predicted present over the 3 epochs in the archipelago of eastern hills between WG and Eastern Ghats. Yet 20 of the species analysed, about half of which are understorey endemics, currently occur there, even if their populations are small and scarce (Pragasam & Parthasarathy, 2009). Despite the contrasted macroclimatic conditions between



these hills and the main WG chain, local microclimatic and/or edaphic conditions could provide localized refugia for evergreen communities. Our SDM modelling captures most major macroecological conditions according to which large-scale species distributions could have been stable or not during the Quaternary. This does not however preclude the past/current existence of cryptic refugia at smaller scales (Ashcroft *et al.*, 2012). This hypothesis could also explain the persistence in unsuitable habitat during the LGM of species displaying significantly more occurrences than random in category 101, and the finding that the understorey tree *G. macrocarpa* had more occurrences in currently unsuitable habitats. However, these cases, even if potentially important to explain diversification events and possible re-colonisation from cryptic refugia, remain minor overall. Finer scale ecological analysis of abiotic and biotic requirements, as well as phylogeographical analyses of putative relict or sink populations, is needed for further insight into these issues.

#### *Limits of the study*

We are aware of and underline the methodological limitations related to the use of SDM, both for the present and for projections into the past (Svenning *et al.*, 2011; Varela *et al.*, 2011). We addressed the statistical performance and relevance of our results based on ten replicate models considering distinct subsets of 10% of occurrence localities for testing. In addition, we designed a specific null model, without subdividing the original data, to address whether the selected climatic variables were actual drivers of species predicted distributions. Both analyses show that our models captured ecologically meaningful drivers of the species distributions. However, the set of occurrences could still be biased given the history of deforestation, especially at low elevations. Furthermore, despite careful analysis prior to choosing among available GCM models, the nature and quality of past climate reconstructions remains a possible source of uncertainty in SDM projections. Lastly, the models should ideally have been evaluated using fossil data, but adequate data for the region, time period and species concerned were unavailable.

#### *Conclusions and perspectives*

In sum, (i) the predicted distributions of most species, apart from the southern-most narrow endemics, remained stable or contracted to stable areas over the last 150kyr, and (ii) species responses were linked to their location along the environmental gradients, beyond phylogenetic proximity. Lastly, (iii) the imprint of past predicted distributions on current populations are evident for 44 species with significantly more current observations than random in pixels that have been climatically stable over the 3 periods or since the LGM, attesting to long-term persistence of these populations within stable areas.

Figure 5 summarizes areas that were climatically stable since the LIG, where local conditions appear to have buffered the species from the effects of climate variability. Superimposing the current protected areas on this map, shows that these zones are not always targeted by conservation policies. For e.g., only 36% of pixels where over 30 species experienced climatic stability over the 3 epochs are protected. Our results can thus help to design useful indicators for future planning of reserves, with the aim of ensuring the persistence of species-rich evergreen forests in the face of ongoing climatic and anthropogenic changes.

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PHYLOGENETIC DIVERSITY IN THE WESTERN GHATS BIODIVERSITY HOTSPOT REFLECTS ENVIRONMENTAL  
FILTERING AND PAST NICHE DIVERSIFICATION OF TREES

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**ABSTRACT**

**Aim:** We addressed how current and past environmental conditions influenced extant patterns of phylogenetic diversity in tropical tree assemblages, depending on constraints exerted on ecological strategies over time and the conservation of these strategies in the process of evolution.

**Location:** Western Ghats region, Western Ghats-Sri Lanka Biodiversity Hotspot, India.

**Method:** Following the stress gradient and historical stability hypotheses, we expected phylogenetic clustering in both harsher environments and areas with historically less stable climates, and overdispersion in opposite conditions. We characterized the phylogenetic structure relative to a null model within and between 297 plots arrayed across broad-scale environmental gradients. To assess the imprint of ancient and recent evolutionary constraints, we calculated mean pair-wise (MPD) and nearest-taxon (MNTD) phylogenetic distances respectively, and related these and phylogenetic turnover indices to geographic and environmental variation.

**Results:** We found non-random phylogenetic structure depending on both current abiotic and historical habitat stability gradients. At broader evolutionary scales (MPD), 1) harsher environments filter closely-related species, while 2) phylogenetic overdispersion suggests niche differentiation in southern stable and least seasonal habitats; however, 3) phylogenetic overdispersion increases with temperature stress at higher elevations. At finer evolutionary scales (MNTD), we found generally increased clustering. Phylogenetic turnover was driven by current abiotic factors, not space, and was highest along the rainfall gradient.

**Conclusions:** Phylogenetic clustering under hydric stress or historical instability suggests functional convergence due to filtering of adapted species. Overdispersion occurs either in least seasonal stable forests or high elevation ecosystems; in the former case, this can be ascribed to conservation of old lineages and opportunities for diversification in refugia, and in the latter to the assemblage of species pools of distinct biogeographic and evolutionary backgrounds (temperate and tropical). Divergence in habitat preferences of closely-related species along the seasonality gradient suggests greater lability of traits related to seasonality than rainfall.

## INTRODUCTION

A complex mix of ecological, evolutionary and biogeographical processes drive species distributions and assemblages from local to regional scales (Leibold *et al.*, 2004; Mittelbach *et al.*, 2007). Environmental filtering is expected to drive species turnover and changing ecological strategies along environmental gradients (Ackerly & Cornwell, 2007). Most emphasis has been put on the influence of current environmental filters, but historical theories (Ricklefs, 1987), especially focussing on climate history (Normand *et al.*, 2011; Ordonez & Svenning, 2015), also stress that past environmental changes can contribute to observed patterns. Analysing the phylogenetic structure of species assemblages adds the temporal dimension needed to address the joint influence of evolutionary and biogeographic dynamics in addition to contemporary factors (González-Caro *et al.*, 2014; Fine, 2015). Stimulated by the increasing availability of phylogenetic information, the development of community phylogenetics (or ecophylogenetics) has provided new concepts and methods for such integration (Webb *et al.*, 2002; Mouquet *et al.*, 2012; Gerhold *et al.*, 2015).

As a result of multiscale biodiversity dynamics, distinct phylogenetic patterns are expected over a spatial hierarchy (Cavender-Bares *et al.*, 2006; Swenson *et al.*, 2007). Based on an assumption of niche conservatism (Wiens & Graham, 2005), the phylogenetic structure of extant biodiversity is expected to reflect present niche-based species dynamics: (i) biotic interactions can entail niche differentiation and phylogenetic overdispersion, or clustering under competitive hierarchy (Kunstler *et al.*, 2012), while (ii) at the larger habitat scale, environmental filtering can prevail and lead to functional and phylogenetic clustering (Gastauer & Meira-Neto, 2014; Carboni *et al.*, 2016). Phylogenetic patterns also convey signatures of the past, as (iii) they are influenced by the historical biogeography of lineages and evolution of biological attributes conferring extant adaptations (Chave *et al.*, 2007; Hardy & Senterre, 2007; Lomolino *et al.*, 2010; Bartish *et al.*, 2016) and (iv) diversification and migration events determine the building of regional biota (Emerson & Gillespie, 2008; Vamوسي *et al.*, 2009; Fine & Kembel, 2011). Both (iii) and (iv) influence extant phylogenetic patterns at local and regional scales. We address here the respective contributions of current niche-based dynamics and past biogeography on the phylogenetic structure of highly diverse rainforests covering broad-scale environmental gradients in South India.

The Western Ghats (WG) of India, with strong environmental gradients and a rich biogeographical history (e.g. Prasad *et al.*, 2009), is well-suited to investigate the role of current environmental filters and historical processes on extant diversity patterns. Firstly, the deeply dissected topography imposes drastic changes in bioclimatic conditions over space and time. Marked



variations in rainfall, seasonality and temperature, the latter closely linked to elevation here, are major drivers of species turnover (Pascal, 1988b; Bonnefille *et al.*, 1999; Barboni *et al.*, 2003; Ramesh *et al.*, 2010a). Species also responded differently to quaternary climatic changes depending on their bioclimatic preferences (Bose *et al.*, 2016). Secondly, the forests of southern WG have served as recurrent refugia since the Early Eocene (Prasad *et al.*, 2009), and are biogeographically delineated from the forests further north characterised by lower historical habitat stability above  $\sim 13^{\circ}\text{N}$  (Radhakrishnan *et al.*, 2007). The predicted higher diversity and endemism in historically stable areas (Graham *et al.*, 2006; Fine, 2015) is supported by a south-north variation in species diversity and endemism (Ramesh & Pascal, 1997; Barboni *et al.*, 2003). Endemism rates decrease from  $\sim 70\%$  in southernmost WG to  $<10\%$  in the far north (Ramesh, 2001). However, the influence of these past and present environmental variations on the phylogenetic structure of tree species across the WG has been little studied (but see Hardy *et al.*, 2012).

We address here two basic hypotheses on the variation of phylogenetic diversity in the WG: 1) a stress-gradient hypothesis (Weiher & Keddy, 1995) and 2) a historical stability hypothesis (Jablonski *et al.*, 2006; Kissling *et al.*, 2012). According to the first hypothesis, only specific ecological abilities that have evolved in specific clades allow local persistence in environmentally stressful sites, leading to greater environmental filtering and phylogenetic clustering (Webb *et al.*, 2002; Kraft *et al.*, 2007). High seasonality and low rainfall conditions may represent ecophysiological limits that not all lineages are able to overcome, depending on inherited adaptations (Anacker *et al.*, 2012). Dry season drought is an important constraint for many tropical plants, expected for understorey trees with shallow roots (Wright, 1992) but also canopy trees (Corlett, 2016). Among other factors, decreasing temperature with elevation also affects tree growth and respiration. Assemblages of closely-related taxa have recently been reported in environmentally constraining contexts such as high elevations (Qian *et al.*, 2014) and in seasonally dry areas (Moro *et al.*, 2015). We thus expect non-random phylogenetic structure along major abiotic gradients, with clustering at high elevations and in seasonally water-stressed areas in central WG and south-eastern leeward slopes. By contrast, conditions of low seasonality and a diversity of resources allow greater niche differentiation, and stronger competition leads to limiting similarity among coexisting plants (Abrams, 1983). Such niche differentiation can cover adaptations of a greater diversity of lineages, so we expect phylogenetic overdispersion (species less related than expected by chance) in southern WG. However, if species niches are not phylogenetically conserved, these basic expectations may be challenged, as we may find for e.g. overdispersion due to environmental filtering under more stressful conditions through convergent evolution in distantly-related species (Cavender-Bares *et al.*, 2004).

According to the second hypothesis, species are differentially excluded from areas experiencing greater historical climate fluctuation, while climate stability enhances persistence and ecological diversification over geological time-scales (Jablonski *et al.*, 2006; Ordonez & Svenning, 2015). Paleoclimatic changes can affect the composition of regional biota based both on climate-related traits and on dispersal abilities during migration (see Ordonez & Svenning, 2015). In other words, less stable areas would harbour assemblages of survivors and/or species favoured by their ability to re-colonize these areas after local extinction (Kissling *et al.*, 2012). This could show up as phylogenetic clustering when niches are conserved and only certain clades have evolved the necessary adaptations, or overdispersion if niches are convergent between distantly-related lineages for instance due to higher immigration into less stable areas (Costion *et al.*, 2015). By contrast, older, more stable rainforest regions as in southern WG (Prasad *et al.*, 2009) should comprise a mixture of distantly-related lineages, which could both persist better through evolutionary time ('museum') and diversify over a broad ecological spectrum ('cradle'). Phylogenetic overdispersion would reflect ancient diversifications at a macroevolutionary scale, but we could also find clustering based on subsequent localized clade divergences and habitat specialization (Kooyman *et al.*, 2011). The hierarchy of evolutionary and biogeographic influences over time is expected to affect the phylogenetic structure differently depending on clade age: Koenen *et al.* (2015) suggested that rainforests are museums for higher level taxa with diverse traits that also provide a stock for ecological diversification over more recent clades.

To test the basic stress gradient and historical stability hypotheses in the context of WG tree communities, we analysed phylogenetic structure along environmental gradients and at different phylogenetic depths (Mazel *et al.*, 2015). A challenge is to use appropriate indices of phylogenetic diversity and relevant null models (null communities drawn from reference species pools) to assess these signatures across time and space. Different measures of within-community phylogenetic relatedness are sensitive to either deeper or more terminal nodes, revealing the influence of older relationships or more recent phylogenetic association of species with congeners or confamilials (Webb, 2000) respectively. Since they capture different time-frames of ecological association and evolutionary adaptation, this allows examining different timescales of evolutionary and ecological dynamics (Mazel *et al.*, 2015). We also defined distinct expectations depending on niche conservatism vs. niche convergence in the phylogeny. For instance, environmental filtering and niche conservatism consistently operating at large and fine evolutionary time-scales would lead to both basal and terminal clustering, while environmental filtering at large time-scales and niche differentiation between close relatives at fine time-scales (and/or colonisation of distantly related lineages from adjacent regions) should result in basal clustering and terminal overdispersion; alternatively, phylogenetic overdispersion in deep nodes

can reflect the legacy of ancient evolutionary differences (older lineage splits), followed by phylogenetic clustering in terminal nodes reflecting environmental filtering of clade-specific habitat preferences acquired over time.

When environmental filtering operates along broad-scale gradients, we also expect higher turnover in phylogenetic composition, reflecting a change of lineages adapted to different environmental conditions. Alternatively, when closely-related species diverge in habitat preferences and occupy dissimilar environments (Fine *et al.*, 2005), we expect lower phylogenetic turnover along the gradient (González-Caro *et al.*, 2014). Therefore, analyzing phylogenetic turnover along gradients allow assessing the strength of environmental filtering of clades with differing adaptations. We thus (i) quantified the phylogenetic structure within and between assemblages in 297 tree communities arrayed across the entire WG region, (ii) examined how this structure varied along broad-scale environmental and historical habitat stability gradients. To capture temporal and spatial variation, we characterised phylogenetic structure using alpha diversity metrics describing basal as well as terminal phylogenetic dispersion, and investigated phylogenetic turnover between pairs of sites at increasing ecological and spatial distances.

## **MATERIAL AND METHODS**

### **Species data and phylogeny**

We used a dataset of 297 plots including 459 species, comprising a) 189 plots located in wet or dry evergreen forests between 8°5' to 11°5'N (Gimaret Carpentier, 1999), b) 12 plots in lower, medium and high elevation forests between 10-12°5'N from Chandrashekara (2004) and c) 96 plots covering a wide array of habitats between 13°30'-15°N in north-central WG (Ramesh *et al.*, 2010b). Species names were checked and updated with The Plant List (2013) and a recent WG flora (Nayar *et al.*, 2014). For a) and b) species accumulation sampling methods were used. For a) all tree species departing from a fixed point until no new species were found were noted, and plots in b) were determined including all trees above 10cm in stem diameter until the species accumulation curve flattened. We therefore verified that species richness of these plots was comparable to plots in c) which comprised complete inventories of all plants within a fixed area of 1ha. Only tree species and plots not located in deciduous formations were included in the analyses and data from plots in c) were converted to presence/absence format to match a) and b).

Each plot was characterised by its location in one of the 19 discrete forest types delineated by Pascal (1988). These comprise 13 wet evergreen forest types classified according to low (0-800m), medium (800-1400m) and high elevation (>1400m), and 3 dry evergreen forests found on eastern slopes south of the Palghat gap (11°N) (Supplementary material Appendix 1, Table

A1). Previous work in the WG underlined major ecological differentiation of forest types related to drought stress above and below 13°N (Pascal, 1986; Barboni *et al.*, 2003). We refer to southern vs. central WG plots and forest types to acknowledge this delimitation.

We used the time-calibrated megaphylogeny of Zanne *et al.* (2014), updated by Qian and Jin (2015), built from gene sequences of land plants available in GenBank. We derived the phylogeny of the regional species pool in the WG forests using PHYLOMATIC v.3, which added additional genus nodes when needed. 85.4% of these species belonged to Eudicots, 13.7% to Magnoliids, while there were only 5 Monocots and a single Gymnosperm.

### **Environmental, historical and spatial predictors**

To assess how the phylogenetic structure of tree communities varied depending on environmental stress and historical habitat stability, we included 1) variables reflecting abiotic stress for plants in the WG, viz. precipitation seasonality, annual rainfall, temperature and elevation (Pascal 1988), and 2) an index of historical habitat stability over the last 150 kyr, derived from a previous study (Bose *et al.*, 2016). Our variables would thus convey the effect of ecological filters of current climate and its dynamics over the Quaternary. The combination of these ecological filters and the evolutionary signature of the niches on the phylogeny would result in a certain phylogenetic structure.

We performed a Principal Component Analysis (PCA) of 19 bioclimatic variables obtained at 30-sec resolution (~1 km) from WorldClim (Hijmans *et al.*, 2005). The first three PCA axes explained 90.4% of the overall variation and represented major environmental gradients devoid of collinearity, (i) a decreasing temperature with elevation gradient, (ii) a south to north increase in seasonal hydric stress (from 3 to 8 months of dry season, with rainfall < 100 mm) and (iii) a west-east decreasing rainfall gradient (annual precipitation from 484 to 6032 mm) (Supplementary material Appendix 1, Fig. A1 a-c).

Historical habitat stability (Fig. A1d) was assessed from Last Inter-Glacial (LIG, ~120-140 kyr BP), following Bose *et al.* (2016). For each 5 arc-min grid cell in the WG, binary maps of potential habitat models were calculated for each species at three periods, namely, present, Last Glacial Maximum (LGM; ~21 kyr BP) and LIG. In each grid cell, we then calculated the number of species potentially occurring at all the three epochs. The higher this number, the greater the number of species that could persist locally over time, thus providing an index of habitat stability (see Bose *et al.*, 2016 for details). The climate stability over this period could have permitted the maintenance of greater ecological diversity and thus capture a greater phylogenetic diversity that reflects the diversity of adaptations acquired in the course of evolution over longer time-periods.

## Statistical analyses

**Alpha phylogenetic dispersion:** We used complementary metrics reflecting phylogenetic structure at different evolutionary depths (Mazel *et al.*, 2015), viz., mean pair-wise phylogenetic distance (MPD) and mean nearest-taxon phylogenetic distance (MNTD), implemented in the *picante* R package (Kembel *et al.*, 2010). The mean pair-wise distance between all species in a community, MPD, is sensitive to deep branching structure, while the mean distance from each species to its closest relative in the community, MNTD, reflects the influence of more recent evolutionary events (Hardy & Senterre, 2007). To avoid inflated phylogenetic dispersion due to a few taxa connected to deep phylogenetic nodes, we excluded the single gymnosperm and the five monocot species in subsequent analyses. We considered only species presence and absence since abundance data was not available for all the plots.

We built the null distribution of these metrics by randomly reshuffling the tip labels of the phylogeny 999 times. We then calculated the standardised effect size (SES) of MPD and MNTD in a community which represents the deviation of the observed phylogenetic structure from a null situation without constraint on phylogenetic structure. Its calculation removes potential bias associated with difference in species richness among plots, as the effect size is divided by the standard deviation of the null model (González-Caro *et al.*, 2014). Negative values of  $MPD_{SES}$  and  $MNTD_{SES}$  indicated phylogenetic clustering, while positive values indicated overdispersion i.e. species found in a plot were on average more (resp. less) closely related than expected by chance. The deviation from the null hypothesis was considered significant at 5% for low quantiles ( $p < 0.025$ , clustering) and high quantiles ( $p > 0.975$ , overdispersion) respectively.

We performed generalised linear models (GLM) of the variation of local phylogenetic structure ( $MPD_{SES}$  and  $MNTD_{SES}$ ) with environmental conditions, and variation partitioning to assess the relative importance of current abiotic gradients and historical habitat stability (varpart, package *vegan* in R). The total percentage of variance explained by the GLM regression was thus partitioned into unique and common contributions of the two sets of predictors (Borcard *et al.*, 1992). We also performed a canonical correspondence analysis (CCA) of the changes in community composition depending on the abiotic and historical stability gradients (ter Braak, 1986) and tested for phylogenetic signal of species scores on the CCA axes using Pagel's  $\lambda$  (Pagel, 1999) as recommended by (2012). The phylogenetic dependence in these key niche traits also allows assessing the strength of niche conservatism under the Brownian model of evolution along the basic environmental gradients expressed in the CCA (Cooper *et al.*, 2010).

**Phylogenetic turnover:** Furthermore, we decomposed the phylogenetic diversity of communities into  $\alpha$ - (within-community) and  $\beta$ - (among-communities) components. The  $\pi$ st metric measures the gain of phyletic divergence between species occurring in different sites compared with those from the same site (Hardy & Senterre, 2007), based on presence/absence data. We calculated both pair-wise  $\pi$ st (PW $\pi$ st) and global  $\pi$ st using the spacodiR package in R (Eastman *et al.*, 2011). PW $\pi$ st was tested against the same null model as above, and a value departing positively from the null hypothesis represented phylogenetic turnover between communities (Hardy, 2008; Hardy *et al.*, 2012).

We performed Mantel tests with 999 permutations of the relationship between pair-wise PW $\pi$ st values and the distances in abiotic, historical and geographic variables among communities (Hardy *et al.*, 2012). We also conducted partial Mantel tests, where all variables other than the focal one were used as covariates. Abiotic and historical stability distances were calculated as Euclidean distances between plots based on rainfall, seasonality, elevation and the historical stability index. We used the plots' geographic coordinates to calculate the spatial distance between communities. Since the region is located at low latitudes the potential area distortion is relatively low.

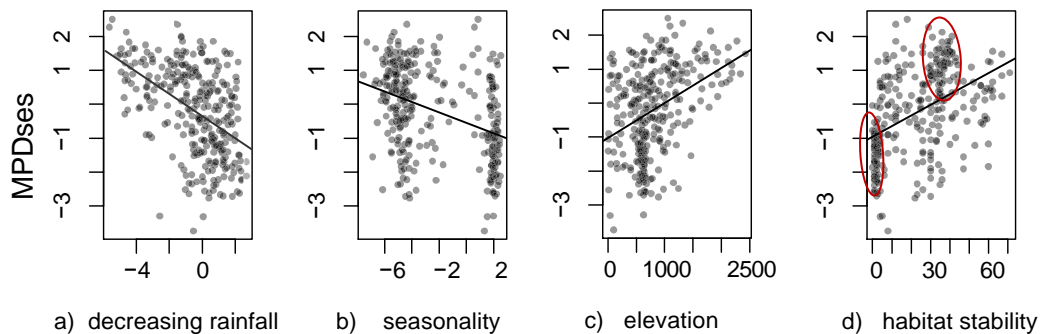
## RESULTS

The CCA analysis represented the main changes in community composition along the environmental gradients. Seasonality, elevation and stability all contributed strongly to CCA Axis1 (50% of variance explained), and rainfall to CCA Axis2 (30%), and were thus major drivers of both changing community composition. In addition, the phylogenetic signal of species scores on these axes represented the level of niche conservatism along the basic gradients. The phylogenetic signal was highly significant along the annual rainfall gradient ( $\lambda=0.46$ ,  $p\text{-value}<<0.001$ ) and less marked along the seasonality gradient ( $\lambda=0.35$ ,  $p\text{-value}<0.001$ ).

### Variations in local phylogenetic structure

We found non-random phylogenetic structure in communities across the WG. First, according to GLM analysis, both MPD<sub>SES</sub> and MNTD<sub>SES</sub> decreased (phylogenetic clustering) at lower rainfall level and increased (overdispersion) with higher rainfall ( $p<0.001$ ). MPD<sub>SES</sub> also decreased with seasonality but increased with higher elevations ( $p<0.001$ ). MNTD<sub>SES</sub> was less significantly predicted by seasonality ( $p<0.05$ , see Table A2a). Statistically overdispersed and clustered plots thus tended to occupy extremes of the abiotic gradients (Fig. 1) as they are expected to be typified by stronger habitat filtering on one end (drier, more seasonal, less stable) and more niche differentiation on the other (wet, less seasonal, more stable). However, some highly over or under-dispersed plots were found at intermediate positions of the gradients.

Historical habitat stability contributed to explain variation in phylogenetic structure in addition to extant climate ( $MPD_{SES}$ ,  $R^2=0.42$ ;  $MNTD_{SES}$ ,  $R^2=0.08$ ). Variation partitioning showed that the unique contribution of current abiotic factors (0.22) explained most variance for  $MPD_{SES}$ , while the unique contribution of historical habitat stability was low (0.04). However, a fair portion was attributed to the joint effect of current and historical predictors (0.16; see Table A2b for details). In fact, least stable plots were also currently most seasonal, and plots of intermediate stability (30-40 on a scale of 0-80) were located at higher elevations (encircled points in Fig. 1d).



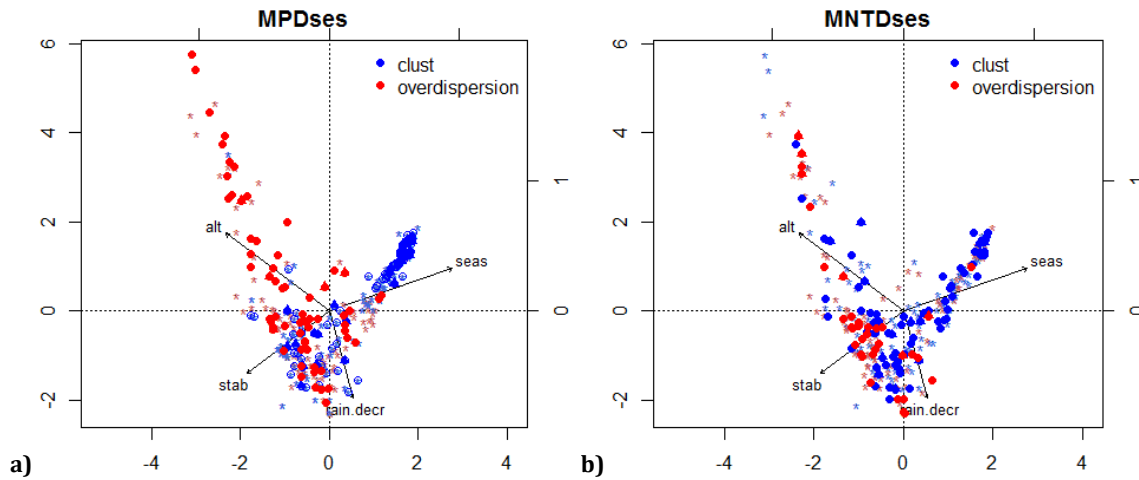
**Figure 1.** Variation of  $MPD_{SES}$  (overdispersed + $MPD_{SES}$ , vs. clustered - $MPD_{SES}$ ) according to a) decreasing rainfall, b) increasing seasonality (PCA scores), c) elevation (m) and d) historical habitat stability, with most seasonal plots in areas of low stability and high elevation plots in areas of intermediate stability encircled. Regression lines are shown.

Figure 2 further shows phylogenetic clustering (blue) and overdispersion (red) along the axes of a CCA representing main changes in community composition along the environmental gradients. Deep phylogenetic clustering was found related to positive scores of sites on CCA Axis1, characterised by greater seasonality and lower historical habitat stability ( $MPD$ , Fig. 2a and 3a). Comparison across forest types (Fig. 4) underlined phylogenetic clustering in forest types of central WG (above  $\sim 13^\circ N$ ), for both  $MPD_{SES}$  and  $MNTD_{SES}$ , whereas basal overdispersion was found in southern forest types ( $MPD_{SES}$ ).

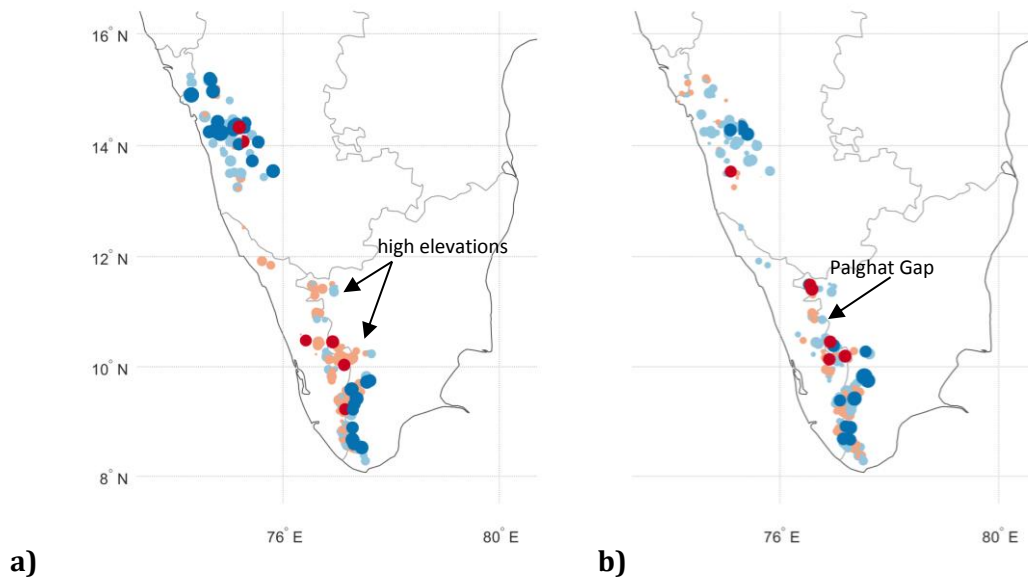
Clustering thus primarily occurred under drier and more seasonal regimes further north (76% of 97 plots departed from the null model,  $MPD_{observed} < MPD_{expected}$ ), while overdispersion occurred under the wet and less seasonal regime in the south (61% of 200 plots  $MPD_{observed} > MPD_{expected}$ ). Departing from the basic north-south gradient, phylogenetic clustering was also found for  $MPD_{SES}$  in dry evergreen forests in the south-east (+CCA Axis 3 not shown; DMM, DMMK, DMO types, in Fig. 4b, upper panel, see the codes in Table A1), and in the southernmost low elevation evergreen forest (DKS).

We observed increased terminal clustering in plots that were basally overdispersed at both high elevations and in less seasonal sites ( $MNTD$ , Fig 2b and 3b), especially in southern WG (clustering increased from 39% to 55% of plots). Details of  $MPD_{SES}$  vs.  $MNTD_{SES}$  values for individual plots

within forest types in Figure 5 shows that these cases also concern high elevation (BGL, LSM types) and neighbouring medium elevation (CMP) forest types in the south.

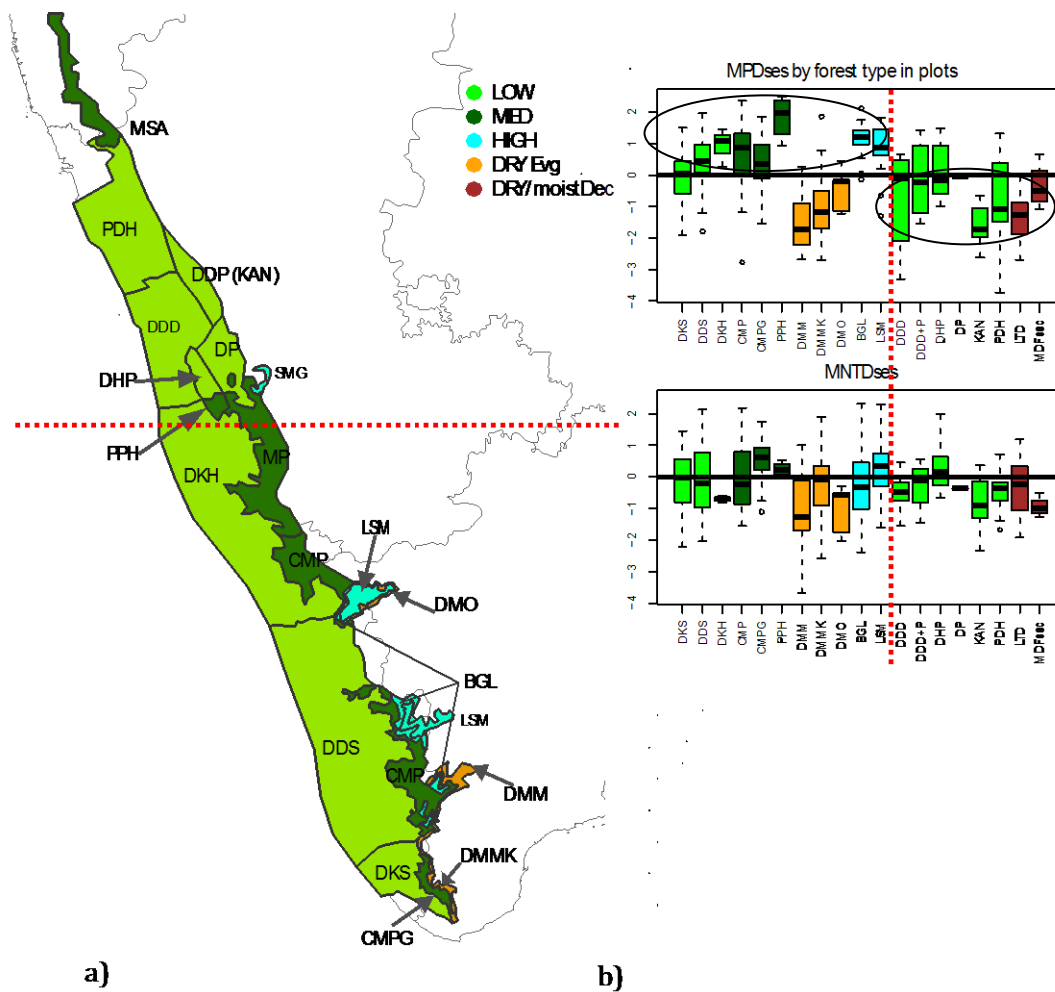


**Figure 2.** Biplot of the CCA of floristic composition where the colour of communities represents phylogenetic clustering (blue) and overdispersion (red) and is darker for plots with stronger negative or positive values respectively, for a)  $MPD_{SES}$  and b)  $MNTD_{SES}$ . Phylogenetic clustering was related to higher seasonality (seas) and overdispersion with lower seasonality, higher elevations (alt) and higher stability (stab) for  $MPD_{SES}$ . An increase in clustering, including higher elevation communities was found for  $MNTD_{SES}$ .

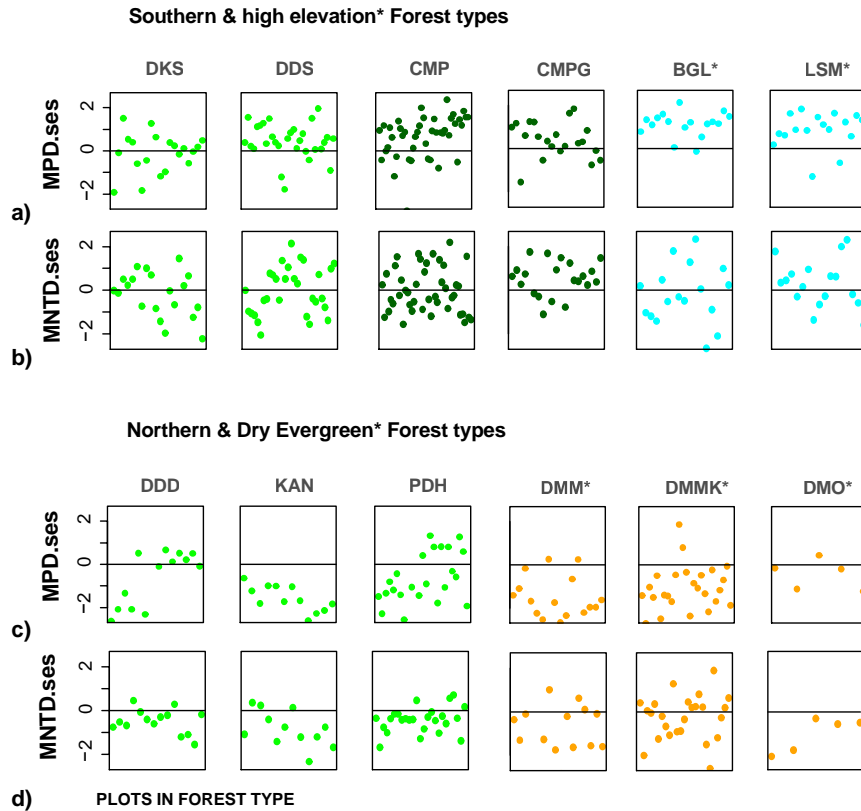


**Figure 13.** Local phylogenetic structure for a)  $MPD_{SES}$  and b)  $MNTD_{SES}$ . Blue to red colour represent low to high SES values. Point size varies according to absolute SES values, and dark colours are used for significant values and light colours for non-significant. Clustering (blue) is more common in northern WG ( $>13^{\circ}N$ ), while more overdispersion is found in southern WG (red). Plots in south-eastern dry evergreen forests are also mostly clustered (blue). For  $MNTD_{SES}$ , more southern plots are phylogenetically clustered.





**Figure 4. a)** Main forest types in the WG categorized into low, medium and high elevation wet evergreen dry evergreen and moist or dry deciduous types (colour code). The red line at 13°N separates northern and southern types. **b)** Distributions of MPD<sub>SES</sub> and MNTD<sub>SES</sub> values in the plots per forest type. Positive and negative SES values indicate overdispersion and clustering, respectively. The red line separates southern (<13°N, left) from central (>13°N, right) types. In top panel, the general trend is overdispersion in southern (+MPD<sub>SES</sub>, ancient evolutionary events), and clustering (-MPD<sub>SES</sub>) in north-central forests. Dry evergreen forests of the south are an exception since they are more clustered. The bottom panel (MNTD<sub>SES</sub>, sensitive to terminal relatedness) shows lowered overdispersion in southern forests, and in some plots more clustering. See Fig. 5 for plot details.

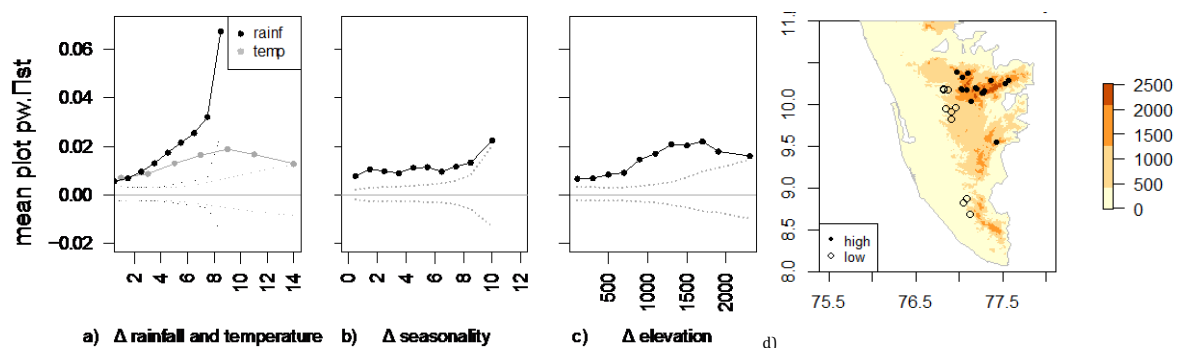


**Figure 14.** Upper panels: southern forest types show **a)** mostly deeper phylogenetic overdispersion (+MPD<sub>SES</sub>) and **b)** greater number of clustered plots (-MNTD<sub>SES</sub>) including at high elevations (BGL, LSM), at finer time-scales. Lower panels: northern forest types above 13°N and three Dry evergreen forest types (DMM, DMMK, DMO) of the south-east displaying **c)** plots generally clustered (-MPD<sub>SES</sub>) at longer evolutionary scales and also **d)** mostly clustered (-MNTD<sub>SES</sub>) at finer evolutionary scales. Plots are coloured according to their location at low, medium and high elevation wet evergreen and dry evergreen formations

### Phylogenetic turnover according to environmental and spatial distances

Distinct species were phylogenetically closer within communities than between communities (global  $\pi_{st}=0.01$ ,  $p<0.001$ ). According to both Mantel and partial Mantel tests on mean pair-wise turnover measures ( $PW\pi_{st}$ ), differences in rainfall, seasonality and elevation were related to phylogenetic turnover (Fig.6), while geographic distance did not contribute in addition to these environmental factors. Annual rainfall contributed the most, and this was also more significant than the lower contributions of seasonality and elevation (Table A3).

Phylogenetic turnover among plots that are increasingly contrasted in annual rainfall levels increases monotonically to a maximum  $PW\pi_{st} \sim 0.07$  (Fig. 6a). However, along the seasonality gradient, phylogenetic turnover was lower (average  $PW\pi_{st}= 0.01$ ), and only increased between plots most contrasted in terms of seasonality (maximum  $PW\pi_{st} =0.02$ , Fig. 6b). For elevation, we observed low variation of  $PW\pi_{st}$  with increasing elevation difference for plots below 900m difference, while  $PW\pi_{st}$  abruptly increased above this difference (Fig. 6c). Since temperature and elevation in the WG were strongly correlated, a similar trend was obtained for phylogenetic turnover between plots of contrasted temperature (in grey in Fig.6a).



**Figure 6.** Phylogenetic turnover (mean  $PW\pi_{st}$ ) as a function of environmental distance for **a)** rainfall and temperature, **b)** seasonality and **c)** elevation. The dotted lines represent the 95% confidence envelopes of the null hypothesis of absence of phylogenetic constraints. **d)** Pairs of plots (solid dot and open circle) with  $>1000m$  elevation difference.

## DISCUSSION

Variations in hydric stress (annual rainfall and seasonality) and historical habitat instability determine phylogenetic structure of tree communities in the WG. Significant phylogenetic signal along the annual rainfall gradient based on species scores of the CCA analysis agrees with that found by Hardy *et al.* (2012) for current and ancestral niches, and significant phylogenetic turnover ( $\pi$ st) supported phylogenetic sorting of species niches among communities along the rainfall gradient.

Local phylogenetic structure covered a broad range of MPD<sub>SES</sub> and MNTD<sub>SES</sub> values from clustering to overdispersion. These results are consistent with the idea that phylogenetic turnover may dominate over large-scale environmental gradients, while assembly processes related to environmental filtering and niche differentiation influence the local community structure (Silvertown *et al.*, 2006; Prinzing *et al.*, 2008). According to our results, 1) harsher environments filter more closely-related species (phylogenetic clustering) in central WG and dry evergreen formations in the south-east; 2) by contrast, in less constrained and more stable habitats of south WG, phylogenetic overdispersion suggests niche differentiation of more distantly-related species. These least seasonal forests could act as both an evolutionary museum and cradle of WG biodiversity (Koenen *et al.*, 2015). Furthermore, 3) phylogenetic overdispersion is found at higher elevations, and points to a mixture of low- and high-elevation species pools with distinct biogeographic and evolutionary backgrounds (Meher-Homji, 1967). Our results underline the potential of the ecophylogenetic approach to decipher the signatures of evolutionary, biogeographic and ecological processes on extant biodiversity patterns (Gerhold *et al.*, 2015).

### ***Harsher and less stable environment filters more closely-related species***

Basal (MPD) and terminal (MNTD) phylogenetic clustering was associated with greater physiological stress and less historical stability in communities, pointing to the fundamental influence of environmental filtering at all phylogenetic scales. Humid formations in south WG benefit from almost year-round water availability, while precipitation seasonality increases northwards and on south-eastern leeward slopes. Annual rainfall also diminishes rapidly beyond the crest of the WG and is exacerbated by strong foehn effects during the monsoon on leeward slopes (Pascal, 1988a). Limited water availability can thus explain increased phylogenetic clustering in both central and southeast forest types. Specifically, central evergreen forests include an impoverished subset of southern species, and local dominance by *Poeciloneuron indicum* can represent an extreme case of such impoverishment (Pascal 1988).

In terms of historical habitat stability, forests beyond ~13°N experienced multiple alternations in climate and alterations in habitat dating from early Paleocene flood basalt volcanism to Miocene

aridity. Greater instability occurred in currently more seasonal areas, and in the Quaternary fluctuations of monsoon regime were greater in the northern half of the region ( $>12^{\circ}\text{N}$ , Bose *et al.*, 2016), making it difficult to separate the respective roles of current and past environments. In variation partitioning, the unique contribution of current environment was much higher than the unique contribution of past stability, but a fair amount of the variation in phylogenetic structure is attributable to their joint effects. To test the influence of past climatic instability in terms of limited migration from refugia (Normand *et al.*, 2011), additional analysis of the mismatch between potential and realized habitats and of the related variations in functional trait composition would be needed (Svenning *et al.*, 2010; Ordonez & Svenning, 2015).

***Distinct causes of phylogenetic overdispersion at high rainfall and low seasonality vs. higher elevations***

In southern WG, where annual rainfall is relatively high and the dry season is shorter, lower constraints due to abiotic stress could entail a stronger influence of competitive interactions and result in limiting similarity and phylogenetic overdispersion among co-existing species (Webb *et al.*, 2002). Over the long-term, i.e. beyond the Quaternary period, the maintenance of these more favourable conditions in this long-standing refuge (Prasad *et al.*, 2009) could have maintained more diverse lineages, and contributed to the phylogenetic overdispersion ("museum" hypothesis, Stebbins, 1974; Jablonski *et al.*, 2006). An exception was the southern-most lowland evergreen forest (DKS), displaying basal phylogenetic clustering (MPD), plausibly due to the presence of "Myristica swamps", characterised by the dominance of a few typically flood-tolerant trees with specific adaptations (e.g., pneumatophores and brace roots).

Deep phylogenetic overdispersion was also found at higher elevations (up to 2700 m asl in WG), where trees endure physiological stress due to lower temperatures, for e.g.  $<13.5^{\circ}\text{C}$  annual mean temperatures in upper montane LSM. Because of greater mist immersion and frost, the establishment and survival of many tropical species would be limited (Das *et al.*, 2015). High-elevation forest fragments, called "shola", are embedded in a matrix of grasslands and basically occur in thalwegs where they are protected from cold winds and fire. Temperature stress at high altitudes could result in phylogenetic clustering, as reported for other taxa like birds, bees, butterflies and microbes, including plants on volcanic mountains, due to environmental filtering (Dossa *et al.*, 2013; Qian *et al.*, 2014). However, contrary to phylogenetic clustering observed under seasonality stress in WG forests, we found phylogenetic overdispersion in higher elevation forests.

While competition can entail functional divergence and phylogenetic overdispersion in least stressful habitats, facilitation in more stressful habitats can also yield phylogenetic

overdispersion, as reported for instance in dry Mexican vegetation (Valiente-Banuet & Verdú, 2007). In this case, facilitation may be easier between species that are not too similar ecologically, hence evolutionarily more distant (Valiente-Banuet & Verdú, 2013). In the case of niche conservatism, the variation of phylogenetic structure with elevation can then be ascribed to the relative importance of different biotic forces viz. competition at lower montane and facilitation in higher montane forests (Callaway *et al.*, 2002; Bryant *et al.*, 2008).

Alternatively, if environmental filtering is indeed the primary driver of phylogenetic structure in montane forests, the evolution of traits needed to cope with high elevation conditions could have occurred independently in distantly-related lineages, as found by Culmsee and Leuschner (2013) in tropical old-growth forests in south-east Asia. Indeed, like insular habitats, biota on mountains can be a complex mix of plants originating from the local adaptation of species occurring at lower elevation, or immigrants of lineages already adapted to distant mountains, that reach the local ecosystem by long-distance dispersal (Merckx *et al.*, 2015). Here the convergence of cold-adapted niches does not preclude species from possessing other traits important in facilitation, like for e.g., the promotion of regeneration of interior shola species due to microclimatic conditions induced by other distantly-related species growing in the fringes or able to regenerate in the open (Nair & Menon, 2000).

### ***Mixed evolutionary background of high-elevation forests***

Previous studies on montane WG forests in fact point to the co-occurrence of species of tropical origin, including congeners of lowland taxa, and species of sub-tropical or even temperate origin (32% of species, Das, 2015). In shola forests, species of tropical origin are restricted to forest interiors in sheltered valleys, while in forest fringes and more exposed grasslands frost-tolerant relics of previous cooler climates are found (Meher-Homji, 1967). The latter include typically temperate genera (*Daphniphyllum*, *Eurya*, *Viburnum*), distinct Himalayan elements (*Mahonia*, *Rhododendron*) or species of subtropical genera also occurring in eastern Himalaya or beyond (Suresh & Sukumar, 1999).

Noticeably the variation of phylogenetic turnover with elevation difference is not smooth, but shows a more abrupt change at around 900-1000 m difference. This trend does not reflect a gradual variation in underlying abiotic drivers, such as for rainfall. Alternatively, it is consistent with the hypothesis that WG forests are derived from two basic species pools, one at low elevations, which could be related to the southernmost richest forests, and one at high elevations, with the distinctive influence of temperate elements. The abrupt increase in phylogenetic turnover between plots at contrasting elevations is more pronounced for endemic species (results not shown). WG montane forests are practically the only habitat of most species in *Ilex*,

*Schefflera*, and *Vaccinium* genera in addition to extra-tropical elements. A number of narrow endemics occur only above 2000 m, e.g., in *Mahonia*, *Magnolia* and *Rhododendron*. Endemics of at least eight families other than the dominant ones abound in shola interiors and are not well-represented in low elevation forests.

### ***Distinctive basal and terminal phylogenetic structure***

Complementary metrics reflect the influence of deeper or more recent phylogenetic structure and allow better understanding the underlying evolutionary drivers (Mazel et al. 2015). The mean nearest taxon distance (MNTD) in communities is more sensitive to the influence of recent lineages, while mean phylogenetic distance (MPD) is sensitive to deep phylogenetic structure. While phylogenetic clustering was basically consistent for MPD<sub>SES</sub> and MNTD<sub>SES</sub>, overdispersion found in MPD<sub>SES</sub> did not translate into overdispersion of MNTD<sub>SES</sub>.

Ancient evolutionary history underlies niche differentiation as expressed by phylogenetic overdispersion in southern WG and high elevation ecosystems. In a topographically and climatically heterogeneous region, extensive specialisation can have been maintained over the long-term (Losos *et al.*, 2003; Cavender-Bares *et al.*, 2004). It does not mean, however, that the taxa present in these ecosystems differentiated a long time ago in the area, but rather that present ecosystems filter ecological strategies that mainly diversified anciently (Bartish *et al.*, 2016). For instance, not all lineages living in wetter forests can survive in drier areas. Phylogenetically clustered forests in harsher central and southeast environments are basically devoid of deep-branching taxa, like Magnoliids. These taxa retained ancestral adaptations to warm and humid periods when they diversified in a rainforest context (Carlucci et al., 2016) (see Fig. S2). They could also evolve over the long term and occupy higher-elevation ecosystems, leading to high diversity of Lauraceae for instance, even though with limited tolerance to stress. They now coexist with distant Eudicot lineages that have differentiated, evolved and migrated over time to occupy comparable habitats at present.

A tendency towards phylogenetic clustering in terminal nodes conversely suggests that more recent diversification did not entail large niche shift among species coexisting in local communities. In southern WG forests, the benign environment may have favoured niche differentiation over the long-term, and climate stability would have limited extinction events and favoured diversification more recently. These forests could thus represent both a former refuge for wet evergreen forest species (museum, basal overdispersion) and a centre of speciation (cradle, terminal clustering) at finer evolutionary time-scales (Koenen *et al.*, 2015). Terminal clustering was also observed in montane forests, especially in BGL. Relatively recent diversification suggested by high levels of endemism (in *Cinnamomum*, *Actinodaphne* and *Litsea*)

would contribute to terminal clustering in this context. *In situ* adaptive divergence, speciation following immigration, or even allopatric diversification due to expansion and contraction over periods of climate change, can account for the diversity of particular clades in this complex mountain landscape.

Phylogenetic turnover between communities also concern evolutionary dynamics at multiple temporal scales. Apart from the turnover of deep-branching groups such as Magnoliids along the gradients, species from the same genus can be found in wet evergreen forests as well as in southern dry evergreen and more seasonal central evergreen forests, suggesting recent speciation events across habitats.  $\pi_{st}$  reached a maximum of 0.07 for annual rainfall compared to 0.02 for seasonality, suggesting that niche traits related to seasonality were more labile than those related to rainfall which display a higher phylogenetic signal. Closely-related species could have diverged in preferences for seasonality and occupied dissimilar environments. The presence of species-rich genera like *Garcinia*, *Drypetes*, *Diospyros*, *Actinodaphne* and *Aglaia* across various habitats, was previously interpreted as evidence of 'ecological vicariance' along the south-north gradient and between western and eastern leeward slopes (Pascal, 1988b; Gimaret-Carpentier *et al.*, 2003). Many species differentiating between these habitats are also endemics, leading to the hypothesis that ecological speciation, possibly along the seasonality gradient, is a driver of diversification in the WG (Pascal, 1988b). Therefore, while terminal clustering in local phylogenetic structure indicates little niche differentiation across close relatives in local communities, niche differentiation has occurred across close relatives now occupying different habitats along the major environmental gradients.

## Conclusion

Lower phylogenetic diversity under stressful or historically unstable conditions can reflect functional convergence due to the selection of adapted taxa. An abrupt change in phylogenetic turnover along the elevation gradient underlines the influence of distinct biogeographic and evolutionary backgrounds at low- and high-elevation. High topographical and habitat heterogeneity of the WG could have favoured the diversification of the flora by parapatric or sympatric speciation, especially in long-term stable areas. Hydric stress is a long-standing and major ecological and evolutionary driver of biodiversity dynamics. Rainfall amount concerns the turnover of deep branching clades, such as Magnoliids, but also turnover at finer phylogenetic scales. On the other hand, many endemics of species-rich genera are found all over the evergreen continuum with species niches within genera being separated especially along the seasonality gradient. These results suggest that seasonality possibly became an important factor more recently, with the establishment and reinforcement of the monsoon regime.



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ROLE OF DIOECY IN THE ECOLOGICAL AND EVOLUTIONARY DYNAMICS OF TREES IN THE WESTERN GHATS: A  
LEGACY OF ARIDIFICATION?

**ABSTRACT**

**Aim:** With the objective of understanding in what conditions separation of sexes (dioecy) has been selected for in the course of evolution and in extant ecosystems, we addressed whether the spatial variation of abiotic stress and historical habitat stability influences the frequency of tree mating systems in a tropical forest.

**Location:** Western Ghats region, Western Ghats-Sri Lanka Biodiversity Hotspot, India.

**Method:** We explored two non-exclusive hypotheses focussing on the particular case of dioecious species: 1) the frequency of dioecious species reflects current environmental filtering, 2) dioecious species underwent preferential diversification related to past environmental conditions. We expected a positive relationship between dioecy and abiotic stress, and no difference between endemic and non-endemic species under Hyp.1 and differential spatial patterns for endemics and non-endemics under Hyp.2. Older lineages could display ancient associations between dioecy and wet-adaptations and we would expect this to be reflected in non-endemic species (niches conserved) under Hyp.2.

We examined the relationship between the proportion of dioecious species in 297 plots and environmental gradients using GLM. We further tested these relationships for endemic and non-endemic species, and acknowledged the influence of phylogenetic and spatial structures using an extended RLQ analyses. Hyp. 2 implies that diversification is linked to both the ecological context and reproductive systems. We thus investigated the role of climatic niche differentiation among congeneric endemics of species-rich genera and its variation according to reproductive systems. Lastly, to test whether older lineages conserved ancient associations, we compared the relative ages of endemic and non-endemic species along the main gradient of seasonal water availability.

**Results:** We found reverse spatial patterns of dioecious species frequency for endemics vs. non-endemics, pointing to different mechanisms selecting for dioecy: conservation of non-endemic dioecious lineages in least seasonal southern forests, vs. diversification of dioecious endemics in more seasonal and unstable environments northward.

**Conclusions:** The refuge effect likely led to non-endemics persisting in less seasonal, historically stable zones due to niche conservation, while ecological speciation in other dioecious genera allowed endemics exploit opportunities for diversification within and beyond the southern refugia. Our analyses could be a first step towards exploring explanations for both the high incidence of dioecy and high endemism in this biodiversity hotspot and we suggest that this is linked to the fact that seasonality became an important factor more recently, with the establishment of the monsoon regime and Miocene aridification.

## INTRODUCTION

Evolutionary changes in sexual systems and environmental factors associated with these changes are central issues of evolutionary biology, as reproductive traits are key parameters of the fitness of organisms. In particular, much interest has been devoted to the emergence and maintenance of separate sexes (dioecy) from combined ones in flowering plants (e.g., Dorken *et al.*, 2002). Both ecological and genetic mechanisms are expected to influence the reproductive success and the evolution of sexual systems: (i) resource allocation to reproduction is asymmetrical for male and female functions; investing in female function is more costly while transmission of genes of male function depends on external factors (pollination), (ii) outcrossing limits the cost of inbreeding compared to selfing, but selfing allows transmitting more genes of parent individuals to their offspring. Basic trade-offs are then expected to influence evolution to separate vs. combined sexes, and to selfing vs. outcrossing systems.

Limitation in resources necessary to pollination and to fruit set may favour differential investment in male and female functions, and ultimately sex separation in plants (Bawa, 1980; Burd, 1994). Environmental constraints can influence resource and pollinator availability and alter the relative advantage of sexual systems depending on their respective reproductive costs (Munoz *et al.*, 2016). Differences in allocation to male and female function (e.g., hermaphrodites decrease seed production and invest in the less-costly male function, Ashman, 2006), lead to accelerating fitness gains for unisexual plants, giving females a demographic advantage over hermaphrodites (Litrico *et al.*, 2005). Resource limitation can hinder seed and fruit production of hermaphrodites more than of females (e.g., Delph, 1990; Spigler & Ashman, 2011), and intensify inbreeding depression (eg., Armbruster & Reed, 2005) with advantages to gender specialists with lower total reproductive costs. Specifically, separate sexes has been found to be favoured by stressful environmental conditions; gynodioecious populations appear closer to dioecious states as resources, especially water, become limiting (Case & Barrett, 2004) and dioecious species are found in drier habitats than monomorphic ones (e.g., Costich, 1995; Weller *et al.*, 1995).

At the community level, monomorphic species may reduce their demographic advantage over dioecious species by investing more in the male function under stressful conditions. Indeed in a recent study covering a large geographical area in central Africa, dioecious plants were shown to have a higher propensity to colonise new or disturbed (i.e. more stressful) areas in tropical forest communities (Réjou-Méchain & Cheptou, 2015). More stressful environments were found to be more easily invaded by comparatively more heterozygous, and thus genetically more diverse, dioecious populations by Costich and Meagher (1992). Along with other studies these findings question traditionally-held hypotheses like Baker's law, which emphasise the selective advantage of selfing rather than outcrossing for colonisers, as they can establish new populations as single



individuals (Baker, 1955). In this context, the high abundance of dioecy in islands - suggesting that the establishment of dioecious plants through colonisation may be more common than expected - has been the object of much debate. Importantly, it also inspired theoretical and empirical studies in various biological contexts beyond dispersal to oceanic islands (cf. Pannell, 2015).

Colonising species are characterised by different phases in their life patterns viz. dispersal and colonisation; initial establishment following colonisation; and post-establishment (Pannell, 2015). Explanations for the abundance of dioecy on islands as well as colonisation of novel environments thus comprise: 1) Arrival explanations, implying an ecological sieve on dispersal traits, with the idea that dioecious species are better dispersers, since certain ecological correlates of dioecy, such as fleshy bird-dispersed fruit (Renner & Ricklefs, 1995), favoured long-distance dispersal of dioecious colonists (Bawa, 1982). The contribution of initial dioecious colonists to the high incidence of dioecy on islands (Sakai *et al.*, 1995b; Schlessman *et al.*, 2014) provided empirical support for theoretical models of association between outcrossing and high dispersal (Cheptou *et al.*, 2009). 2) Establishment explanations imply a sieve of reproductive traits and associated fitness outlined above, including pollinator preferences and longevity or woody growth form. Lastly, 3) regarding the post-establishment phase, enhanced survival leading to speciation as well as the local evolution from other sexual systems towards dioecy also contributed to the high incidence of dioecy in islands, possibly as an inbreeding avoidance mechanism (Sakai *et al.*, 1995b; Ito, 1998; Le Péchon *et al.*, 2010). Interestingly, in Hawaii, dimorphism in the overall flora was associated with wetter habitats, but dimorphic *endemics* were associated with a shift to dry habitats (Sakai *et al.*, 1995a; Sakai *et al.*, 2006). In New Caledonia, post-colonisation diversification of dioecious lineages rather than local evolution contributed to the high incidence of dioecy (Schlessman *et al.*, 2014).

Episodes of historical climate changes like the Pleistocene glaciations or late Neogene aridification caused contractions to and expansions from refugia, and the latter also opened up new adaptive zones that spurred range expansion and diversification in certain lineages (Crisp *et al.*, 2004; Fujita *et al.*, 2010). Paleoclimatic changes can filter regional species pools based both on climate-related traits and on dispersal abilities during migration (cf. Ordonez & Svenning, 2015). Less climatically stable areas would harbour assemblages of survivors and/or species favoured by their ability to colonize these areas (Kissling *et al.*, 2012) and the distribution of species would therefore reflect both habitat preferences and colonisation history. The role of environmental constraints on the evolution of mating systems is expected to translate over the long-term into patterns of diversification reflecting the influence of past environments. The diversity and the adaptations of extant dioecious lineages can then reflect these past dynamics.

A high proportion of dioecy in rainforest trees is found on all continents. In the forests of Western Ghats of India (WG), an escarpment running along India's south-western coast at elevations c. 1200 m, the local incidence of dioecy is elevated (20%, Krishnan & Ramesh, 2005) compared to global levels (ca. 6% Renner & Ricklefs, 1995). Much research has focused on factors influencing the evolution of dioecy and its correlates viz. woody habit, inconspicuous flowers, fleshy fruits etc. (Vamosi & Vamosi, 2004), but the factors affecting current abundance and distribution of dioecious species, especially in tropical forest communities, have received less attention (cf. Matallana *et al.*, 2005; Vamosi & Queenborough, 2010).

The climate of the WG region of the Western Ghats-Sri Lanka biodiversity hotspot is more variable than most equatorial rainforests because there is a distinct dry season, which increases from south to north and from west to east due to the timing of the monsoon winds. This latitudinal gradient in seasonality drives species turnover at the macroscale (Davidar *et al.*, 2007) and variations in annual rainfall and temperature due to the complex topography also determine marked changes at mesoscales (Pascal, 1988; Bonnefille *et al.*, 1999; Barboni *et al.*, 2003; Ramesh *et al.*, 2010a). Importantly, the present climatic conditions are a product of past geomorphological evolution. The rise of the Himalayas and subsequent establishment of the monsoon regime (11-5 Ma) brought about a major shift in climate, along with the onset of aridification in large parts of the Indian peninsula in the late Neogene (Morley, 2000; Guo *et al.*, 2008; Patnaik *et al.*, 2012). As the arid zone spread southwards, previously widespread wet evergreen forests were largely replaced by deciduous forests to the north and east of the WG. Orographic rainfall on the western windward slopes of the WG provided the necessary humid environment to ensure the persistence of wet evergreen forests here (Meher-Homji, 1980). However, the seasonal reversing monsoon winds introduced a south to north regional gradient of seasonality within the WG during this period (Gunnell, 1997; Patnaik *et al.*, 2012).

The more climatically stable and least seasonal southern WG forests have served as recurrent refugia since the Eocene (Prasad *et al.*, 2009), while species with distributions in zones of progressively increasing seasonality further north would have faced extinction or adapted to changing conditions in the late Neogene. Decreasing species richness, endemism (Ramesh & Pascal, 1997; Ramesh, 2001) and phylogenetic diversity have been linked to the increasingly harsh current abiotic conditions from south to north (Gimaret Carpentier, 1999) and lower historical habitat stability (Bose *et al.* 2016), suggesting that northern WG forests have lower diversity because fewer lineages have successfully colonised them, or that they have been colonised relatively recently, leaving less time for diversity to build up in these habitats, or a combination of these factors (Wiens *et al.*, 2013).

We investigate here the influence of these past and present environmental constraints on the distribution and abundance of dioecious tree species in WG rainforests. We consider whether and how the variation of abiotic stress and resource limitation related to water availability, and historical habitat stability influences the frequency of mating systems along abiotic gradients. In addition, a majority of evergreen tree species are endemic to WG (63%, Ramesh & Pascal, 1997), while non-endemic species can be found in other rainforests of Asia. We consider two basic and non-exclusive hypotheses concerning the ecological and evolutionary dynamics of mating systems in this area.

**Hypothesis 1:** The frequency of dioecious species in WG rainforests reflects current environmental filtering. A relative advantage of dioecious species is expected in more stressful conditions along the environmental gradients, related to resource and pollinator limitation. Under this hypothesis, we expected that the proportion of dioecious species would increase along the south-north seasonality gradient. If environmental filtering is the only driver of dioecious tree distributions, the pattern was expected to be the same for endemic and non-endemic species of WG.

**Hypothesis 2:** Dioecious species underwent preferential diversification in WG related to past environmental conditions (local evolution). It means that (i) environmental stresses and (ii) the advantage of dioecious species in colonizing new habitats, can have driven speciation events. This scenario implies specific patterns of dioecious endemics reflecting the role of these drivers, while non-endemic species should reflect only the role of current environmental filtering (Hyp. 1). On the other hand, older lineages could also display ancient associations between dioecy and adaptations to least water-stressed conditions under which early angiosperms diversified, which we would thus expect under Hyp 2, to be reflected in non-endemic dioecious species (niches conserved) that were not the result of local evolution to novel more stressful conditions like the dioecious endemics (niches diverged).

## MATERIAL AND METHODS

### *Species data and phylogeny*

We used a dataset of 297 ~1-ha plots including 459 species, comprising a) 189 plots located in southern wet or dry evergreen forests between 8°5' et 11°5'N from Gimaret-Carpentier(1999) and Pascal(2004) , b) 96 plots covering a wide array of habitats between 13°30'-15°N in north-central WG (Ramesh *et al.*, 2010b), and c) 12 plots between 10-12°5'N from Chandrashekara (2004). Each plot was further characterised by its location in one of 19 discrete floristic types delineated by Pascal (1988), that are distributed along the latitudinal seasonality gradient. These comprise 16 wet evergreen forest types classified according to low (0-800 m), medium (800-

1400 m) and high elevation (>1400 m), and 3 dry evergreen forests found on eastern slopes south of the Palghat gap (11°N) (Fig. S1 and Table S1).

We used the time-calibrated megaphylogeny of Zanne *et al.*, (2014), updated by Qian and Jin (2015), built from gene sequences of land plants available in GenBank. We derived the phylogeny of the species using PHYLOMATIC v.3, which added additional species in genus nodes when needed.

### ***Species reproductive traits***

Reproductive traits may be important in reflecting species ecological strategies related to historical disturbances and stressful environments. We thus focussed on sexual systems along with dispersal mode, which are traits related to colonisation, dispersal and persistence in challenging conditions. Using a field-based morphological trait database ([www.biotik.org](http://www.biotik.org)) as well as various flora of southern India (Fyson, 1915; Gamble, 1915-1934; Sasidharan, 2006) and regional flora (<http://florakarnataka.ces.iisc.ac.in>, [kerala.plants.in](http://kerala.plants.in)) as references, the species were classified according to their sexual systems as hermaphrodite, dioecious, monoecious or polygamous. Polygamodioecious species were classified as dioecious as the perfect flowers found in these species are often functionally unisexual (Flores & Schemske, 1984). Dispersal syndrome can be inferred from information on the type of diaspore; fleshy (drupe, berry, arillated, ficus-type), corresponding to animal- or bird-dispersed, and dry dehiscent (pod, capsule, follicle) and dry indehiscent (achene, winged/diptero-type) corresponding to wind, explosive or gravity-based dispersion. Dispersal modes were additionally evaluated based on the flora and field-based literature (Ganesh & Davidar, 2001; Puyravaud *et al.*, 2003; Tadwalker *et al.*, 2012).

### ***Environmental and historical predictors***

Floristic composition from south to north in the WG is marked by a change in phenology, with tall dense evergreen forests (at least 95% evergreen stems) giving way to shorter semi-evergreen (40-80% evergreen) forests at c. 14°N, where the length of the dry season increases to >5 mo. These forests can be distinguished on the basis of their pollen signal, potentially indicating two distinct biomes with different responses to drought stress (Barboni *et al.*, 2003). Between 13°15'-14°N there is a gradual transition from *Dipterocarpaceae* to *Diospyros* dominated forests, with the disappearance of sciaphilous species sensitive to drought, leading to forests composed of species of the common pool with wider ecological amplitude and new species adapted to the longer dry seasons (Pascal, 1986).

The WG forests north of ~13°N are not only characterised by higher seasonality, but also lower historical climate and habitat stability, having experienced multiple alternations in climate - with accompanying cycles of contraction and colonisation of species distributions - dating from the early Paleocene flood basalt volcanism, to the Miocene aridity. The effect of more recent

Quaternary climate fluctuations, especially reduced rainfall, was also stronger in northern WG according to global circulation models. The predicted higher diversity and endemism in historically stable areas (Graham *et al.*, 2006; Fine, 2015) is supported by a south-north decrease in species diversity and endemism in the WG (Ramesh, 2001).

To assess how the proportion of dioecy/sexual systems varies depending on environmental stress and historical habitat stability, we first performed a Principal Component Analysis (PCA) of 19 bioclimatic variables obtained at 30-sec resolution (~1km) from WorldClim (Hijmans *et al.*, 2005). The first three PCA axes explained 90.4% of the overall variation and represented the major environmental gradients devoid of co-linearity, (i) a decreasing temperature with elevation gradient, (ii) a south to north increase in seasonal hydric stress (from 3 to 8 months of dry season, with rainfall < 100 mm) and (iii) a rainfall gradient (annual precipitation from 484 to 6032 mm) that decreases from west to east and increases from south to north (Fig. S2 a-c). These results were consistent with previous regional scale analyses (Pascal, 1988). An index of historical habitat stability reflecting the south-north gradient was derived from a previous study (Bose *et al.*, 2016).

Historical habitat stability since Last Inter-Glacial (LIG, ~120-140 kyr BP) was assessed for 5 arc-min grid cells in the WG, from binary maps of potential habitat models calculated for each species at three periods, namely, present, Last Glacial Maximum (LGM; ~21 kyr BP) and LIG. In each grid cell, we calculated the number of species potentially occurring at all the three epochs. The higher this number, the greater the number of species that could persist locally over time, providing an index of habitat stability (Fig. S2 d), see Bose *et al.*, 2016 for details). We used this historical habitat stability index as a proxy for longer-term climatic instability. The increasing south to north seasonality gradient is also an indicator of regions that historically underwent a shift from less seasonal to more seasonal patterns with the establishment of the monsoon regime.

### ***Statistical analyses***

We characterised the frequency of dioecious trees in rainforests along basic environmental gradients related to resource availability and abiotic stresses. Specifically, we addressed the influence of the major hydric stress gradient related to rainfall seasonality, which broadly varies from south to north in the WG. Under Hyp. 1, we expected significant and positive relationship between dioecy and environmental stress. To test this, we examined the relationships between the proportion of dioecious species in each plot and environmental gradients using GLM and compared the patterns for endemic and non-endemic species. We also compared the proportion of dioecious endemic or non-endemic species in plots located in different forest types.

We further characterized and tested these relationships by performing RLQ analyses. This multivariate approach allows addressing the relationship between species attributes and local

environmental conditions through the patterns of occurrence and co-occurrence of species in communities along the gradients (Dolédéc *et al.*, 1996; Raavel *et al.*, 2012). We acknowledged the influence of phylogenetic and spatial structures in the analysis of the relationship between environment and traits using an extended RLQ analyses (ESLTP, Pavoine *et al.*, 2011). Before this, we tested for spatial autocorrelation in the environmental variables and phylogenetic signal in trait variables. The lack of spatial autocorrelation in an environmental variable indicates that it is not affected by space and should be omitted from the ESLTP analysis (Pavoine *et al.*, 2011). We tested this using Moran's I test (Thioulouse *et al.*, 1995) with 999 randomisations. Phylogenetic signal of the sexual systems was quantified using the D statistic (Fritz & Purvis, 2010) which describes tree-wide patterns in trait conservatism for binary data. This was calculated using 1000 replicated simulations in the function *phylo.d* in the *caper* R package (Orme *et al.*, 2012). This measure of phylogenetic signal was compared to both a random shuffle of trait values at the tips of a phylogeny and a Brownian threshold model. If the D statistic is 1 the distribution of the trait is random with respect to phylogeny;  $D > 1$  indicates that the distribution of the trait is more labile than random expectation; a D of 0 corresponds to a Brownian threshold model and  $D < 0$  when traits are less variable than the Brownian motion expectation i.e. highly conserved (Fritz and Purvis 2010).

To select reproductive traits which have separately significant correlations with the environmental factors we applied the multivariate version of the fourth-corner analysis and an appropriate null model (Model 4 in Dray & Legendre, 2008) using the function *funtest* in Pavoine *et al.*, (2011). We applied this approach to environment and trait on the one hand, and space and trait matrices on the other hand. The null model assumes that the environmental and spatial variables are fixed, and that the species are randomly distributed in either space or environment whatever their traits and phylogeny. We also tested the significance of the connection between the trait and environment matrices using a multivariate statistic that measures the global significance of trait-environment relations with sequential testing of Model 2 (permutation of sites) and Model 4 using *randtest.rlq* function with 49000 permutations, *ade4* R package (Dray *et al.*, 2014).

Under Hyp. 2, we expected that dioecious and non-dioecious species would display differential patterns, due to specific diversification events having influenced the emergence of dioecious taxa in the area. Therefore, we performed separate RLQ analyses of endemic and non-endemic taxa. To account for past environmental conditions, we included the index of historical habitat stability in addition to current environmental predictors in the RLQ analyses.

Hyp. 2 implies that the diversification of species in the WG is linked to both the ecological context and reproductive systems. We analyzed the evolutionary dynamics of reproductive systems and

climatic niches and their relationship. Multispecies comparisons could suffer from phylogenetic mismatching i.e. comparing species traits among species with very different evolutionary histories (Thuiller *et al.*, 2004). Focusing on species within a single genus allows controlling for phylogenetic history and the explicit examination of reproductive trait and niche difference between species. We investigated the role of climatic niche differentiation among congeneric endemics of species-rich genera and whether this varied according to reproductive systems.

For this we 1) calculated and compared predicted niche occupancy (PNO) profiles of congeneric species of the 15 most species-rich dioecious and non-dioecious genera along different niche axes using the R package *phyloclim*. PNO takes the likelihood surface from the MaxEnt species distribution model output and relates it to the raster input layers to calculate a species probability of occurrence at a given environmental value (Evans *et al.*, 2009). PNO profiles can be calculated along a single or several axes of the climatic niche, for instance, separately along the seasonality gradient or all the niche axes comprising rainfall, seasonality and temperature. We then 2) quantified and tested niche overlap based on Schoener's D (Warren *et al.*, 2008) between pairs of congeneric species based on PNO profiles including all niche axes, and lastly 3) tested for a difference in pair-wise niche overlap values for all dioecious vs. all non-dioecious genera using a one-way ANOVA with 2 levels. If speciation is associated with niche conservatism, species within a genus should have more similar niches; alternatively, if speciation is associated with niche divergence, closely-related species should have less similar niches.

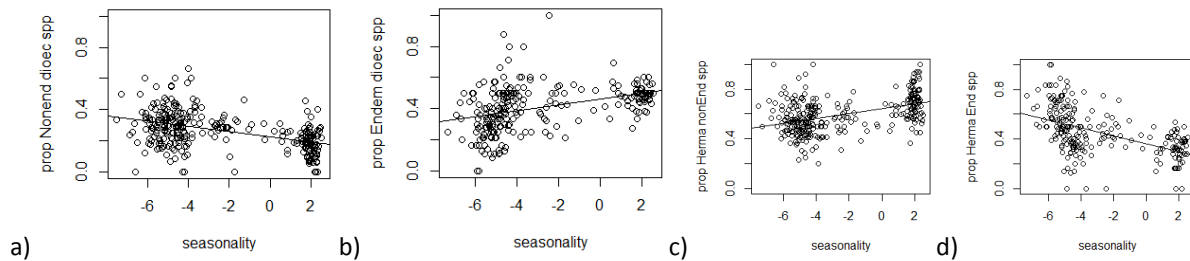
According to Hyp. 2 ecological differentiation could have occurred within dioecious genera in novel harsher environments due to their capacity for dispersal/colonisation and ability to withstand environmental stress. We thus expected that pairs of endemics within dioecious genera would have lower overall niche overlap than pairs of endemics of non-dioecious genera since they would include a larger range of niches due to greater differentiation between congeneric species.

Lastly, to test the implication of Hyp. 2 that older lineages could display ancient associations between dioecy and adaptations to least water-stressed conditions and this should be detectable in the case of non-endemic dioecious species that did not undergo niche divergence, we compared the relative ages (terminal branch lengths) of endemic and non-endemic dioecious species along the seasonality gradient and tested whether they were different using a Mann-Whitney Wilcoxon test.

## RESULTS

The proportion of dioecious species varies along the seasonality gradient (Hyp.1), and this pattern is distinct for endemic and non-endemic species (Hyp.2). According to the GLM analyses, the proportion dioecy among non-endemic species decreases significantly with seasonality and

the pattern is inversed for endemic species, where dioecy increases significantly with seasonality (Fig.1 a-b). In areas of high seasonality, the mean proportion of dioecy among non-endemics ( $\sim 0.3$ ) is lower than the mean proportion of dioecy among endemic species ( $\sim 0.45$ ).

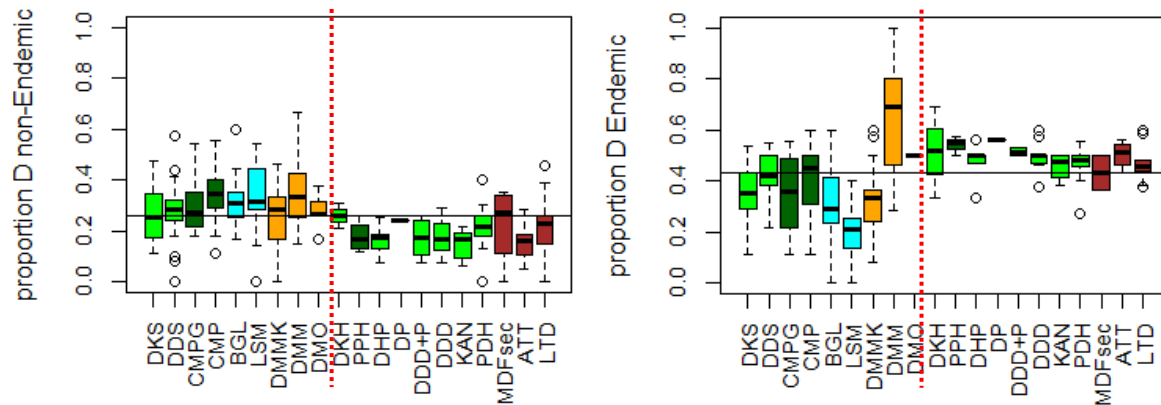


**Figure 1. Proportion of a) non-endemic dioecious b) endemic dioecious c) non-endemic hermaphrodite and d) endemic hermaphrodite species along the seasonality gradient**

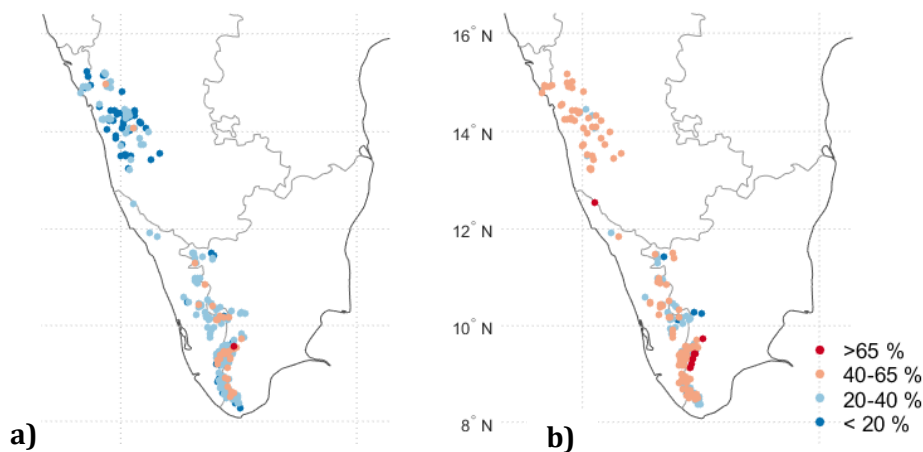
The proportion of hermaphrodite species follows the opposite pattern (Fig. 1 c-d); hermaphrodites increase significantly with seasonality among non-endemics and decrease among endemics. The proportion of hermaphrodites among endemic species is significantly correlated with lower temperatures and higher annual rainfall according to the GLM.

The proportion of dioecy among non-endemics is on average higher in plots located in the least seasonal southern WG forest types compared to northern WG forest types. By contrast, the proportion of dioecy among endemics is relatively higher in plots located in more seasonal forests further north and two dry evergreen forests in the south (Fig. 2). Endemics belonging to the most species-rich dioecious genera such as *Actinodaphne*, *Aglaia*, *Diospyros*, *Garcinia* and *Litsea* strongly contributed to the pattern of increasing dioecy with seasonality. Other endemic species also present in drier forests belonged to less speciose dioecious genera viz. *Dimorphocalyx*, *Flacourtia*, a dioecious fig *Ficus beddomei*, *Heritiera*, *Hydnocarpus*, *Knema*, *Myristica*, *Vepris*, and polygamodioecious species of *Discospermum* and *Reinwardtiadendron*.





**Figure 2.** The proportion of dioecious species among a) non-endemic and b) endemic species in plots according to their location in different forest types. The horizontal line represents the median proportion of dioecious species and the red vertical line separates forests above and below  $\sim 13^\circ\text{N}$ . The three dry evergreen forests (orange) are located in southern WG. The frequency of dioecy is highest among endemic species in plots located in northern forests with high seasonality and southern dry evergreen forests.



**Figure 3.** Proportion of dioecious species among a) non-endemic and b) endemic species in plots of the WG

Finally, the proportion of dioecy among non-endemics displays a strong south to north decreasing pattern but dioecy among endemics is relatively high (40% or more) in a number of plots in the southern WG as well, with the highest proportions in the dry evergreen forests on the eastern slopes in the south (Fig. 3).

The value of  $\mathbf{D}$  (Fritz & Purvis, 2010) and its associated probabilities indicated that the phylogenetic pattern of dioecy in the overall phylogeny is significantly non-random ( $p=0$ ), and this pattern is similar to the Brownian model ( $p=0.86$ ).  $\mathbf{D}$  is less than 0 for dioecy ( $\mathbf{D} = -0.18$ ) as well as for the other sexual systems, indicating that sexual systems are a conserved trait. In other words, closely-related species resemble each other more than expected under Brownian motion evolution for these traits. We found significant spatial autocorrelation in the environmental variables using Moran's I test.

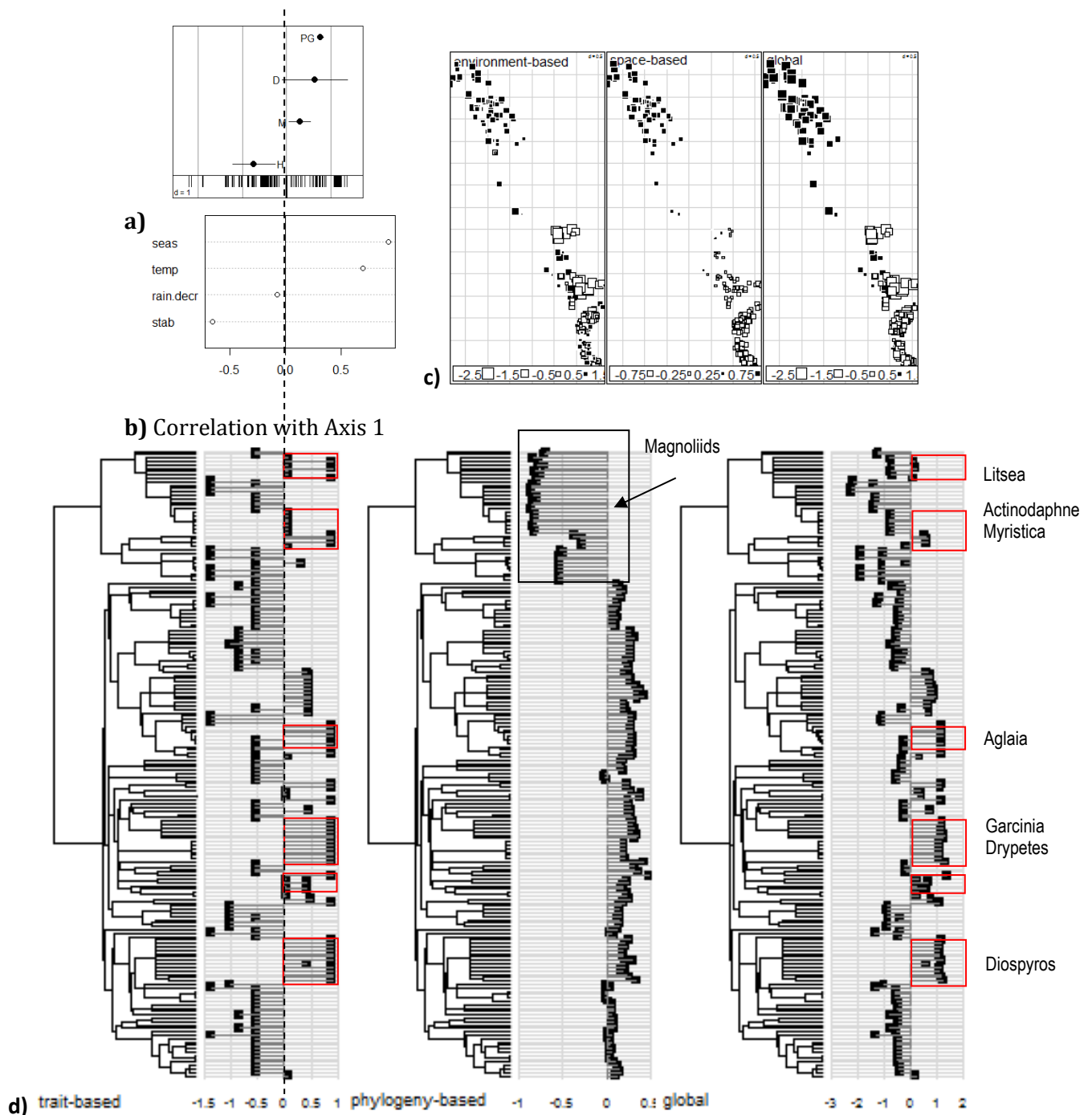
Of the 459 species present in the plots, 58.2% were hermaphrodite, 28.9% dioecious, 6.1% monoecious and 6.75% polygamodioecious. The majority of species in plots were animal or bird dispersed (hermaphrodite 78% and dioecious 91%). The reproductive traits of sexual systems

and dispersal modes were significantly correlated with environmental variables and all, apart from dispersal modes for non-endemic species, are spatially structured according to the fourth-corner analyses. The traits of fruit type and fleshy vs. dry were not significant and therefore not included in the analyses. The global statistic of the connection between these traits and environment matrices was significant for both Models 2 and 4 for non-endemic species ( $p < 0.001$ ). The lowest significance ( $p < 0.05$ ) was obtained using Model 4 compared to the Model 2 ( $p < 0.001$ ) for endemic species.

The first axis of the extended RLQ analysis for endemic species, explained a major part (75%) of the total variation in the structure of species in plots (2nd axis 22.7%). In terms of the distribution of traits, endemic species with positive scores on RLQ Axis1 tend to be polygamous or dioecious with zoochorous dispersal while those with negative scores are hermaphrodite with bird-dispersed seeds (Fig. 4a). The distribution of species within plots was mainly differentiated according to seasonality and historical stability status (highest positive and negative scores respectively along Axis 1, Fig. 4b).

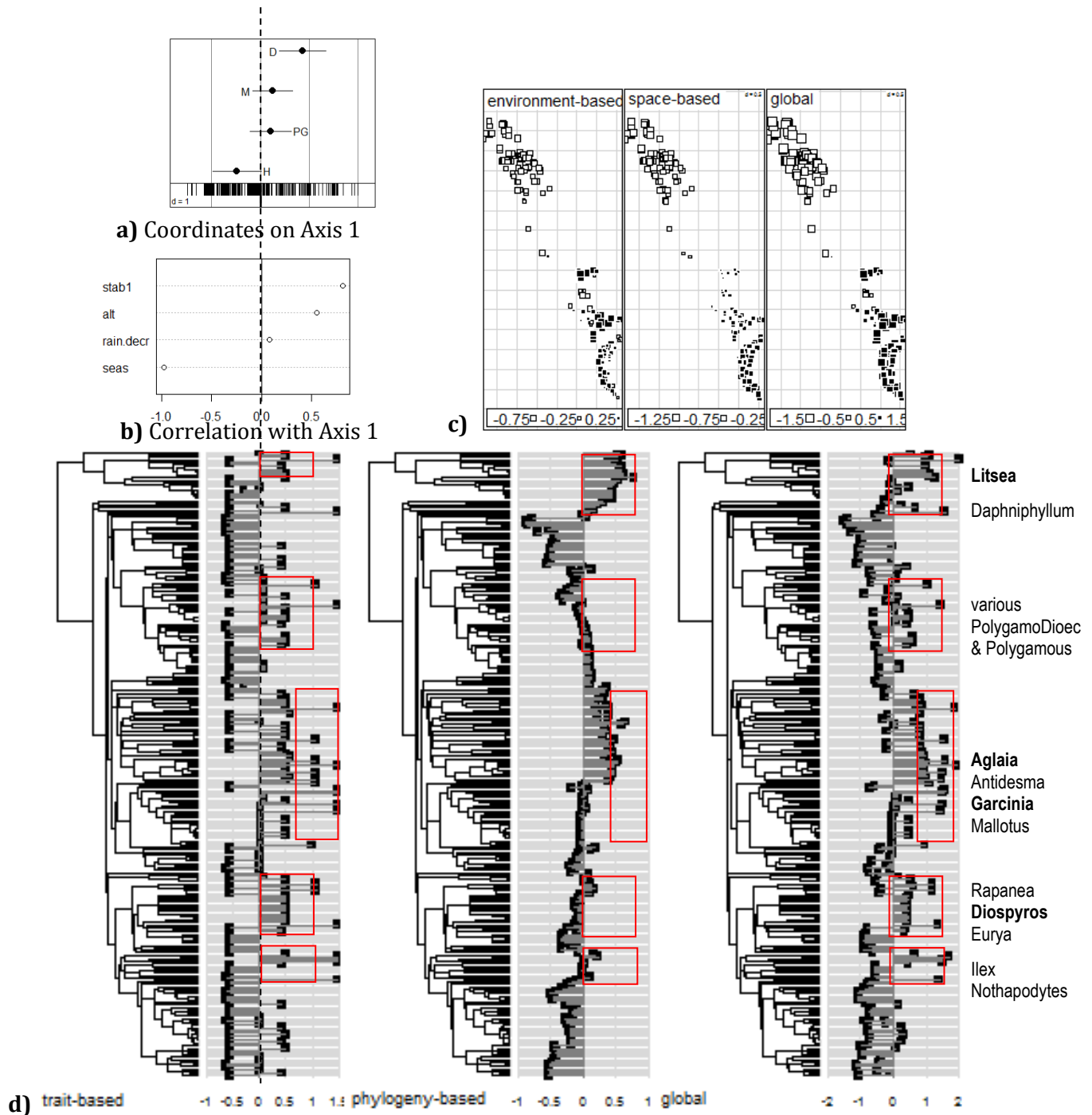
The positive side of this RLQ axis corresponds to areas of greater historical disturbance, higher seasonality and lower elevations/higher temperatures located further north and along coastal lowlands (black squares Fig. 4c). In contrast, the negative side of this axis corresponds to areas that were more stable in terms of historical climates, with low seasonality, and are also associated with higher elevation/lower temperatures. From a spatial perspective, these areas are located mostly in the southern WG including the high elevations on either side of the Palghat gap (white squares Fig. 4c).

The dot charts with coordinates of species along RLQ Axis 1 beside the phylogenetic trees in Fig. 4d, show how lineages are structured in space, and highlight the dominance of endemics of dioecious genera in northern plots (Fig. 4d left panel). Specifically, endemics of dioecious genera like *Actinodaphne*, *Aglaia*, *Diospyros*, *Drypetes*, *Garcinia* and *Litsea* are shown to have more species associated with the positive RLQ Axis1 (higher seasonality, lower historical stability and elevation). Apart from the phylogenetic constraint which acts mainly upon species of the Magnoliids to occupy high elevation areas of lower seasonality (Fig. 4d middle panel), the selection of traits is mirrored in the global community structure (Fig. 4d right panel).



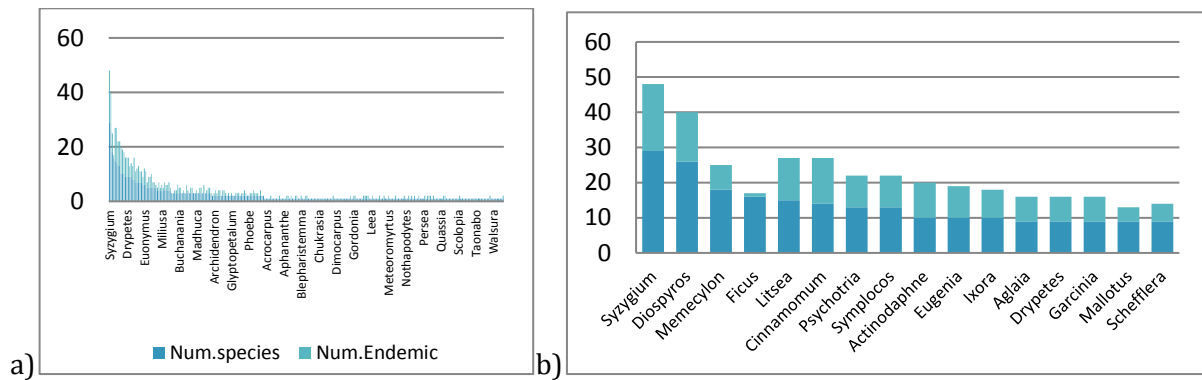
**Figure 15.** Extended RLQ analysis for endemic species alone: **a)** Coordinates of dioecious (D) & polygamous (PG) species increase along Axis 1 which is **b)** positively correlated to plots of higher seasonality (seas). Hermaphrodites (H) have negative scores along Axis 1 which is negatively correlated with plots of greater historical habitat stability (stab). **c)** Plot coordinates are represented in geographic space as black squares (positive Axis 1, northern plots) and white squares (negative, southern and high elevation plots). **d)** The coordinates of the species are a sum of a combination of trait (left panel) and phylogenetic (middle) variables, which are given by a dot plot beside the phylogenetic tree of endemic species. Dioecious species (highlighted in red) are associated with positive Axis 1 and therefore more likely to be found in northern wg. The phylogeny-based panel (centre) shows the separation of Magnoliids (negative scores, southern wg) from Eudicots (positive scores, northern wg). The resulting global pattern (right panel) shows the phylogenetic constraint acting mainly on Magnoliid dioecious genera (*Litsea*, *Actinodaphne*) whereas this is less for other dioecious genera.

In the RLQ conducted on non-endemic species (Axis 1 explained 85% of variance, Axis 2, 11.5%), these patterns are reversed. Non-endemic dioecious species are most strongly associated with areas of higher stability and lower seasonality of southern plots while non-endemic hermaphrodite species with wind or animal dispersed seeds are associated with areas further north (Fig. 5a-c). While a few species-rich genera had dominated in contributing to the observed patterns for dioecious endemic species, in the case of non-endemics, dioecious species, while including a few species of the species-rich dioecious genera, are better represented by a large variety of genera having one or a few species (red squares, Fig. 5d left panel). Dioecious Magnoliids of for instance, *Litsea*, *Neolitsea*, *Daphniphyllum* genera reflect the joint effects of phylogeny and traits. Despite phylogenetic constraints acting on for instance, *Diospyros* (Fig. 5d. middle panel), the selection on dioecy and polygamy is mirrored in the global community structure (Fig. 5d right).

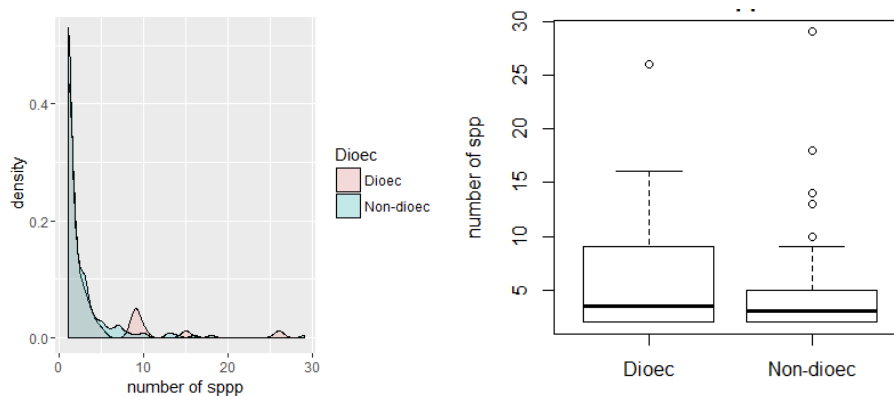


**Figure 16** RLQ-ESLTP analysis for only non-endemic species: **a)** Coordinates of dioecious (D) species increase along Axis 1 which is **b)** positively correlated to plots of higher stability (stab), shown in **c)** as black squares (positive Axis1) for plots located in southern wc and at high elevations. **d)** In the trait-based panel (left) non-endemic dioecious species (highlighted in red) are associated with positive Axis 1 and therefore more likely to be found in southern wc and high elevations, whereas non-endemic hermaphrodites (negative coordinates) are associated with plots further north of higher seasonality negatively correlated with Axis 1.

To investigate the role of climatic niche differentiation among congeneric endemics of species-rich genera and whether this varied according to reproductive systems, we focused on the 15 most species-rich genera (>9 species) in the wg. Almost half of these genera are entirely dioecious or polygamodioecious viz. *Diospyros*, *Litsea*, *Actinodaphne*, *Aglaia*, *Drypetes*, *Garcinia* and *Mallotus*, each including four or more endemic species (Fig. 6). In a comparison of the number of species in dioecious and non-dioecious genera, dioecy appears to be overrepresented among species-rich genera (Fig. 7).



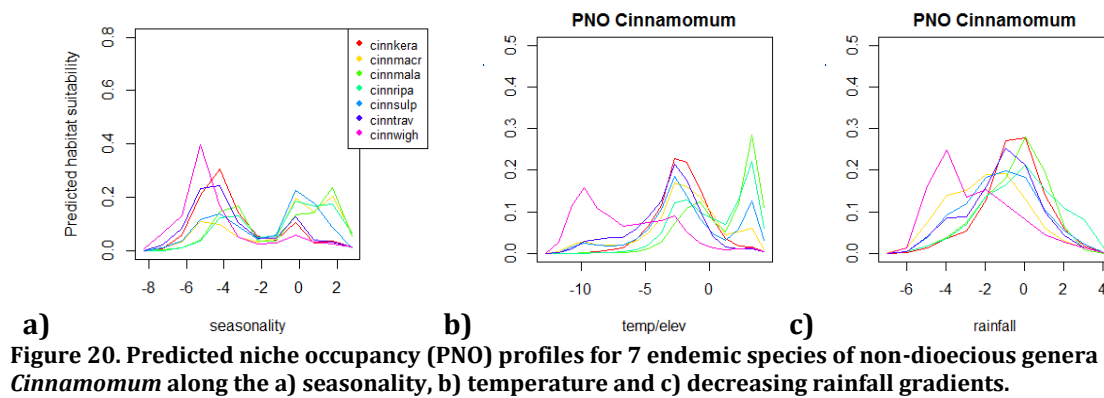
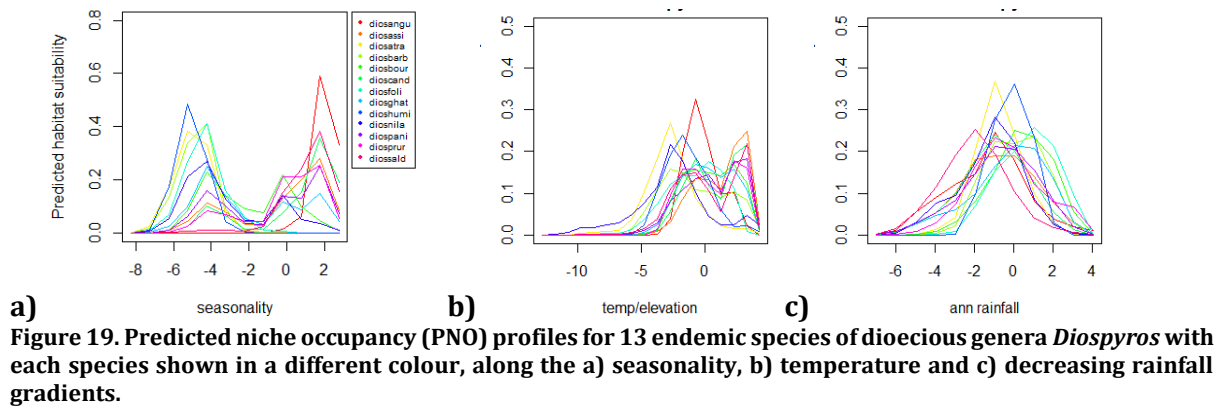
**Figure 17. Genera in the WG showing a) all genera b) the 16 most species-rich genera, with the number of non-endemic species (abscisse) in blue and endemic in red.**



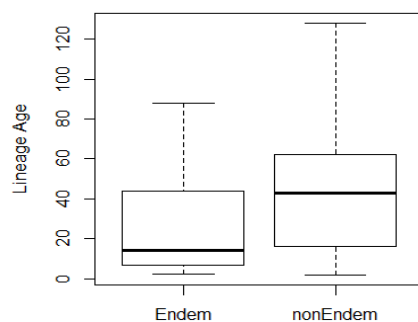
**Figure 18. a) Frequency of dioecious species compared to non-dioecious and b) dioecy is overrepresented among species-rich genera in the box plot of number of species for dioecious vs. non-dioecious genera with more than one species.**

The PNO profiles of endemics of species-rich genera showed little niche differentiation along the annual rainfall gradient, and greater differentiation along the seasonality gradient (Figs. 8-9). Most dioecious genera followed a similar pattern to *Diospyros* (Fig. 8), with a bimodal peak for seasonality at low and high values, indicating that endemic species within the genera have a preference for either high or low seasonality habitats. Some non-dioecious genera include one endemic species distributed in areas of higher seasonality, but the predicted habitat suitability is lower than for dioecious species in these areas (Fig. 9a). *Litsea* (Lauraceae), like the non-dioecious *Cinnamomum* (Lauraceae, Fig. 9b) and *Symplocos*, additionally displayed multiple peaks along the temperature/elevation gradient, indicating niche differentiation especially at higher elevations.

According to the one-way ANOVA, dioecious vs. non-dioecious genera are significantly different ( $p=0.007$ ) based on the pair-wise niche overlap for each group. Dioecious genera display lower overall niche overlap. By contrast non-dioecious genera display overall higher niche overlap.



Lastly, the mean (and standard deviation) age of non-endemic dioecious species with a majority of occurrences in southern WG was 44.78 Myr ( $\pm 33.45$ ) with a median age of 42.92, which pointed to their older age compared to dioecious endemics (mean 24.1 Myr  $\pm 23.65$ ) of median age 14.33 Myr (Fig. 10). These two groups were significantly different in terms of their ages according to the Mann-Whitney Wilcoxon test (function `wilcox.test` in R).



## DISCUSSION

We found distinct patterns for endemic and non-endemic species in terms of association between dioecy and harsher environmental conditions. The proportion of dioecy increased significantly with seasonality both in plots and within forest types above  $\sim 13^{\circ}\text{N}$  and in dry evergreen forests of the south, but this was only true for endemic species. By contrast, non-endemic dioecious species were associated instead with zones of stability in southern WG. The RLQ results confirmed this pattern, and also showed that certain dioecious genera with numerous endemic species were associated with higher seasonality and lower historical stability, whereas a larger number of less speciose dioecious genera with non-endemic species were associated with regions of high stability in southern WG. This pattern could be attributed to a refuge effect, where niche conservation led to non-endemic dioecious species persisting in less seasonal and historically stable zones, while ecological speciation in certain dioecious genera resulted in their endemics exploiting the opportunities for diversification within and beyond the southern refugia in the course of time.

Other species, not belonging to the most species-rich dioecious genera, also contributed to the increasing frequency of dioecious endemics with seasonality. These have widespread distributions, and are found all along the latitudinal seasonality gradient, pointing to their broader physiological niches allowing for persistence under a broad set of conditions. All but four of the 60 dioecious endemic species are either bird or animal dispersed, which would have facilitated colonization, but this does not set them apart from hermaphrodites which are also largely zoochorous in the WG.

In fact, non-endemic species with other reproductive traits were also filtered by the harsher environmental conditions, suggesting selection due to traits conferring drought tolerance other than those associated with dioecy. The non-endemic hermaphrodites associated with higher seasonality were largely animal-dispersed but comprised more wind-dispersed species than other sexual systems according to the RLQ results. These included deciduous species for instance of *Terminalia* and *Xylia*, which are dominant in some central WG plots (Ramesh *et al.*, 2010a). Field-based studies report the observation of a transition zone between  $13\text{--}14^{\circ}\text{N}$  leading to forests composed of species of the common pool with wider ecological amplitude and new species adapted to the longer dry seasons (Pascal, 1986), which would include species of different sexual systems. One or more endemic species of the hermaphrodite genera *Psychotria* and *Memecylon*, both of which usually comprise of understory shrubs or small tree species, also have more northern distributions. The success of these species here could be linked to the fitness gains offered by the increased potential for outcrossing due to the heterostyly prevalent in many *Psychotria* species (Sakai & Wright, 2008). Interestingly, all Hawaiian species of *Psychotria* are



dioecious, this apparently having evolved due to dystyly (Bawa, 1982). *M. umbellatum* dominates in forests with the longest dry seasons (5-7 months) and occur in plots found on lateritic outcrops and in areas of the Deccan traps (Ramesh *et al.*, 2010a) suggesting adaptations to these harsher conditions.

In the detailed fourth-corner significance testing for each trait and environmental predictor pair among endemics, dioecy is significantly and positively associated with higher temperatures and seasonality and negatively associated with historical habitat stability according to Model 2 (permutation of sites), but this is no longer significant under Model 4 (permutation of species). The global statistic of the trait-environment connection is also less significant for Model 4 than Model 2. This indicates the strong influence of the sharp environmental gradients on species distributions as compared to sexual systems in the WG, but is also due to the fact that dioecious endemics are also found in relatively high proportions in the less seasonal stable south.

We found more support for Hyp. 2 as our results point to the likely ecological divergence and adaptation to new niches along the seasonality gradient of endemic dioecious species. In other words, the preferential diversification of dioecious species in the seasonally drier central WG and on southern leeward slopes could have resulted in the distinct spatial pattern of reproductive systems of endemic species.

The PNO profiles for the species-rich dioecious genera, which were associated with areas of higher seasonality and low historical habitat stability in the RLQ and contributed most strongly to the high proportion of dioecy in plots (*viz.* *Actinodaphne*, *Aglaia*, *Diospyros*, *Garcinia* and *Litsea*), all showed bimodal peaks along the seasonality gradient. This is in agreement with previous studies on the WG that have shown that endemic species of certain species-rich genera displayed varying tolerances to increasing seasonality, or 'ecological vicariance', where species of the same genus could be found at both extremes of the seasonality gradient (Pascal, 1988; Gimaret-Carpentier *et al.*, 2003). Secondly, in a previous study we found that the response of certain congeneric endemic species to Quaternary climatic fluctuations were related to their distinct habitat preferences, beyond the phylogenetic affinities (Bose *et al.*, 2016). This suggests that niche evolution could have played a role in the origin of some of the endemic species within species-rich genera.

Thirdly, in studies of phylogenetic turnover along broad-scale environmental gradients in the WG, the high turnover along the rainfall gradient suggesting conservation of niche traits related to rainfall preferences, was contrasted to the low phylogenetic turnover along the seasonality gradient (Hardy *et al.*, 2012; Bose *et al.*, *in prep.*), indicating that close relatives occupy dissimilar positions along the latter gradient. Thus, traits related to seasonality may be more evolutionarily labile for certain clades. In particular, the potential for evolution and ecological diversification within the above speciose dioecious genera was greater along the seasonality gradient as their

PNO profiles indicate stronger niche conservatism along the rainfall gradient with highly overlapping niches, but greater divergence of niches along the seasonality gradient.

A possible scenario would be the diversification of these species-rich genera driven by the increase in seasonality from south to north in WG in the mid-Miocene. The shift in habitat to increased seasonality further north could have led to the disappearance of less-tolerant lineages, opening up new areas for colonisation by dioecious species with bird and animal dispersed seeds and greater drought tolerance, i.e. a better ability to both reach novel, more stressful environments and for the seedlings to develop there. In addition, the lowered floristic diversity after the shift to more seasonal conditions may have limited competition of dioecious colonists with non-dioecious ones, mitigating the disadvantages of dioecy and facilitating the establishment of dioecious colonists (Heilbuth *et al.*, 2001).

The southern WG represents both a former refuge for wet evergreen species and an active centre of speciation (cf. De Franceschi, 1993) from where colonisation of new locations towards the north or south eastern slopes could have taken place. Another possibility is that ancestor species of these lineages were already present in those locations, and the opening up of opportunities and reduced competition could have led to niche evolution and diversification. The observed vicariance between species of certain genera has been observed between southern and northern areas, but also between the western and eastern leeward slopes of the WG. The latter phenomenon, observed for instance in the case of pairs of species of *Actinodaphne*, *Aglaia*, *Diospyros* has been attributed to allopatric speciation, where species would have derived from a widely distributed ancestor that underwent differential selection on either side of the WG (Gimaret-Carpentier *et al.*, 2003).

The comparison of pair-wise niche overlap between species-rich dioecious and non-dioecious genera pointed to greater niche conservatism in species of non-dioecious genera. In other words, greater divergence in niches occurred within dioecious genera leading to lower niche overlap and less conservation of niches, presumably along the seasonality gradient. The steepness of this gradient could have favoured diversification through parapatric or sympatric speciation.

While our results point to a possible case of adaptive radiation through ecological speciation with greater niche separation along the seasonality gradient in the case of some dioecious genera, it is not evident why this phenomenon did not affect all genera equally. An ability to withstand stressful conditions and avoidance of inbreeding contribute to explaining the relative advantage of dioecious genera. However, not all dioecious genera display high incidence in stressful areas, which mainly concern those with either numerous or widespread endemic species. We found that dioecy is overrepresented among the species-rich genera in our study plots, and in Hawaii the number of species in dioecious genera is almost twice that of hermaphrodites (Bawa, 1982).

Possible explanations could be linked to why these genera are more speciose than other genera in the WG. Studies regarding the effect of dioecy on diversification are not conclusive, with the finding that some lineages exhibit high diversification and others low (Käfer *et al.*, 2014; Sabath *et al.*, 2016). Some authors indicate that dioecious lineages are most speciose when they possess all of certain morphological traits (woodiness, plain flowers and fleshy fruit) and occur in the tropics (Vamosi & Vamosi, 2004), but this is the case for many dioecious lineages in the WG. Lastly, traits such as self-incompatibility are said to inherently encourage speciation via increased genetic diversity (Vamosi & Vamosi, 2011).

In Hawaii, only dimorphic endemics were associated with a shift to dry habitats while dimorphism in the overall flora was associated with wetter habitats (Sakai *et al.*, 1995a; Sakai *et al.*, 2006) which could reflect an earlier association between the ancestral character of dioecy and ancestral traits related to adaptations to the least water-stressed conditions of early angiosperm diversification (Feild *et al.*, 2009) in the non-endemic flora. Indeed, separation of sexes is probably an ancestral or at least very ancient character, independently of the history of the WG, or Hawaii, and older lineages might display these ancient associations between dioecy and other ancestral niche traits (Hyp. 2). A possible explanation for why all dioecious genera do not display high incidence in stressful areas could thus be that lineages of non-endemic dioecious species occurring in southern WG being more ancient than those of dioecious endemics, they could have retained this ancient association. This explanation is consistent with the hypothesis of southern WG being a refuge for these more ancient lineages that did not evolve to tolerate greater seasonality. Non-endemic dioecious species were positively associated with zones of high stability and negatively associated with high seasonality, including those of genera belonging to the Magnoliids found at higher elevations such as *Ilex*, *Daphniphyllum*, *Neolitsea* and *Ternstroemia*. It is also consistent with the diffused distribution of the trait of dioecy in the phylogenetic tree of non-endemics in contrast to the more clustered distribution of dioecy within diversified genera in the endemic phylogeny which is coherent with more recent adaptive radiation.

Other potential explanations for the observed patterns or avenues for further research that are beyond the scope of this article may involve 1) ecological plasticity, a characteristic often associated with dioecious plants that present for instance physiological and morphological specialisations of each sex to different microhabitats, and one that is favoured by the strong variation in environmental conditions in space and time; and 2) genetic diversity and polyploidy in these lineages. A recent study found an association between dioecy and polyploidy, the latter leading to characteristics that may contribute to the establishment and success of species in novel ecological settings (Glick *et al.*, 2016). In particular polyploidy is believed to facilitate colonisation

of new and harsh environments (Hijmans *et al.*, 2007; Ainouche *et al.*, 2008), in which separate sexes may be advantageous for their more efficient use of resources for reproduction. However, this association does not occur in all clades. In the WG, it has been suggested that the adaptive flexibility of *Diospyros* could result from its high number of chromosomes, allowing frequent rearrangements (De Franceschi, 1993), but this information is not available for the other genera. Polyploidy could in fact increase phenotypic plasticity or the tendency of a genotype to produce different phenotypes under different environmental conditions, which could lead to diversification in certain cases (Pfennig *et al.*, 2010).

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## GENERAL DISCUSSION AND CONCLUSION



## 1. OVERVIEW

In the course of this work, we attempted to understand the impact of ecological, biogeographical and evolutionary processes on the current biodiversity of WG tree species. While much attention has been focussed on current ecological processes, recent research points to the importance of evolutionary processes and historical contingency in explaining patterns of biodiversity across spatial scales. Evolutionary and ecological processes at the origin of biodiversity hotspots like the WG with high levels of endemism are complex and would potentially reflect interacting aspects of climatic, biogeographic as well as geological history (Harrison & Noss, 2017).

With this view in mind, the present study set out to assess the impact of past and present environmental conditions on current taxonomic distributions and extant patterns of phylogenetic and reproductive trait diversity of the WG tree species. We posed a few basic and general hypotheses linked to the impact of environmental variation in time and changing conditions in space, and tested them along broad-scale gradients covering a major part of the WG. To summarise, we expected persistence in stable areas (historical climate stability-related hypothesis) where species could escape extinction and accumulate in refugia (museum hypothesis) and eventually display elevated speciation rates (cradle hypothesis) over the long term. The stability of climate here implies the stability of particular climatic conditions that are expected to be favourable to a large number of species e.g. warm and wet (*cf.* tropical conservation hypothesis), which characterised the niches of early angiosperms (Feild *et al.*, 2009). Climatic conditions can vary in space, and different locations along abiotic gradients would be more or less suitable to species with different niche preferences or tolerances. In particular, only specific ecological abilities, that would have evolved in specific clades, would have allowed persistence under harsher environmental conditions (stress gradient hypothesis).

Past and present climatic variations are key drivers of both ecological and evolutionary dynamics in the WG. They drive both the distribution of tree species (chapter 1), their assembly in extant communities and long-term evolutionary dynamics (chapter 2), and patterns of dioecious species distributions (chapter 3). They also likely played a role in the diversification of some predominantly dimorphic clades of the WG flora. We found varying levels of niche conservatism along different environmental gradients and variation in phylogenetic structure between subsets of the larger 'tropical moist forest' habitat type in the WG. Our results contradict the idea of a local-regional spatiotemporal divide and point to the influence of macroevolutionary diversifications on the contemporary pattern of local community assembly in the WG.

### ***Species ecological strategies determine responses to quaternary climate variation***

In accordance with previous studies on the WG, our models of species distributions based on current conditions strongly support the importance of variation in annual rainfall, temperature and precipitation seasonality as drivers of endemic tree distributions (chapter 1). We did not find evidence of quaternary refugia within the WG. However, by comparing the trajectories of species modelled distributions over the last ~150 kyr, we showed that fluctuating monsoon rains and changing temperatures or seasonality during the glacial-interglacial cycles induced habitat dynamics that drove distributional changes over time and determined the current contours of species' distributions. Importantly, the responses of species varied, depending strongly on their respective positions along the environmental gradients i.e. their ecological strategies. Based on this analysis we were able to produce an index of habitat stability since the LIG which portrayed a strong south to north trend of decreasing stability.

### ***Current climate and its Quaternary dynamics determine current phylogenetic structure***

Using variables that would convey the effects of ecological filters, be it of current climate or its past dynamics (represented in our index of habitat stability derived in the previous chapter) we tested the stress gradient and historical climate stability hypotheses to explain the phylogenetic structure of WG tree assemblages. The logic behind using the latter index was that climatic stability over the last 150kyr could have permitted the persistence/maintenance of more ecological diversity, allowing us to capture a greater phylogenetic diversity (reflecting the diversity of adaptations acquired over the long-term).

#### ***...in agreement with expectations***

We found that current climatic factors i.e. hydric stress in terms of annual rainfall amounts and seasonality of rainfall, and their dynamics since the LIG jointly explained variation in phylogenetic structure in the WG. Filtering by the strong south to north gradients of decreasing stability and seasonality and the west-east gradient of decreasing annual rainfall were reflected in the basic phylogenetic structure of local communities in plots arrayed across the WG. Conserved niches in deeper nodes resulted in most phylogenetically overdispersed and clustered plots occupying extremes of these broad-scale gradients, environmental filtering being stronger under harsher conditions. A general tendency towards phylogenetic clustering in terminal nodes conversely indicates the domination of subsequent diversification (many short branch lengths within clades), consistent with the high overall rate of endemism in the WG.

*...and contrary to expectations of the stress gradient hypothesis*

In contrast to our expectations involving conserved niches, rather than increasing phylogenetic clustering in local communities with increasing stress along the elevation gradient, our results revealed the coexistence of distantly-related species in communities at higher elevations. This indicated convergent evolution towards cold adaptation in species of tropical, subtropical or temperate origin and also reflected the coexistence of two major angiosperm clades, Magnoliids and Eudicots. Thus, phylogeny is a poor proxy for traits when niches represent convergent evolution between distantly-related species. This highlights the justifiable criticism of community phylogenetic analyses based on the assumption that closely related species are more ecologically similar than distant ones (Webb *et al.*, 2002), and the need for considering alternative scenarios.

*Positive phylogenetic turnover*

The overall positive phylogenetic turnover is in keeping with the general finding for studies conducted at a deep taxonomic scale in the presence of strong environmental gradients (cf. Vamosi *et al.*, 2009). Similar to previous findings based on a part of the same dataset (13°30'-15°N) using the same (50 plots, Hardy *et al.*, 2012) and different methods (96 plots, Swenson, 2011), phylogenetic turnover was significantly correlated with annual rainfall and seasonality gradients but not space, highlighting the role of environment rather than dispersal limitation in the replacement of plant lineages across space in the WG. However, our study which spans the entire elevation gradient in the WG (>2000m) provides new evidence for the likely distinct biogeographic and evolutionary backgrounds of low- and high-elevation species pools. In fact, up to a difference of 900-1000m, the elevation span of plots included in previous studies, phylogenetic turnover is low for plots at contrasting elevations. It is only after this, up to a difference of 1700m, that turnover abruptly increases.

***Current climate and its Quaternary dynamics determine reproductive trait structure***

Finally, we found that the variation of abiotic stress and resource limitation related to water availability and historical habitat stability influences the frequency of mating systems along environmental gradients. Our results further point to the likely ecological divergence and adaptation to new niches along the seasonality gradient, i.e. the preferential diversification of dioecious species in the drier northern WG, leading to opposing spatial patterns of dioecious species frequency for endemics and non-endemics along the seasonality gradient. Different mechanisms may have selected for dioecy: conservation of non-endemic dioecious lineages in least seasonal southern WG forests, vs. diversification of dioecious endemics in more seasonal and unstable environments northward.

While seemingly dealing with different aspects of the plant biodiversity of the WG (taxonomic, phylogenetic, sexual systems), linked mainly by the marked influence of past and present environmental variations in shaping the patterns we observe today, the three chapters are closely interlinked and feed into each other on various levels. I illustrate this below with two examples related to the different levels of niche conservatism we found along different environmental gradients. I then go on to explore the macroevolutionary contingency of habitat-lineage pools and how it affects patterns of local phylogenetic structure in habitats with different abiotic conditions

## 2. THE STORY THAT CONGENERIC ENDEMICS TOLD: NICHE LABILITY

According to our results in chapter 1, the response of certain congeneric endemic species to Quaternary climatic fluctuations were related to their distinct habitat preferences, beyond phylogenetic affinities. Indeed, a pattern they ascribed to "ecological vicariance", was observed in the field and studied by previous researchers at FIP (Pascal, 1988; De Franceschi, 1993; Gimaret Carpentier, 1999). Species of the same genus were restricted to either wet or dry formations, or displayed a differential capacity to tolerate seasonality or low temperatures or to adapt to certain edaphic conditions within humid forests. We could conclude at this stage that this diversity of niches at fine taxonomic scales arose as a result of evolutionary events that predate the Pleistocene.

Chapter 2 provides additional pieces to this puzzle. The tendency towards clustering in terminal nodes suggested that more recent diversifications did not entail large niche shifts among species coexisting in local communities. This seemed to contradict the hypothesis of ecological vicariance. However, it refers to local differentiation *within* communities whereas the vicariance concerns variation along gradients, highlighting the importance of incorporating both within (alpha) and between (beta) community metrics of phylogenetic dispersion. The variation in phylogenetic turnover along different gradients is telling; the strong phylogenetic signal in niche traits related to rainfall preferences and high lineage turnover along the rainfall gradient was contrasted to the low turnover along the seasonality gradient. This indicates that close relatives occupy dissimilar positions along the latter gradient, suggesting that traits related to seasonality preferences, like drought tolerance or avoidance, may be more evolutionarily labile for certain clades than others.

In chapter 3, we made the connection between the shift from wetter to seasonally drier abiotic conditions and dioecy. For one, many of the genera in question displaying the above vicariance were dioecious or polygamodioecious. Secondly, explanations of the high incidence of dioecy in islands included autochthonous evolution towards dioecy, and in some places endemic (i.e. locally evolved) dioecious species were associated with a shift to dry habitats, whereas dioecy in the overall flora was associated with wetter habitats (Sakai *et al.*, 1995; Sakai *et al.*, 2006). This could point to a more ancient association of dioecy with traits conferring adaptation to humid

conditions and a more recent encountering of drier (novel) habitats where dimorphic species might have been able to escape competition with monomorphic species.

While our analysis of the patterns of frequency in dioecious species along the seasonality gradient does not fully explain ecological vicariance in all genera along other gradients such as elevation, this could constitute a first step towards explaining both the high incidence of dioecy and high endemism in the WG. We suggest that these explanations are linked to the fact that seasonality became an important factor more recently, with the establishment and reinforcement of the monsoon regime and the aridification of large areas of the Indian peninsula in the Miocene (Guo *et al.*, 2008; Patnaik *et al.*, 2012). Fossil records of flora and fauna also indicate warm and humid conditions in the early Neogene shifting to cooler and drier conditions during the late Neogene (Patnaik & Prasad, 2016).

The literature provides some support for our hypothesis. For e.g. the dispersal into India from other Gondwanan landmasses is indicated as having occurred around the mid-Miocene for Garciniaee which have a crown age of ~20 Ma (Ruhfel *et al.*, 2016). This suggests that some of the diversification of this polygamodioecious clade could have coincided with time that central/northern WG experienced increased seasonality. Regarding possible allopatric speciation, we could hypothesise that populations of species having established on both versants of southern WG, would have subsequently experienced contrasting conditions on the wind- and leeward slopes, not due to WG orogeny, which would have predated their arrival into India, but due to Himalayan orogeny and the onset of the monsoon regime. Although we were limited by the resolution of available phylogenetic trees for the WG species in our ability to verify if the time of diversification of dioecious endemics coincided with the onset of seasonality here, we provide hypotheses that can be tested in the future. Specifically, we highlight the importance of taking into consideration the role of geological history and global paleoclimatic trends in the deepening of the climatic gradients in the WG and the impact this could have on biota.

Our results suggest that whether it is easier to shift in space or to evolve in the face of climate change could depend on the one hand on (i) the presence of lineages that can readily adapt to and take advantage of opportunities offered by novel conditions by dint of their ability to successfully colonise and occupy harsher conditions, and on the other hand (ii) the age of the lineage and the relative strength/constraining force of associations between ancient trait states. Other possible factors like spatial configuration of the contrasting environments and phenotypic plasticity (Edwards & Donoghue, 2013; Donoghue & Edwards, 2014) not treated here, are also of potential importance. In sum, different lineages, with different biogeographical and evolutionary histories would respond differently to the onset of a new climatic regime, as suggested by the differences in sexual systems in the WG.

### 3. CONSERVATION OF ANCESTRAL PREFERENCES IN SOUTHERN REFUGIA

The concept of a museum involves the persistence of species of ancient lineages in climatic refugia. These are (i) old and historically stable areas that have not been affected by glaciations or extreme temperature fluctuation (Harrison & Noss, 2017) and (ii) offer the particular conditions of high temperature and moisture that decrease extinction (Rolland *et al.*, 2014) associated with such 'museums' in the tropics. The idea of a museum also implies preservation, or conservation of ancient niche adaptations. Indeed, a region may also function as a museum because it (iii) matches the environment in which lineages from a particularly early epoch originated or survived. Further, wet habitats appear to function as museums containing older lineages and dry habitats as cradles containing younger ones, although a habitat could be both a museum and a cradle (Bartish *et al.*, 2016).

In terms of historical climate stability, firstly, the gradient of habitat stability since the LIG in the WG (chapter 1) is represented by the number of species that could persist locally over time, and southern WG represent the area that provided long-term stability for the maximum number of species. This index likely mirrors past conditions, at least since the last major event, i.e. the onset of the monsoon that deepened the seasonality gradient and affected conditions on leeward slopes. Secondly, fossil pollen records indicate the presence of widespread rainforests in the Indian subcontinent dating back to the late Palaeocene-early Eocene, when excessive humid climates prevailed due to the equatorial position of the Indian plate combined with a long-term global warming phase spanning the Palaeocene-Eocene Thermal Maxima (PETM) and early Eocene Climatic Optima (EECO) (Prasad *et al.*, 2009).

This abiotic environment is currently matched only in southern WG where elements of this flora persist in refugia, as indicated by the strong resemblance between a number of the most common fossil flora of this period and the extant pollen flora of southern WG (Prasad *et al.*, 2009). Molecular phylogenetic studies report the persistence of ancient lineages here for a variety of taxa (Biju & Bossuyt, 2003; Roelants *et al.*, 2004; Joshi & Karanth, 2013). Thus, indications are that southern WG forests function as a museum by providing stable conditions for ancient lineages with conserved preferences for high rainfall and low seasonality habitat conditions.

The deep-branching clade of Magnoliids - retaining ancestral adaptations to warm and humid periods during which they diversified in a rainforest context (Carlucci *et al.*, 2016) - influences the phylogenetic structure in WG plots. Species of this clade co-exist with distant Eudicot lineages that have also differentiated, evolved and migrated over time to occupy conditions favourable to both in the forests of the south and at higher elevations, contributing to basal phylogenetic overdispersion. Magnoliids contribute significantly more species compared to a null model prediction to the composition of plots here. However, they are significantly underrepresented in

low elevation plots further north with >6 months of dry season and lower annual rainfall levels, and plots in the dry evergreen forests of southern leeward slopes, contributing to basal phylogenetic clustering there. However, some clades that include Lauraceae, are over-represented in certain low elevation northern forests (e.g. PDH, Table 2 of the Introduction) despite the longer dry season, as annual rainfall levels are very high.

Unsurprisingly, high lineage turnover along the rainfall gradient particularly concerned the turnover of deep-branching clades such as Magnoliids. Such older lineages likely retain environmental tolerances to occupy communities in habitats presenting similar environments across continents (Hardy & Senterre, 2007; Graham *et al.*, 2009). Indeed, Hardy *et al.* (2012) found that specific clade adaptations to the rainfall gradient in the WG corresponded to those in central Panama, although the two regions did not have species in common. Niche phylogenetic signal was driven mostly by several families, including many in the Magnoliid clade, adapted to high rainfall in both regions. It follows that conservation of niches related to rainfall is deeply rooted in the origin of clades showing adaptive trends, rather than being a result of re-organisations of species adaptations within specific biogeographic contexts (Hardy *et al.*, 2012).

Finally, non-endemic dioecious species, including those belonging to the Magnoliids such as *Daphniphyllum*, *Ilex*, *Neolitsea* and *Ternstroemia*, were positively associated with zones of high stability and negatively associated with high seasonality (chapter 3). They also belonged to lineages that were on average older than those of endemic dioecious species and might thus reflect an ancient association between dioecy and ancestral wet adaptation. Their presence in southern WG is in keeping with the hypothesis that such forests are a refuge for these more ancient lineages (museum) that did not evolve to tolerate greater seasonality. On the other hand, dioecious endemics of genera that displayed greater niche lability (see previous section) are also found under humid low seasonality conditions of southern WG, suggesting that this comprised the original niche of these genera. The forests of southern WG could have constituted a centre for secondary diversification (cradle) as suggested for *Diospyros* (De Franceschi, 1993), from whence species diversified through adaptive radiation and occupied different positions along the gradient.

#### 4. MACROEVOLUTIONARY CONTINGENCY

Different habitats, and plant communities occurring in these habitats, have their specific species pools. Habitats (e.g. a moist tropical forest) are connected into persistent networks (e.g. all moist tropical forest found in the world) maintaining global 'habitat-lineage pools' (Gerhold *et al.*, 2015). The particular evolutionary history of lineage pools of distinct habitat types should be reflected in the lineage composition and hence phylogenetic structure of extant communities that are sampled from these pools. Bartish *et al.* (2016) found for e.g. that dark and moist habitats

contain high diversities of lineages dating back to globally moist epochs like the Palaeocene/Eocene; warm habitat types were similarly linked to warm climates of the Miocene, and cold habitats to a period of global cooling and glaciations in Europe.

It follows from our above example of Magnoliids that the evolutionary history of moist tropical forest habitat-lineage pools have an effect on the composition of local communities sampled from them in the WG (phylogenetic-patterns-as-cause, Gerhold *et al.*, 2015). Champion and Seth (1968) categorised WG forests into moist tropical, dry tropical, montane subtropical and montane temperate forests. The moist tropical forest habitat-type is further sub-divided into a) tropical wet evergreen, b) tropical semi-evergreen, c) tropical moist deciduous and d) littoral and swamp forests. The question is, do sub-habitats of the moist tropical forest habitat type have separate enough histories or lineage pools to have a similar effect to lineage pools of more strongly differentiated habitat types such as moist tropical forest vs. montane forests or grasslands for instance?

#### *Contrasting phylogenetic structure*

Extant communities of evolutionary old habitats can source their species from a wider range of major old lineages than communities in young habitat types leading to higher phylogenetic dispersion in local communities of older habitat types compared to younger ones according to Gerhold *et al.* (2015). An evolutionary interpretation of Webb's (Webb *et al.*, 2002) standard parameters suggested by the authors is that early diversification would lead to greater mean phylogenetic distances and a high rate of diversification more recently would lead to lower phylogenetic distances among closely-related species.

Our use of metrics reflecting phylogenetic structure at different evolutionary depths allowed us to additionally examine different timescales of evolutionary and ecological dynamics. The general trend of overdispersion at deeper phylogenetic scales in the southern WG contrasted to the general trend of clustering at these scales in communities further north. This appears to support the idea of them being different habitat types. In southern WG the maintenance of favourable conditions through different geological epochs could have maintained more diverse lineages here and ancient evolutionary history possibly underlies niche differentiation (older lineage splits that would have occurred elsewhere, Bartish *et al.*, 2016). Lineage pools of ancient habitat types (like the wet evergreen subsets of moist tropical forests) may have diversified for long periods leading to higher phylogenetic dispersion of incumbent angiosperm species pools (Gerhold *et al.*, 2015) - as we found in southern forests. On the other hand younger habitat types would have experienced diversifications more recently (they may not have existed before) with only limited immigration from more ancient habitat types due to the prevalence of niche conservatism (Prinzing *et al.*, 2001); is this the case for northern forests (>13°N)?



*Conditions in northern forests are more recent*

While Prasad *et al.* (2009) term it a Paleogene refuge (in the sense that the flora includes relicts of Paleogene lineages) we suggest that the southern WG might be a late Neogene (post mid-Miocene) refuge as it was this period that was marked by major drying events since the late Palaeocene-early Eocene period of widespread rainforests in the Indian subcontinent. We can thus say that forests in the northern half of the WG where dry seasons exceed 4-5 months/year reflect conditions that were established more recently. But did it achieve the status of a distinct, and younger, habitat type with a distinct habitat-lineage pool? Does basal clustering here point to more younger lineages with recent diversifications and fewer lineages in the habitat-lineage pool of moist tropical forests that are seasonally dry? Is community composition limited by this habitat-lineage pool? Would we have found different patterns if we had used different species pools for southern and northern forests in our null models?

*Along the south to north stress and stability gradients*

The predicted higher diversity and endemism in historically stable areas (Graham *et al.*, 2006; Fine, 2015) is supported by a south-north decrease in species diversity and endemism in the WG (Ramesh & Pascal, 1997; Ramesh, 2001). This suggests that fewer lineages have successfully colonised northern WG forests, or that they have been colonised relatively recently leaving less time for diversity to build up in these habitats, or a combination of these factors (Wiens *et al.*, 2013). Alternatively, northern forests could include an impoverished subset of southern species.

Floristic composition from south to north in the WG is marked by a change in phenology, with tall dense evergreen forests (at least 95% evergreen) giving way to shorter semi-evergreen (40-80% evergreen) forests at c.14°N, where the length of the dry season increases to >5 mo. Barboni *et al.* (2003) distinguished these forests on the basis of their pollen signal, potentially indicating two distinct habitats (the authors use the word 'biomes' here) of different phenology, i.e. with different responses to drought stress and precipitation seasonality. Between 13°15'-14°N there is a gradual transition from *Dipterocarpus*- to *Diospyros*-dominated forests, with the disappearance of sciaphilous species sensitive to drought (Pascal, 1988). This could be a signature of changing conditions in the late Neogene, as species with distributions in zones of progressively increasing seasonality further north would have to face extinction, adapt, or persist in refugia - if their ecological amplitude was not wide enough to survive in this newly changed and fragmented landscape. The shift in moisture conditions and disappearance of less-tolerant lineages, could then have opened up new areas for colonisation, including from the outside, by species of lineages better adapted to seasonally dry conditions.

### Older lineages

An example of 'relicts' of former evergreen forests are the "Kan" forest islets (forest type DDP, see Table 2, Introduction) between 14-15°N. Evergreen species persist in 'edaphic refugia' with less rain (<2000mm) and through long dry seasons due to the moisture holding capacity of soils. Along with a neighbouring forest types, these edaphic facies are characterized by i) an absence or rarity of species more common in southern evergreen forests, ii) high importance value of *Diospyros* species, and iii) an abundance of heliophilous (e.g. *Aporosa lindleyana*) and light-tolerant evergreen species (Pascal, 1988; Barboni *et al.*, 2003). Our results reflected this limited immigration of more ancient lineages (Magnoliids) into plots further north and in the leeward slopes of the WG.

Secondly, older lineage could include those that were (perhaps more anciently) filtered by other abiotic or biotic factors (see Chapter 2). For instance, waterlogging (e.g. *Myristica* swamps), or particular edaphic conditions ("Kan" forests) filtered species with adaptations or ecological plasticity to persist in these conditions. Patchily distributed elsewhere in the WG, *Poeciloneuron indicum* (*Poeciloneuron* Bedd.<sup>1</sup> is one of the six genera endemic to the WG) becomes almost monodominant in facies characterized by particular soils rich in iron and alumina in forests further north, along with other species of the Calophyllaceae family. This has been attributed to its competitive edge to colonise and establish here thanks to the early development of a deep tap root and copious seeding (Kadambi, 1942; Pascal, 1988). The genus is particularly informative in this context because its appearance has been placed in the late Oligocene (Ruhfel *et al.*, 2016). A fossil leaf impression of this species in north-east India is indicative of the more widespread distribution of both rainforests and of *P. indicum* during this period (28.4-23 Ma) coinciding with the 'Late Oligocene Warming' phase (Srivastava & Mehrotra, 2013). Apart from climate, the authors ascribe its disappearance from north east India to the change in latitude compared to the paleolatitude of the fossil locality (from 10-15°N to ~27°N), where the WG is today located. Thus, it is clearly sampled from the wet evergreen/ moist tropical forest habitat-lineage pool.

Calophyllae, a subclade of the Calophyllaceae family (stem age ~100Ma) of the ancient clusoid clade, includes genera *Poeciloneuron*, *Calophyllum*, *Mammea* and *Mesua* present in the WG, all which have WG endemic species apart from *Mesua*. It was found to have a very long stem (stem age ~ 60Ma) and have diverged only within the last 35 Myr or so (Ruhfel *et al.*, 2016). Calophyllae is thus an example of a lineage with ancient evolutionary roots, and adaptations to wetter

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<sup>1</sup> *Poeciloneuron* comprises two species, *P. indicum* and *P. pauciflorum* displaying high interspecific morphological and wood anatomical variation - to the point that it has been proposed that the latter, restricted to southern WG, be placed in a new monotypic genus *Agasthiyamalaia* (Rajkumar & Janarthanam, 2007).

conditions, but displaying more recent diversification - blurring the old-wet-overdispersion and young-dry-clustering distinction.

*Combination of lineages from multiple habitat-lineage pools?*

The assembly of a community occurs through short-distance dispersal from adjacent patches of other habitat types or from refuges, and long-distance dispersal between plots of the same habitat type (Gerhold *et al.*, 2015). We can probably say that local communities in northern forests reflect the varying influence of both *older* lineages from the wet evergreen habitat type (i) persisting in refugia, (ii) having species with wide ecological amplitudes, or (iii) anciently filtered by other abiotic factors; and *younger* lineages (i) that are a result of immigration from neighbouring habitat types (e.g. deciduous lineages of the moist or dry deciduous forest types), or (ii) southern lineages that diversified more recently (e.g. species of some dioecious genera, Chapter 3).

These forests are possibly at the intersection of two more distinct habitat types, with elements of the habitat-lineage pool of each: i.e. tropical semi-evergreen forests in the transition between wet evergreen and moist deciduous types. Indeed, the contrasting north vs. south, clustered vs. overdispersed phylogenetic structure is not absolute. This is especially so in forests above 13°N which, despite their local communities being on average more clustered, include plots displaying basal overdispersion. Here the relative importance of older lineages may be greater than younger lineages. On the other hand, the contribution of lineages from the lineage pool of an ancient wet evergreen habitat type that only relatively recently diversified (e.g. Calophyllaceae and Garcinieae, Ruhfel *et al.*, 2016) would result in the co-occurrence of more closely-related species or local phylogenetic clustering (e.g. *Poeciloneuron* facies with confamilial species).

In sum, our results, based on extant communities in contemporary habitats, are informative of the macroevolutionary impact of the habitat-lineage pools from which communities are sampled. They point to the interaction between macroevolutionary diversification and local co-existence, blurring widely-held distinctions based on differences in spatiotemporal scales of local vs. regional or ecological vs. macroevolutionary. Importantly, for the purposes of this thesis, these interactions are strongly mediated by both the present-day climatic conditions in the habitat, their recent dynamics, as well as the paleoclimates that prevailed during the different geological periods that different lineages diversified in. In a very general way, wetter(drier) paleoclimates dominated at more ancient (recent) geological periods, leading to older (younger) lineages with extant species potentially displaying conserved niches of their ancestors co-existing in habitats that present wetter (drier) conditions today. However, no habitat type is absolute nor always strongly demarcated. In a region with strong environmental gradients, extreme ends of a dominant abiotic gradient or the combined influence of multiple gradients leading to conditions that are experienced by trees as ecophysiological extreme, can be linked by areas of

intermediate conditions. This could lead to different habitat-lineage pools or combinations of thereof, each with their particular evolutionary histories, being reflected in local communities in this habitat that are sampled from these pools.

## 5. LIMITATIONS OPEN PERSPECTIVES

The present work is among very few analyses of broad-scale patterns at the regional scale in the WG (c.f. Gimaret-Carpentier *et al.*, 2003; Davidar *et al.*, 2005; Davidar *et al.*, 2007; Ramesh *et al.*, 2010) especially spanning all the major environmental gradients across 7-8 degrees of latitude. It is one of the first attempting community phylogenetic analyses at this scale. However, we have only been able to get a partial understanding of biogeographical and evolutionary events at the origin of the various aspects of plant diversity. Indeed, the lack of more such large-scale studies is also an indication of the paucity of data, but for this very reason it also presents much opportunity for more focussed data collection, hypotheses testing and discoveries in the future in this complex and fascinating biodiversity hotspot.

Our study is limited in its inferences by the data available for quantitative analyses; we hope however, that it opens up new perspectives and proposes hypotheses that motivate further testing. Inferences regarding biogeographical history is usually based on a) data on contemporary species distributions; b) past climate reconstructions; c) fossil data to ascertain species past locations and data on their related ancestors to estimate divergence times; and d) genetic sequences or morphological data to reconstruct phylogenies. While many other tropical forest areas in Africa, South America and Asia increasingly comprise large-scale permanent plots that are connected to a worldwide network of plots following a common protocol (e.g. RAINFOR or CFTS forest plot networks), in the WG there are few such initiatives. The FIP is practically the sole repository of accessible data on plots covering a large area. However, we need to combine two datasets, which although collected by botanists common to both, might lead to uncertainties related to differences in research aims and sampling protocols used. There remain gaps in the data and a lack of plots between 11°5'-13°N needed to be compensated with one of the rare publications that included plot data from the Kerala Forest Research Institute, which could also contribute uncertainties related to differing protocols. Although our metrics of phylogenetic dispersion are standardised by the mean and variance of the metrics of null assemblages and should not be influenced by variations in species richness, we verified that species richness of between plots from the different datasets were indeed comparable and used only species presence-absence information. Secondly, we did not have access to any plots located in the northern-most area of the WG between 16°-20°N. An analysis of these northern-most forests, where seasonality and historical climate instability is even greater, might throw further light on the issues raised in our work.

*SDMs, current climate and past climate reconstructions*

The development of SDM has allowed the modelling of the multiple species occurring in tropical rainforests, and advances in presence-only modelling permits the use of data contained in atlases and natural history collections, especially valuable in the context of hyper-diverse tropical forests that lack inventories arrayed across the entire region. However, we acknowledge the methodological limitations related to the use of SDM, both for the present and for projections into the past (Varela *et al.*, 2009; Svenning *et al.*, 2011). We attempted to address the statistical performance and relevance of our results in Chapter 1, by using multiple replicate models with distinct subsets of 10% of occurrence localities for testing. In addition, we designed a specific null model, which showed that our models captured ecologically meaningful drivers of the species distributions. Our choice of climate dataset (WorldClim) among the many available alternatives, like for instance remotely-sensed data, was supported by this and the fact that the climate-distribution association was strongest in the WG compared to other rainforests in Central Africa or South America (Deblauwe *et al.*, 2016) using this data. The latter also indicates the relatively strong influence of current abiotic factors on species distributions here. However, despite careful analysis prior to choosing among available GCM models, the nature and quality of past climate reconstructions remains a possible source of uncertainty in SDM projections.

*Fossil data and Phylogenetic resolution*

We were unable to access adequate fossil data for the region, time period and species concerned and were thus unable to evaluate species distribution models projected into past climatic conditions based on their fossil locations in the LIG or LGM. More generally too, fossil data for the ancestors of tree species in the WG is hard to come by, which affects the calibration of phylogenies. Most important, and easier to improve, is the fact that molecular genetic work for better phylogenetic reconstruction is lacking for many tree species, especially endemic ones. Much more research effort has been focussed on amphibians or on fauna than on plants, and phylogeographical studies on WG plants are not numerous (e.g. Deshpande *et al.*, 2001; Kuttapetty *et al.*, 2014).

Thus, while our phylogeny reflects the most current understanding of phylogenetic relationships among families and genera for angiosperms, the resolution among species is poorly defined. A number of lower taxa are represented as polytomies, i.e. with the same node age for congeneric species, in the phylogeny. Although this allows for phylogenetic analyses of species-rich assemblages lacking pre-existing molecular or phylogenetic information, phylogenetic dispersion metrics could be sensitive to polytomies. However, according to Swenson (2009), when most basal nodes are bifurcating and the lack of resolution is terminal, as in our case, the loss of statistical power is minimised. Also, lower phylogenetic resolution generally causes false negative

(under-estimation of overdispersion and clustering) results rather than false positives (over-estimation), i.e. the  $MPD_{SES}$  and  $MNTD_{SES}$  values would be closer to the null expectation and there is reduced power to detect non-random community phylogenetic structure. This is more important when using larger trees such as ours. Given this, we focussed on values that were significantly higher or lower than expected with regard to the null assemblages, not having detected many values of significance when applying multiple-comparison corrections to control the false discovery rate of multinomial tests (e.g. Benjamini & Hochberg, 1995).

Our lack of a fully resolved tree was more crucial in terms of testing hypotheses, for instance in Chapter 3. We were limited in our ability to identify and compare sister species between dioecious genera to see whether and when their niches diverged, or to identify ancestor species and compare possible ancestral niches with divergent ones. We were unable to conduct simple tests such as comparing the phylogenetic distances and niche distances between species within genera, as congeneric species often had the same node age. Lastly, we were also unable to verify whether the timing of diversification of dioecious endemics coincided with the deepening of the seasonality gradient, which would have given more weight to our findings. However, the literature supports some of our hypotheses for certain clades. For instance, dispersal into India and subsequent diversification of certain dioecious clades after the mid-Miocene (Ruhfel *et al.*, 2016) would coincide with time that central/northern WG experienced increased seasonality. Our work thus retains value in the sense that we provide perspectives for future work, and highlight the need for studies yielding genetic sequences, especially on endemic tree species. The hypotheses we propose can then be further tested when progress in phylogeny reconstruction would allow for finer analyses.

#### *Biotic interactions and species traits*

Our aim was to study the impact of broad past and present environmental gradients on the spatial patterns of different aspects of WG biodiversity, but biotic interactions are also of great importance in community assembly, albeit possibly at smaller scales. They are also increasingly being included in distribution models. For our analyses of patterns of distribution of plant mating systems, the non-inclusion of the role of pollinators is an important limitation. Reproduction in plants, especially in fragmented landscapes, is limited by the diversity or abundance of pollinators, and this is especially important for obligate outcrossers (Nayak & Davidar, 2010). There exist only a handful of studies on pollinators or dispersal modes of WG trees, and only one on the effect of pollinator limitation and plant breeding systems on their reproduction, which unfortunately only concerns the Eastern Ghats (Nayak & Davidar, 2010).

There is little verifiable information on other basic characteristics and biology of the trees in our dataset, such as dispersal mode and mating systems. The few studies that exist only concern a

certain number of species (e.g. Ganesh & Davidar, 2001; Devy & Davidar, 2006; Tadwalkar *et al.*, 2012) or focus on a single species. As a result, we combined, compared and contrasted publications, a field-based morphological trait database ([www.biotik.org](http://www.biotik.org)) as well as various flora of southern India (Fyson, 1915; Gamble, 1915-1934; Sasidharan, 2006), regional forest department flora and global databases (e.g. Renner, 2014) to compile this information. The different sources sometimes provided conflicting information, which might have introduced some uncertainty. Additionally, there has not been much work done on cryptic dioecy or other mechanisms of self-incompatibility in other mating systems of the WG trees, which information would have nuanced our results in Chapter 3. In the context of dioecious species, detailed studies on ecological plasticity would also be pertinent. Such plasticity would also possibly play a role in the context of the survival of populations of species in zones where conditions are less suitable such as in edaphic facies (e.g. *Poeciloneuron*, the species of which display high intra-specific variation, see Chapter 2) or forest fragments outside the evergreen zone (e.g. WG endemic species in eastern hills that connect the WG and the Eastern Ghats, see Chapter 1). Another important aspect that has been raised in the WG (Krishnan, 2001) and elsewhere and only touched upon in Chapter 2 is the particularity of understorey species, that can benefit from the micro-climatic conditions below the forest canopy.

The advantages of studying broad-scale trends was made clear by the present work, but this needs to be complemented by more detailed research. For example, we infer competition in southern WG forests and we consider facilitation as a possible mechanism at high elevations, as we infer conserved vs. convergent niches, however this would need to be verified by precise field-based studies. In this context, given the key role of strong environmental gradients in determining past and current forest dynamics in the WG, an investigation of functional traits is an important perspective. Our findings could contribute to decisions on which traits, out of the myriad possible traits, future studies could focus on. For instance, the potential importance of traits related to drought-resistance/tolerance or avoidance along the seasonality gradient and hydraulic conductivity-related traits like wood or leaf vein density (e.g. Swenson & Enquist, 2007) along the rainfall gradient are most apparent. The regulation of hydraulic and photosynthetic processes in the temperate-tropical adaptations for Magnoliaceae species, meant that different ecophysiological traits were conserved across divergent lineages of this family (Liu *et al.*, 2015). Studies on ecophysiological traits and determination of conservation, convergence or divergence of niche traits could thus also throw light on such issues as well as the ancestral ecophysiological contexts of lineages (Feild *et al.*, 2009). In association with information on the geological epoch in which lineages diversified and the associated paleoclimate, this would provide a more complete picture of the macroevolutionary contingency on patterns of local phylogenetic structure we observe today.

## 6. IMPLICATION FOR CONSERVATION

The immediate future of this hotspot faces greater threat from direct human activity than climate change, as the Indian government increasingly bows to pressure to allow developmental activities within the WG. For instance, between two recommendations of plans for the protection of the WG requested by the previous government, - the first by a panel of ecologists in 2011 and the second a commission set up to review the first - the area recommended as ecologically sensitive areas (ESA), i.e. out of bounds of industrial development, went from 3/4 to about 1/3 of the total area of the WG. Under pressure of interest groups in the sectors of mining, quarrying other heavy industry and politicians, the boundaries have since been redrawn in three successive government notifications of ESAs, each one reducing the proposed area further.

Conservation planning traditionally focuses more on patterns (species rarity and richness) rather than processes like persistence (genetic diversity) (Moritz, 2002). In recent years as threats to biodiversity mount, evolutionary processes that maintain and generate biodiversity are being recognized as factors that need to be included in conservation strategies (Rolland *et al.*, 2012). Our results provide clear indications of the evolutionary potential of different areas of the WG. having relatively higher or lower phylogenetic diversity

It has been argued that preserving a site with highly diverse, distantly-related species may be more beneficial than preserving one with many closely-related taxa (Lyashevskaya & Farnsworth, 2012; Diniz-Filho *et al.*, 2013). The rationale is that the extinction of most phylogenetically distinct species would result in a greater loss in terms of the variety of strategies, that may then reduce the ability of biota to persist in the face of change (Devictor *et al.*, 2010). However, while overdispersed plots in the WG may comprise distantly-related species and a larger pool of lineages, our results indicate that these are communities are located in the most stable areas, which have been buffered from the effects of long-standing climatic changes or fluctuations, and might continue to be in the future. According to our results they largely comprise species with conserved preferences for high moisture levels lasting almost throughout the year, unlike evergreen species further north that were able to withstand or adapt to the imposition of seasonality in the Miocene. The former if exposed to change would like face greater threat than the latter. Trees in seasonally dry forests would remain vulnerable to climatic fluctuations because of their location in already stressful environments. However, during the LGM when the summer monsoon was weakened, distributions of evergreen endemic species here contracted but still persisted in populations in the areas of higher rainfall - although not all were able to recover their previous distributions of the LIG between the LGM and the present. However, species in both seasonal and less seasonal areas of the WG are under greater threat of proposed changes in land use leading to fragmentation, than imminent climate change.



In this context, the existing protected area (PA) network takes on increased importance as it can provide connectivity between populations in a fragmented landscape. We propose areas where species have been buffered from the effects of climate variability since the LIG and potentially further back in time. Our results show that these areas are not always targeted by conservation policies in the WG as only a portion of stable habitat zones fall into the current PA network, and this mainly concerns southern WG.

The plots of southern WG are valuable in terms of conservation of evolutionary functions of communities as both a museum and a cradle of diversity. On the other hand, areas of low phylogenetic diversity further north include lineages that are specially adapted to specific conditions that allowed them to persist in the face of long-standing environmental change, and are particular to the area (e.g. the 'Kan' forests, *Poeciloneuron* facies and *Myristica* swamps).

Dioecious species are thought to be under greater threat in situations of climate change and associated fragmentation especially given their need for the presence of a male and a female tree, and pollinators in proximity in order to reproduce. However, the "vicariant" endemic dioecious species of the WG appear to show an ability to survive under moisture stress and even colonise what might have been fragmented landscapes in the Miocene. If our hypotheses prove true, this could be significant in terms of response of endemic species to changing conditions.

The WG was high on a list of most irreplaceable protected areas based on a recent study in *Science*, ranking second in terms of 'irreplaceability' of multiple threatened taxa and first when this concerned amphibians alone (Le Saout *et al.*, 2013). Our analysis is specific to trees but this has implications for the many forest-dwelling amphibians, birds and animals that depend on these forests. Animals, especially those having a host-plant relationship, may track plant species distributions (Condamine *et al.*, 2012) and studies specific to the WG point to the persistence of humid-forest dwelling relict taxa over the long term in southern refugia (Joshi & Karanth, 2013), making the conservation of these forests all the more important.

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## ANNEXE 1

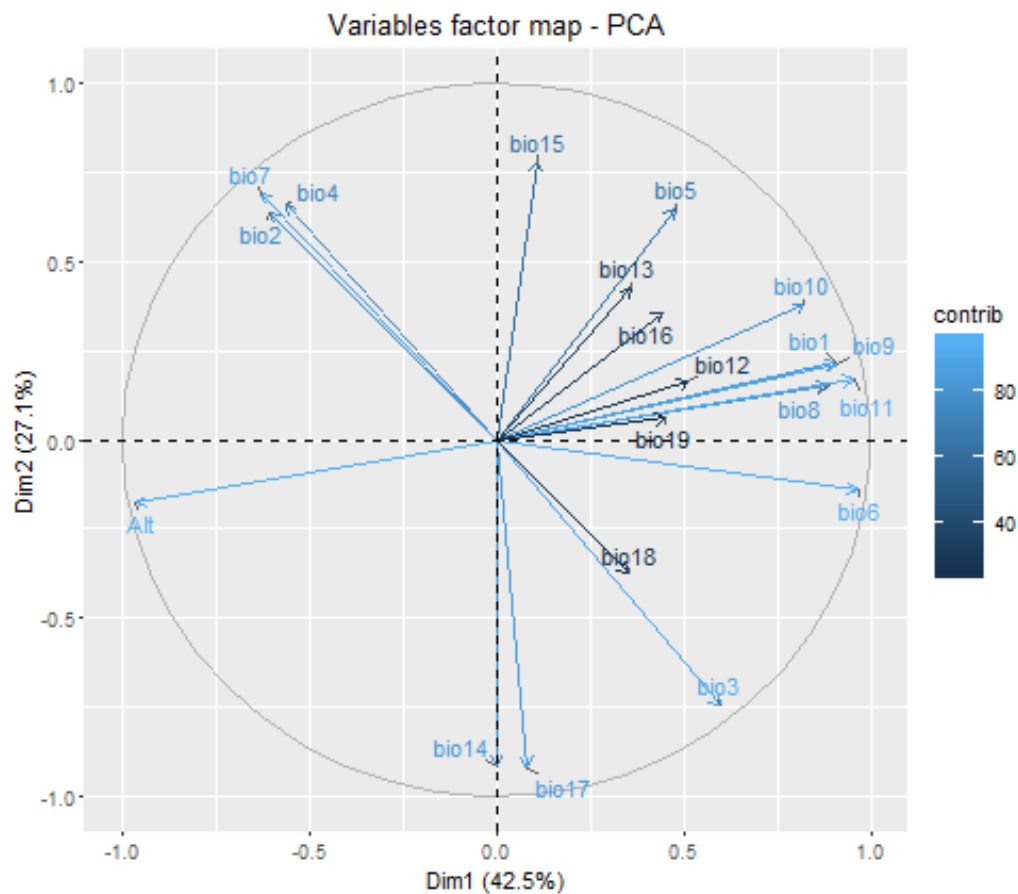
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**Appendix S1** PCA of 19 bio-climatically significant variables (bio 1-19) and elevation

**Appendix S2** Results of the multiple regression analysis of species scores on CA axes

**Appendix S3** Results of multinomial test for 44 significant species

**APPENDIX S1** Principal components analysis (PCA) of 19 variables (BIO1–BIO19; Table S1) and elevation extracted from WorldClim database for the Western Ghats area in India.



**Figure S1** Plot of the first two PCA axes of 19 variables (BIO1–BIO19) and elevation extracted from WorldClim database for the Western Ghats area in India.

**Table S1** 19 WorldClim bioclimatic variables.

Variable	Description	Variable	Description
BI01	Annual mean temperature	BI010	Mean temperature of the warmest quarter
BI02	Mean diurnal temperature range	BI011	Mean temperature of the coldest quarter
BI03	Isothermality (BI01/BI07)	BI012	Annual mean precipitation
BI04	Temperature seasonality (Coefficient of Variation)	BI013	Precipitation of the wettest month
BI05	Maximum temperature of the warmest month	BI014	Precipitation of the driest month
BI06	Minimum temperature of the coldest month	BI015	Precipitation seasonality (Coefficient of Variation)
BI07	Temperature annual range (BI05 – BI06)	BI016	Precipitation of the wettest quarter
BI08	Mean temperature of the wettest quarter	BI017	Precipitation of the driest quarter
BI09	Mean temperature of the driest quarter	BI018	Precipitation of the warmest quarter
		BI019	Precipitation of the coldest quarter
		Alt	Elevation

**APPENDIX S2** Detailed results of the multiple regression analysis of the species scores on CA Axis 1 and CA Axis 2 according to the mean species ecological preferences. The predictors of the most parsimonious model, based on AIC analysis with the *step* function, are included in the tables: temp.mean, mean temperature; rain.mean, mean rainfall; season.mean, mean seasonality preference of species.

**Table S2** Multiple regression analysis of the species scores on (a) CA axis 1 and (b) CA axis 2.

(a)	Estimate	Std. error	<i>t</i>	Pr(>  <i>t</i>  )
(Intercept)	0.071772	0.055829	1.286	0.200
temp.mean	0.159510	0.025815	6.179	$3.84 \times 10^{-9**}$
season.mean	0.116076	0.029040	3.997	$9.17 \times 10^{-5**}$
I(temp.mean <sup>2</sup> )	-0.005732	0.003750	-1.528	0.128
I(season.mean <sup>2</sup> )	0.031963	0.007095	4.505	$1.16 \times 10^{-5**}$

$**P < 0.001$ ;  $*P < 0.01$

Residual standard error: 0.4652 on 190 degrees of freedom; multiple  $R^2$ , 0.4829; adjusted  $R^2$ , 0.472; *F*-statistic: 44.36 on 4 and 190 d.f.;  $P < 2.2 \times 10^{-16}$

(b)	Estimate	Std. error	<i>t</i>	Pr(>  <i>t</i>  )
(Intercept)	-0.12453	0.09206	-1.353	0.17774
temp.mean	0.08505	0.03057	2.782	0.00595*
season.mean	-0.16702	0.02393	-6.981	$4.72 \times 10^{-11**}$
rain.mean	-0.02899	0.05590	-0.519	0.60461

$**P < 0.001$ ;  $*P < 0.01$

Residual standard error: 0.5265 on 191 degrees of freedom; multiple  $R^2$ , 0.2983; adjusted  $R^2$ , 0.2873; *F*-statistic: 27.07 on 3 and 191 d.f.;  $P = 1.236 \times 10^{-14}$

**APPENDIX S3** Results of multinomial test on the pixel categories 001,011,101,111 showing the 44 species with significant  $P$ -values ( $P < 0.05$ ) adjusted  $P$ -values after correction ( $P_{adj.}$ ) and deviation from the model null of each species for the respective pixel categories. The species have been categorized in terms of their position on the CA plot (Fig. 3). Species at the extreme negative end of CA axis 1 have more current occurrences located in pixels 111 than expected by chance and most other species (positive CA axis 1) have more current occurrences in pixels that have been stable across the three periods (111) or stable since the LGM (011 for species with contracting distributions over time) than expected by chance.

(a) Negative CA axis 1

Species	Family	001	011	101	111	$P$	$P_{adj.}$	Mean elev.
South WG, < 12° N								
<i>Apollonias arnottii</i>	Lauraceae	-59.21	0.25	<b>297.67</b>	<b>165.12</b>	0.0040	0.0236	1100.66
<i>Calophyllum austroindicum</i>	Clusiaceae	-37.95	-16.23	N/A	<b>218.52</b>	0.0104	0.0492	1071.22
<i>Cinnamomum keralaense</i>	Lauraceae	-80.52	-18.05	N/A	<b>413.88</b>	0.0000	0.0000	937.34
<i>Diospyros nilagirica</i>	Ebenaceae	-59.26	-33.10	N/A	<b>104.63</b>	0.0005	0.0042	1073.08
<i>Euonymus crenulatus</i>	Celastraceae	<b>216.92</b>	-54.73	N/A	<b>48.56</b>	0.0005	0.0042	1394.68
High-altitude								
<i>Elaeocarpus recurvatus</i>	Elaeocarpaceae	-100.00	-81.23	N/A	<b>129.24</b>	0.0001	0.0013	1941.47
<i>Gordonia obtusa</i>	Theaceae	-100.00	-46.64	N/A	<b>41.73</b>	0.0066	0.0353	1226.82
<i>Litsea wightiana</i> var. <i>tomentosa</i>	Lauraceae	-100.00	-90.37	N/A	<b>154.61</b>	0.0000	0.0000	1867.65
<i>Litsea wightiana</i> var. <i>wightiana</i>	Lauraceae	N/A	-55.97	N/A	<b>101.28</b>	0.0000	0.0000	1750.48
<i>Symplocos foliosa</i>	Symplocaceae	N/A	-84.44	N/A	<b>26.39</b>	0.0111	0.0492	1930.00
<i>Syzygium tamilnadensis</i>	Myrtaceae	-64.29	-3.57	N/A	<b>207.45</b>	0.0002	0.0022	1510.52
Widespread								
<i>Elaeocarpus munronii</i>	Elaeocarpaceae	-75.15	-43.06	-4.09	<b>33.45</b>	0.0012	0.0090	1151.78
<i>Lasianthus jackianus</i>	Rubiaceae	-81.30	7.89	-100.00	<b>74.38</b>	0.0008	0.0062	993.84
<i>Litsea floribunda</i>	Lauraceae	-63.57	-48.19	-1.84	<b>26.28</b>	0.0067	0.0353	880.31
<i>Holigarna arnottiana</i>	Anacardiaceae	-38.98	-5.56	-38.86	<b>31.08</b>	0.0000	0.0000	237.11
<i>Artocarpus hirsutus</i>	Moraceae	-52.94	-72.78	-0.69	<b>35.63</b>	0.0000	0.0000	274.21
<i>Holigarna nigra</i>	Anacardiaceae	-25.62	<b>179.18</b>	-84.51	-4.73	0.0000	0.0000	838.98
<i>Litsea laevigata</i>	Lauraceae	0.75	<b>101.50</b>	-65.83	-12.68	0.0085	0.0425	545.13



## (b) Positive CA axis 1

Species	Family	001	011	101	111	P	P <sub>adj.</sub>	Mean elev.
<i>Aglaia barberi</i>	Meliaceae	-45.06	N/A	<b>112.28</b>	-55.52	0.0000	0.0000	545.06
<i>Diospyros candolleana</i>	Ebenaceae	-2.91	N/A	<b>29.25</b>	-53.65	0.0015	0.0108	425.83
<i>Knema attenuata</i>	Myristicaceae	-13.01	N/A	<b>37.28</b>	-27.23	0.0046	0.0264	470.32
<i>Hopea parviflora</i>	Dipterocarpaceae	13.24	-22.43	<b>54.31</b>	-37.51	0.0022	0.0143	367.06
<i>Poeciloneuron indicum</i>	Clusiaceae	-31.37	15.33	<b>75.53</b>	-38.16	0.0027	0.0170	679.95
<i>Croton malabaricus</i>	Euphorbiaceae	-28.79	-100.00	<b>58.53</b>	<b>49.87</b>	0.0019	0.0132	599.23
<i>Flacourtia montana</i>	Flacourtiaceae	-42.94	N/A	<b>25.24</b>	<b>18.66</b>	0.0021	0.0141	462.29
<i>Gymnacranthera canarica</i>	Myristicaceae	-77.91	N/A	<b>136.79</b>	<b>44.71</b>	0.0005	0.0043	264.71
<i>Leptonychia moacurroides</i>	Sterculiaceae	-38.28	-100.00	<b>125.51</b>	<b>59.43</b>	0.0058	0.0323	720.08
<i>Otonephelium stipulaceum</i>	Sapindaceae	-48.61	-22.31	<b>88.68</b>	<b>87.91</b>	0.0000	0.0000	609.20
<i>Turpinia malabarica</i>	Asteraceae	-39.25	-80.63	<b>79.62</b>	<b>75.63</b>	0.0001	0.0013	727.75
<i>Ormosia travancorica</i>	Fabaceae	-59.32	-21.97	<b>75.58</b>	<b>99.59</b>	0.0006	0.0049	745.34
<i>Cinnamomum malabathrum</i>	Lauraceae	-20.92	15.42	-32.90	<b>35.28</b>	0.0029	0.0177	354.40
<i>Drypetes elata</i>	Euphorbiaceae	-25.22	-100.00	-16.97	<b>93.49</b>	0.0107	0.0492	573.99
<i>Euonymus indicus</i>	Celastraceae	-84.13	-100.00	-21.57	<b>63.04</b>	0.0000	0.0000	641.99
<i>Humboldtia brunonis</i>	Fabaceae (Caesalpinioideae)	-100.00	N/A	-75.24	<b>37.37</b>	0.0001	0.0013	579.18
<i>Hydnocarpus pentandra</i>	Flacourtiaceae	-26.09	-100.00	3.11	<b>18.03</b>	0.0089	0.0434	282.45
<i>Mallotus stenanthus</i>	Euphorbiaceae	-39.53	75.38	-40.27	<b>98.15</b>	0.0000	0.0000	785.95
<i>Myristica malabarica</i>	Myristicaceae	27.83	N/A	-44.59	<b>28.74</b>	0.0111	0.0492	237.64
<i>Psychotria nigra</i>	Rubiaceae	-50.82	<b>51.75</b>	-27.67	<b>42.22</b>	0.0000	0.0000	831.30
<i>Reinwardtiodendron anamallayanam</i>	Meliaceae	-33.44	<b>281.60</b>	45.37	<b>20.63</b>	0.0002	0.0022	599.08
<i>Memecylon malabaricum</i>	Melastomataceae	-39.44	<b>177.49</b>	6.25	<b>107.91</b>	0.0000	0.0000	339.55
<i>Humboldtia vahliana</i>	Fabaceae (Caesalpinioideae)	-16.87	<b>241.07</b>	194.26	-35.03	0.0005	0.0042	374.38
<i>Palaquium ellipticum</i>	Sapotaceae	0.40	<b>128.70</b>	-7.43	-40.10	0.0075	0.0385	800.11
<i>Hydnocarpus macrocarpa</i>	Flacourtiaceae	-65.59	<b>250.73</b>	N/A	N/A	0.0003	0.0031	678.08
<i>Kingiodendron pinnatum</i>	Fabaceae	<b>54.13</b>	N/A	-59.89	-56.81	0.0002	0.0022	519.67

## ANNEXE 2

**Table A1.** List of the 19 evergreen forest types in the Western Ghats

Acronym	Forest Type	Annual Rainfall (mm)	Dry season (mo)	Mean temp. coldest month(C)	Latitudes covered
Wet Evergreen: plains and low elevation types					
DKS	<i>Dipterocarpus indicus</i> - <i>Kingiodendron pinnatum</i> - <i>Strombosia ceylanica</i>	2000-5000	2-3	>23	8°-9°N
DDS	<i>Dipterocarpus indicus</i> - <i>Dipterocarpaceae bourdillonii</i> - <i>Strombosia ceylanica</i>	2000-5000	2-3	>20	9°-11°N
DKH	<i>Dipterocarpus indicus</i> - <i>Kingiodendron pinnatum</i> - <i>Humboldtia brunonis</i>	2000-6000	4-5	>20	11°-13°N
DHP	<i>Dipterocarpus indicus</i> - <i>Humboldtia brunonis</i> - <i>Poeciloneuron indicum</i>	5000-8000	4.4-5.5	>20	13°-13°5N
DP	<i>Dipterocarpus indicus</i> - <i>Persea macrantha</i>	>2000	5-6	>20	13°-14°N
DDD	<i>Dipterocarpus indicus</i> - <i>Diospyros candolleana</i> - <i>Diospyros oocarpa</i>	3500-7000	5-6	>20	13°-14°4N
DDD+P	<i>Poeciloneuron indicum</i> facies of DDD				
PDH	<i>Persea macrantha</i> - <i>Diospyros</i> spp. - <i>Holigarna</i> spp.	2000-6000	6-7	>23	14°4-15°5N
DDP/KAN	<i>Diospyros</i> spp. - <i>Dysoxylum malabaricum</i> - <i>Persea macrantha</i> (kan forest)	1500-2000	6-7	23-24.5	14-15°N
Wet Evergreen: medium elevation types					
CMPG	<i>Cullenia exarillata</i> - <i>Mesua ferrea</i> - <i>Palaquium ellipticum</i> - <i>Gluta travencorica</i>	2000-5000	2-3	16-23	8°-9°N
CMP	<i>Cullenia exarillata</i> - <i>Mesua ferrea</i> - <i>Palaquium ellipticum</i>	2000-5000	2-4	16-23	9°-12°N
MP*	<i>Mesua ferrea</i> - <i>Palaquium ellipticum</i>	2000-5000	4-5	17-22	12-13°5N
PPH	<i>Palaquium ellipticum</i> - <i>Poeciloneuron indicum</i> - <i>Hopea ponga</i>	5000-7000	4-5	18-20	13°-13°5N
MSA*	<i>Memecylon umbellatum</i> – <i>Syzygium cumini</i> – <i>Actinodaphne angustifolia</i>	5000-6500	5-7	17-23	15°5-20°N
Wet Evergreen: high elevation types					
BGL	<i>Bhesa indica</i> - <i>Gomphandra tentandra</i> - <i>Litsea</i> spp	3000-5000	2-3	13.5-16	9°-11°5N
SMG*	<i>Schefflera</i> spp - <i>Meliosma arnottiana</i> - <i>Gordonia obtusa</i>	>2000	3-6	13.5-17	13°-13°5N
LSM	<i>Litsea</i> spp - <i>Syzygium</i> spp - <i>Microtropis</i> spp.	900-6000	0-4	<13.5	10°-11°5N
Dry Evergreen forest types					
DMMK	<i>Diospyros foliosa</i> - <i>Mitrephora heyneana</i> - <i>Miliusa</i> spp. - <i>Kingiodendron pinnatum</i>	1200-1500	4-6	>23	8°-9°N
DMM	<i>Diospyros foliosa</i> - <i>Mitrephora heyneana</i> - <i>Miliusa</i> spp.	1200-1500	4-5	>23	9°-10°N
DMO	<i>Diospyros ovalifolia</i> - <i>Memecylon lushingtonii</i> - <i>Olea gladiifera</i>	1200-1500	4-6	16-23	11°-11°5N
Plots in transition zone between evergreen and deciduous domains (21 plots in Moist and 8 in Dry Deciduous)					
LTD (Moist deciduous)	<i>Lagerstroemia microcarpa</i> - <i>Tectona grandis</i> - <i>Dillenia pentagyna</i>	1500-2000	4-7	25-31	
ATT (Dry deciduous)	<i>Anogeissus latifolia</i> - <i>Tectona grandis</i> - <i>Terminalia tomentosa</i>	<1500	7-8	25-31	

\* Plots in study not found in these forest types

**Table A2:** Result of GLM and variation partitioning for MPD<sub>SES</sub> and MNTD<sub>SES</sub> with a) only current abiotic variables and b) with historical stability and current abiotic variables including percentage of variance of MPD<sub>SES</sub> and MNTD<sub>SES</sub> explained by seasonality + rainfall + elevation (X1) and historical habitat stability (X2)

### 3a)

#### MPDses. Model 1: Current abiotic variables only

Coefficients:

	Estimate	Std. Error	t value	Pr(> t )	
(Intercept)	-0.4240730	0.1296022	-3.272	0.00120	**
Seas	-0.1976774	0.0247070	-8.001	2.9e-14	***
Decr. rain	-0.4052341	0.0419469	-9.661	< 2e-16	***
Elev	-0.0005950	0.0001972	-3.017	0.00278	**

AIC: 865.87 R-sq. (adj) = 0.379 Deviance explained = 38.5%

#### MNTD.ses Model 1: Current abiotic variables only

Coefficients:

	Estimate	Std. Error	t value	Pr(> t )	
(Intercept)	-0.2776554	0.1258212	-2.207	0.028107	*
Seas	-0.0851241	0.0239862	-3.549	0.000450	***
Decr. rain	-0.1480508	0.0407231	-3.636	0.000328	***
Elev	-0.0002985	0.0001915	-1.559	0.120041	

AIC: 848.28 R-sq. (adj) = 0.0734 Deviance explained = 8.28%

### 3 b)

#### MPDses. Model2: Current abiotic variables + historical habitat stability

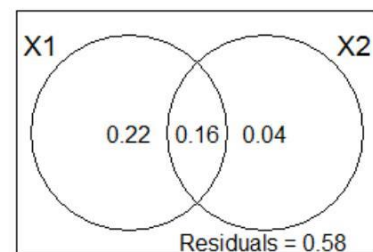
Coefficients:

	Estimate	Std. Error	t value	Pr(> t )	
(Intercept)	-0.9102471	0.1702959	-5.345	1.82e-07	***
Seas	-0.0852657	0.0357583	-2.385	0.0177	*
Decr. rain	-0.3658149	0.0418245	-8.746	< 2e-16	***
Elev	-0.0002879	0.0002049	-1.405	0.1611	
Stability	0.0215741	0.0050839	4.244	2.96e-05	***

AIC: 848.12

R-sq. (adj) = 0.413

Deviance explained = 42.1%



VARIATION PARTITIONING

X1: ~Seas + Rain + Elev; X2: Stability

#### MNTD.ses Model2: Current abiotic variables + historical habitat stability

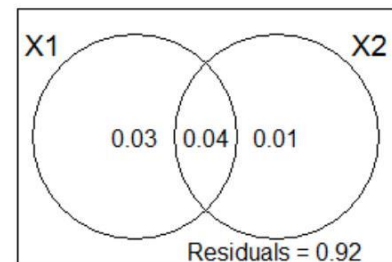
Coefficients:

	Estimate	Std. Error	t value	Pr(> t )	
(Intercept)	-0.5057483	0.1724154	-2.933	0.00362	**
Seas	-0.0288349	0.0377516	-0.764	0.44560	
Decr. rain	-0.1233862	0.0425133	-2.902	0.00399	**
Elev	-0.0001314	0.0002094	-0.628	0.53071	
Stability	0.0098849	0.0051352	1.925	0.05521	.

AIC: 846.53

R-sq. (adj) = 0.0819

Deviance explained = 9.43%



VARIATION PARTITIONING

X1: ~Seas + Rain + Elev; X2: Stability

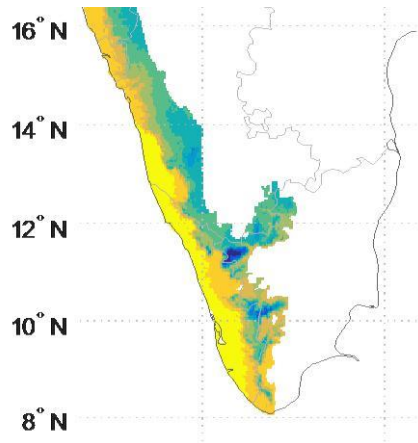
Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

**Table A3.** Results of Mantel tests for correlation between phylogenetic turnover & environmental gradients

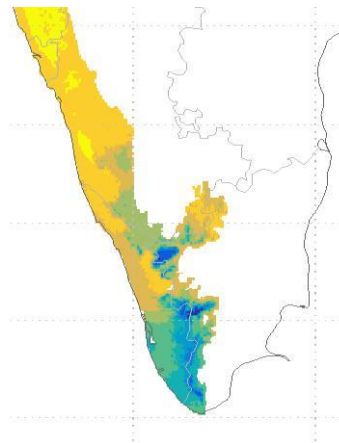
pwPlst	Mantel	Partial Mantel
Temperature	0.166 ** $p=0.001$	0.062 $p=0.03$
<b>Seasonality</b>	0.075 ** $p=0.001$	<b>0.051*</b> $p=0.009$
<b>Annual precipitation</b>	<b>0.261**</b> $p=0.001$	<b>0.214**</b> $p=0.001$
Distance	0.039 $p=0.022$	-0.03ns
<b>Stability</b>	0.043. $p=0.049$	0.035 $p=0.12$
<b>Elevation</b>	0.19 ** $p=0.001$	<b>0.063*</b> $p=0.01$

Signif. codes: 0 '\*\*\*' / 0.001 '\*\*' / 0.01 '\*' / 0.05 '.' / 0.1 ' ' 1

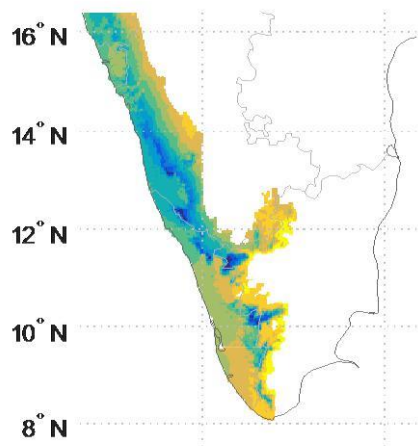
# Supplementary Figure A1.



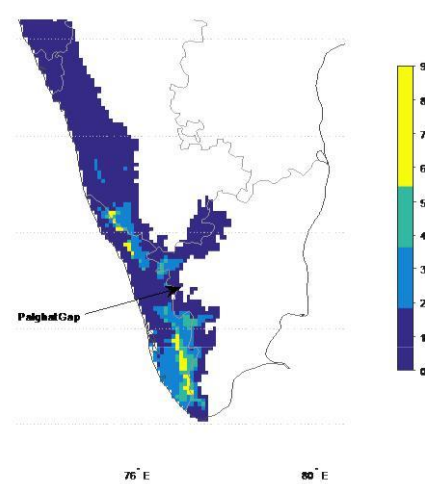
a) West-east decrease in temperature/  
increase in elevation gradient



b) North-south decreasing  
seasonality gradient



c) Annual rainfall gradient



d) Historical habitat stability gradient

Climate-based variables (PCA axes 1 to 3). Dark blue to yellow colour indicates low to high a) temperature (mean monthly in °C), b) seasonality, c) high to low monsoon rainfall and d) past habitat stability, as the number of species predicted present in each grid cell (indicated in the colour scale) since the Last Interglacial (LIG).

**Title: Influence of past and present environmental heterogeneity on the ecology and biogeography of tree species of the Western Ghats biodiversity hotspot**

**Keywords:** species distribution model, biogeography, phylogenetic, biodiversity hotspot, moist tropical forest, India

**Abstract:** Multiple and entangled ecological and evolutionary processes determine the architecture of biodiversity in space and time. Deciphering these influences is key to understanding fundamental questions relating to the current distribution and assemblage of species, the susceptibility of species to environmental change, and the influence of the biogeographic context on diversification. In the face of ongoing and large-scale habitat alterations of climatic and anthropogenic origin in species-rich tropics, this understanding is all the more important to inform conservation strategies. This is particularly the case in the Western Ghats of India which, along with Sri Lanka, is one of the eight hottest global biodiversity hotspots and one of the most densely populated. Little is known about the ecological and biogeographical drivers of Western Ghats biodiversity, and the basic objective of the thesis is to characterize the role of past and present environmental conditions on the distribution and diversification of Western Ghats tree species. We did this by integrating species distribution models and the analysis of phylogenetic and reproductive trait variation across broad-scale gradients in this region spanning 8 degrees of latitude.

First, we examined how past environmental fluctuations could have influenced endemic species distributions over time. We modelled the potential distribution of tree species over the last glacial cycle, and identified basic scenarios of species stability/expansion, contraction, and migration (article 1). Second, we investigated the phylogenetic structure of tree communities to characterize the legacy of past adaptations and the signatures of current environmental filters along gradients (article 2). We found lower phylogenetic diversity under hydric stress or historical instability, suggesting filtering of lineages with specific adaptations. Overdispersion occurs either in least seasonal and more stable forests or in high elevation ecosystems; in the former case, this could be ascribed to ecological diversification over the long term and conservation of old lineages in refugia, and in the latter, to the assemblage of species pools of distinct biogeographic and evolutionary backgrounds (temperate and tropical). Lastly, we addressed in what conditions separation of sexes (dioecy) has been selected for in the course of evolution and in extant ecosystems. We found reverse spatial patterns of dioecious species frequency for endemics and non-endemics, pointing to different mechanisms selecting for dioecy: conservation of non-endemic dioecious lineages in least seasonal southern WG forests, vs. diversification of dioecious endemics in more seasonal and unstable environments northward (article 3).

The results concur to highlight the key role of environmental gradients and biological adaptations in the biogeography and ecology of Western Ghats trees. They stress the importance of long-term evolutionary processes and climatic variations in shaping current species pools and patterns of tree species diversity in a highly diverse yet little studied region.

## **Titre : Impact de l'hétérogénéité environnementale passée et présente sur l'écologie et la biogéographie des espèces d'arbres dans le hotspot de biodiversité des Western Ghats**

**Mots clés :** modèles de niche, biogéographie, phylogénétique, hotspot de biodiversité, forêt tropicale humide, Inde

**Résumé :** Des multiples processus écologiques et évolutif interdépendants déterminent l'organisation de la biodiversité dans le temps et l'espace. Déchiffrer ces influences est indispensable pour comprendre les mécanismes régissant la distribution et les assemblages actuels d'espèces, la sensibilité des espèces aux changements environnementaux, et l'influence du contexte géographique sur la diversification. Face aux modifications climatiques et anthropiques à large échelle des habitats dans les tropiques, cette compréhension est devenue un enjeu pressant pour informer les politiques de conservation. Cet enjeu est particulièrement criant dans les Western Ghats d'Inde et au Sri Lanka, un des huit plus chauds point chauds de biodiversité et l'un des plus densément peuplés. Les processus écologiques et biogéographiques responsables de la biodiversité élevée des Western Ghats restent mal connus. L'objectif de cette thèse est de caractériser le rôle des conditions environnementales passées et présentes dans la distribution et la diversification des espèces d'arbres des Western Ghats. Nous présentons ici une étude intégrant des modèles de distributions d'espèces et l'analyse des traits phylogénétiques et reproductifs le long de gradients environnementaux de cette région couvrant 8 degrés de latitude.

Dans une première partie nous avons cherché à comprendre comment les fluctuations environnementales passées ont pu influencer la distribution des espèces endémiques. Nous avons modélisé la distribution potentielle des espèces d'arbres durant le dernier cycle glaciaire et identifié quatre scénarios : stabilité, expansion, contraction et migration (article 1). Dans une deuxième partie, nous avons analysé la structure phylogénétique des communautés d'arbres afin de caractériser l'héritage des adaptations passées et la signature du filtrage environnemental contemporain (article 2). Nous avons observé une faible diversité phylogénétique dans les zones les plus arides ou historiquement moins stables, ce qui suggère la sélection de lignées adaptées. Au contraire, une surdispersion phylogénétique a été observée dans les régions à faible saisonnalité ou à haute altitude. Le premier cas peut être attribué à une diversification sur le long terme et à une conservation des lignées dans des refuges ; le second correspond à l'assemblage de pool d'espèces provenant de contextes biogéographiques et évolutifs distincts (i.e. tempéré et tropical). Enfin, nous avons investigué les conditions dans lesquelles la séparation des sexes (dioécie) a été sélectionnée au cours de l'évolution et dans les écosystèmes actuels. Nous avons observé des patrons spatiaux opposés entre espèces endémiques et non-endémiques. Cela suggère des mécanismes différents à l'origine de la sélection des espèces dioïques : conservation des lignées non-endémiques dioïques dans les zones à faibles saisonnalités dans le sud des WG, et diversification des endémiques dioïques dans les zones instables à fortes saisonnalité plus au nord (article 3).

Les résultats soulignent le rôle clé des gradients environnementaux et des adaptations biologiques dans la biogéographie et l'écologie des arbres des Western Ghats. Ils soulignent l'importance des processus évolutifs et des fluctuations climatiques dans la constitution des pools d'espèces et les patrons de diversité géographiques d'aujourd'hui dans une région diverse et pourtant mal connue.