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# Phylogenetic turnover in tropical tree communities: impact of environmental filtering, biogeography and mesoclimatic niche conservatism

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## ABSTRACT

**Aim** We addressed the roles of environmental filtering, historical biogeography and evolutionary niche conservatism on the phylogenetic structure of tropical tree communities with the following questions. (1) What is the impact of mesoclimatic gradients and dispersal limitation on phylogenetic turnover and species turnover? (2) How does phylogenetic turnover between continents compare in intensity with the turnover driven by climatic gradients at a regional scale? (3) Are independent phylogenetic reconstructions of the mesoclimatic niche of clades congruent between continents?

**Location** Panama Canal Watershed and Western Ghats (India), two anciently divergent biogeographic contexts but with comparable rainfall gradients.

**Methods** Using floristic data for 50 1-ha plots in each region, independent measures of phylogenetic turnover ( $\Pi_{ST}$ ) and species turnover (Jaccard) between plots were regressed on geographic and ecological distances. Mesoclimatic niches were reconstructed for each node of the phylogeny and compared between the two continents.

**Results** (1) The phylogenetic turnover within each region is best explained by mesoclimatic differences (environmental filtering), while species turnover depends both on mesoclimatic differences and geographic distances (dispersal limitation). (2) The phylogenetic turnover between continents ( $\Pi_{ST} = 0.009$ ) is comparable to that caused by mesoclimatic gradients within regions ( $\Pi_{ST} = 0.010$ ) and both effects seem cumulative. (3) Independent phylogenetic reconstructions of the mesoclimatic niches were strongly correlated between the two continents ( $r = 0.61$ ), despite the absence of shared species.

**Main conclusions** Our results demonstrate a world-wide deep phylogenetic signal for mesoclimatic niche within a biome, indicating that positive phylogenetic turnover at a regional scale reflects environmental filtering in plant communities.

## Keywords

Assembly processes, community phylogenetics, environmental filtering, neutral communities, phylodiversity, phylogenetic signal, phylogenetic turnover, species turnover, tropical rain forest.

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## INTRODUCTION

Which factors determine species assemblages in natural communities and species turnover in space and/or across habitats (beta diversity) is a central issue in community ecology. Three

broad categories of factors are usually recognized (e.g. Cavender-Bares *et al.*, 2009).

1. Biogeography summarizes historical contingency related to speciation and large-scale dispersal, causing species assemblages to differ on a large scale, for example among continents.

2. Ecological factors refer to species–environment interactions (environmental filtering) and inter-species interactions (competition, facilitation, predation), causing species assemblages to differ among habitat types, notably following ecological gradients.

3. Neutral factors refer to stochastic processes such as ecological drift (random demographic fluctuations due to finite community size) and dispersal limitation, causing random fluctuations of species composition among local communities as well as a spatial dependency in species composition, even under homogeneous environmental conditions. Neutral factors also involve speciation and ecological drift at the metacommunity scale, two processes that, for instance, largely control the global biodiversity expected at equilibrium in Hubbell's (2001) neutral theory of biodiversity.

Adaptive species traits and their impact on population dynamics, ecological adaptations and colonization are main keys to deciphering the relative importance of these factors on community patterns, which remains a subject of controversy (e.g. neutral versus niche assembly theories). Indeed, these traits determine how individuals respond to resources in a given environment and hence define the impact of ecological factors on the fate of a species in a given community. However, which traits are sufficiently influential to determine a species' niche is not well understood and species traits are rarely known for all species, notably in species-rich communities. As an alternative, the integration of phylogenetic information into community data analysis has been proposed as a surrogate for analysing the variation of species traits, under the assumption that closely related species are more similar than more distant ones (Webb, 2000; Webb *et al.*, 2002). 'The tendency for related species to resemble each other', named phylogenetic signal, is indeed ubiquitous (Blomberg *et al.*, 2003). Niche conservatism (i.e. the tendency of the niche of taxa within a clade to be stable over evolutionary time; Wiens *et al.*, 2010) can generate a phylogenetic signal, and a non-random phylogenetic structure in ecological communities is then expected to reflect niche-related processes. This framework has been therefore used to address the relative importance of niche-related processes versus neutral processes in structuring species assemblages (e.g. Cavender-Bares *et al.*, 2004, 2006; Hardy & Senterre, 2007). Specifically, in situations where a phylogenetic signal occurs on niche-related traits and environmental filtering largely determines the difference in species composition between communities, we expect species in a given community to be on average more phylogenetically related than species from distinct communities. This pattern is called spatial phylogenetic clustering (Hardy, 2008) but can also be referred to as (positive) phylogenetic turnover because there is a turnover of clades between communities beyond the one expected if species turnover was independent of the phylogeny. If, by contrast, adaptive traits are labile and/or species assemblages are determined by purely neutral processes, no spatial phylogenetic structure is expected. Hence, testing for phylogenetic turnover among local communities can be interpreted as a test of community neutrality when species niches display a phylogenetic signal. For instance, Parmentier & Hardy

(2009) showed that phylogenetic turnover among plant communities occurred when species turnover was driven by ecological gradients but not when it was driven only by dispersal limitation (see also Swenson, 2011).

Furthermore a phylogeny essentially describes the amount of shared evolutionary history between species. Hence, it can help interpret community patterns in terms of both biogeographic and ecological factors. The amount of biogeographic history shared by two species necessarily decreases with divergence time (i.e. the age of the most recent common ancestor). Disjunct communities on distinct continents are then expected to display higher phylogenetic divergence between species from different continents than between species from the same continent, as long as speciation occurs at a faster rate than inter-continental migration. Hence, phylogenetic turnover can also arise from biogeographic processes in a neutral fashion. So far, no study has addressed the relative importance of niche versus biogeographic processes on the phylogenetic turnover among communities, while it raises important questions. For example, consider (1) disjunct communities occurring in similar ecological conditions but situated on different continents and (2) nearby communities occurring in different ecological conditions. What is the relative strength of the phylogenetic turnover in the two situations? An additional question arises if two sets of disjunct communities from distinct continents occur along comparable ecological gradients: does phylogenetic turnover among continents increase when comparing local communities in more dissimilar environments? The answer should depend on the pattern of niche evolution.

A central issue here is that the occurrence and strength of phylogenetic signal and community phylogenetic structuring strongly depend on phylogenetic, spatial and ecological scales (Emerson & Gillespie, 2008; Vamasi *et al.*, 2009). At particular scales (shallow phylogenetic scale and weak ecological gradient), niche phylogenetic signal and/or community phylogenetic structuring are often not observed or can even be reversed by convergent evolution, potentially leading to spatial phylogenetic overdispersion (e.g. phylogenetically overdispersed oak communities, Cavender-Bares *et al.*, 2004; evolutionary radiations of several clades on islands, Emerson & Gillespie, 2008). The latter pattern might also result from the competitive exclusion of sister taxa within local communities due to niche overlap (Hardy & Senterre, 2007) or from other biotic interactions (e.g. clade-specific pathogens enhancing negative interactions between related species, Webb *et al.*, 2006). At a deep phylogenetic scale (e.g. spermatophyte or angiosperm communities), phylogenetic niche conservatism has been well documented at a regional scale over steep ecological gradients (e.g. ecological niche conservatism in central European flora, Prinzing *et al.*, 2001) but also over moderate gradients (e.g. phylogenetic turnover among tropical evergreen forest plots along an elevation gradient, Hardy & Senterre, 2007), or at a biogeographic scale over contrasted environments (e.g. world-wide biome conservatism, Crisp *et al.*, 2009). However, what is the pattern at a biogeographic scale for moderate ecological gradients (i.e. gradients that do not change the type of vegetation formation)? For

example, if at a regional scale we observe a phylogenetic turnover within evergreen forests over a moderate ecological gradient (e.g. related to mesoclimatic variation) as a result of environmental filtering combined with a phylogenetic niche signal, does the underlying niche conservatism extend at a large biogeographic scale? In other words, if some clades are more adapted to one or the other end of the ecological gradient in a given region, do the same clades show the same adaptations in a similar ecological context but at the opposite side of the earth? The answer to this question has important consequences for understanding the way species niche evolves or adjusts according to regional conditions (Donoghue, 2008).

Here, we use two datasets of tree inventories in 50 1-ha plots made in the central Western Ghats (south India) and in the watershed of the canal area in central Panama, both regions where evergreen rain forests or semi-deciduous moist forests constitute the dominant natural vegetation. In each continent, plots were sampled in an area characterized by mesoscale climatic gradients inducing notably moderate rainfall variations across the landscape. We used a method to partition phylogenetic divergence between species within and among plots in a pairwise fashion (Parmentier & Hardy, 2009), so as to get measures of phylogenetic turnover essentially independent from species turnover. We addressed the following questions related to the ecological and biogeographic factors structuring communities and the pattern of niche conservatism. (1) In each continent, is there significant spatial phylogenetic clustering (positive phylogenetic turnover)? (2) Do the data support our hypothesis that phylogenetic turnover is mostly driven by mesoclimatic gradients while species turnover is both affected by ecological gradients and dispersal limitation? (3) Is there a phylogenetic turnover between continents and how does it compare in intensity with the ecologically driven turnover occurring at a regional scale? (4) Is there a correlation in the reconstructed mesoclimate niches for clades between the two continents (i.e. does niche conservatism observed over moderate ecological gradients at a regional scale extend world-wide)? We will show that a phylogenetic turnover of similar magnitude results both from environmental filtering along the rainfall gradients and from biogeography, and that mesoclimate niches display a world-wide deep phylogenetic signal within the evergreen tropical forest biome.

## MATERIALS AND METHODS

### Datasets

In each region our analyses were based on inventories of trees with a d.b.h. > 10 cm in 50 1-ha plots (sometimes smaller plots) situated in moist to wet forests dominated by evergreen species.

The dataset available for Panama contained 55 plots provided by the Center for Tropical Forest Science (CTFS; R. Condit and S. Lao) and described in Chave *et al.* (2004) ('Marena' plots; most are also described in Pyke *et al.*, 2001; Condit *et al.*, 2002; CTFS, 2011). We discarded five plots (33, 35, 37, 38, 39 in Chave *et al.*, 2004) occurring above 600 m to limit the elevation gradi-

ent. The remaining 50 plots were distributed over an area of 50 km (north–south axis) by 60 km (east–west axis) across the watershed of the Panama Canal. Plot elevation ranged from 50 to 410 m while rainfall at the plot locations ranged from 1850 mm (close to the Pacific coast) to 3300 mm (close to the Atlantic coast). The dry season lasts from 3 to 4 months between December and April according to plot location. In the 50 selected plots, a total of 586 taxa were identified as species or morphospecies among a total of 21,683 trees. Most plots were of 1 ha (100 × 100 m) but four of them were smaller (0.32 ha).

The dataset available for Western Ghats contained 96 1-ha plots within the Karnataka State (central Western Ghats) in south India, where all trees with girth > 10 cm were inventoried and identified (Ramesh & Swaminath, 1999; Ramesh *et al.*, 2010a). The dataset is available from Ramesh *et al.* (2010b). For the purpose of comparison with the Panama dataset, we selected 50 forest plots dominated by evergreen species (0 to 30% deciduous species), which mostly occur in the wettest areas (plots corresponding to formations WE1, WE2 and SE in Ramesh *et al.*, 2010a) and we considered only trees with a d.b.h. > 10 cm. The plots were distributed over an area of c. 245 km (north–west–south–east axis) by 55 km (north–east–south–west axis) on the western slope of the Ghats that receives the south–west monsoon from June to October. Plot elevation ranged from 55 to 1050 m, while rainfall at plot locations ranged from 1500 mm (on the eastern side of the Western Ghats) to 8500 mm (south of the Western Ghats) (Pascal, 1988; Ramesh *et al.*, 2010a). According to location, there is a 4–6 month dry season. In the 50 selected plots, a total of 294 species were identified among a total of 19,555 trees with d.b.h. > 10 cm.

### Floristic and phylogenetic turnover

A matrix of inter-plot floristic turnover was computed using the 1 – Jaccard index of similarity (as defined in Legendre & Legendre, 1998) from the species list. Phylogenetic turnover was assessed using the  $\Pi_{ST}$  statistic defined by Hardy & Senterre, (2007).  $\Pi_{ST}$  is defined as  $1 - \text{MPDw}/\text{MPDa}$  where MPDw and MPDa represent the mean phylogenetic distance between distinct species sampled within plots and between plots, respectively. MPDw and MPDa were estimated as:

$$\text{MPDw} = 1/N \sum_k \left( \sum_i \sum_{j \neq i} \delta_{ij} p_{ik} p_{jk} / \sum_i \sum_{j \neq i} p_{ik} p_{jk} \right)$$

$$\text{MPDa} = \frac{1}{N(N-1)} \sum_k \sum_{l \neq k} \left( \sum_i \sum_{j \neq i} \delta_{ij} p_{ik} p_{jl} / \sum_i \sum_{j \neq i} p_{ik} p_{jl} \right)$$

where  $N$  is the total number of plots,  $\delta_{ij}$  is the phylogenetic distance between species  $i$  and  $j$ ,  $p_{ik} = 1$  if species  $i$  occurs in plot  $k$ , otherwise  $p_{ik} = 0$  (and similarly for  $p_{jl}$  for species  $j$  in plot  $l$ ). The formula for MPDa corrects a typographic error in equation (16) of Hardy & Senterre (2007) where the  $j \neq i$  were missing. In addition to the global estimate,  $\Pi_{ST}$  was estimated for each pair of plots (Parmentier & Hardy, 2009). Note that if species are

more related within plots than between plots, spatial phylogenetic clustering or (positive) phylogenetic turnover occurs, and  $\Pi_{ST} > 0$ . If species are less related within plots than between plots, spatial phylogenetic overdispersion (negative phylogenetic turnover) occurs, and  $\Pi_{ST} < 0$ .

Phylogenetic distances were assessed from a dated phylogenetic tree of angiosperm families (Davies *et al.*, 2004) within which genera and species were treated as polytomies using PHYLOMATIC (Webb & Donoghue, 2005). We expected the  $\Pi_{ST}$  statistic to be little influenced by the poor phylogenetic resolution at low taxonomic levels, because the large majority of pairs of species used to compute MPD belong to distinct families (96.3% for our datasets).

For each dataset, we assessed which variables best explained species turnover and phylogenetic turnover using Mantel tests and partial Mantel tests. The explanatory variables were the logarithm of spatial distances, and the absolute differences of rainfall, dry season length, and elevation. Spatial distances were log-transformed because it improved substantially the linear relationship with species turnover (see also Pyke *et al.*, 2001; Davidar *et al.*, 2007). For Mantel tests,  $1 - \text{Jaccard}$  or  $\Pi_{ST}$  was tested against each variable in turn. For partial Mantel tests,  $1 - \text{Jaccard}$  or  $\Pi_{ST}$  was tested against each variable in turn using all the other variables as covariables.

The phylogenetic turnover between continents was assessed by the mean  $\Pi_{ST}$  value between plots from Panama and the Western Ghats. As the phylogenetic turnover proved well correlated with the difference in rainfall within each continent, we also distinguished inter-continental phylogenetic turnover for pairs of plots with limited (< 500 mm), strong (> 1000 mm but < 3500 mm) and very strong (> 3500 mm) rainfall difference.

### Phylogenetic signal and correlation in mesoclimatic niches between continents

For each dataset, to characterize the realized mesoclimatic niche of each species with respect to environmental gradients (rainfall, dry season length, elevation), we used Pearson's correlation coefficient between the species abundance and the value of the environmental variable across plots. For simplicity, these correlation coefficients were treated as species niche traits quantifying the relative propensity of the species to occur at one or the other end of the environmental gradients in the particular context of each dataset, although they are in fact proxies for the realized niches and thus also depend on the biotic contexts and not only on the species' intrinsic characteristics. We also considered alternative measures characterizing the realized niche (i.e. abundance-weighted mean environmental values, species scores following a canonical correspondence analysis; results not shown), but an advantage of the correlation coefficients over these is that low-frequency species for which the realized niche cannot be characterized precisely have a low weight in subsequent analyses because the correlation coefficient approaches zero. Moreover, species occurring in at least five plots and showing a restricted distribution along the environmental gra-

dients always occurred at one or other end of the gradient so that species–environment relationships should be adequately represented by a linear model.

The phylogenetic signal in adaptation patterns towards environmental gradients was assessed by the autocorrelation of the niche trait (Pearson's correlation) according to the topology of the tree, using Moran's *I*-statistic for a set of phylogenetic distance intervals (Diniz-Filho, 2001). Phylogenetic signal was tested for each niche trait separately for each dataset by complete randomization of the species at the tips of the phylogenetic trees.

Finally, we assessed whether there is a correlation in phylogenetic patterns of species niche traits between continents. First, for each dataset, we reconstructed the ancestral niche trait values for each node of the trees using MESQUITE (module 'Parsimony Ancestral States' that estimates node values for continuous characters by minimizing the number of squared character changes between successive nodes along the phylogeny; Maddison & Maddison, 2005). Then, for the set of nodes shared between the phylogenetic trees of the two datasets, we plotted the reconstructed niche trait values on a scattergram where each axis represents a continent. We tested the correlation of niche trait values between Panama and the Western Ghats using family nodes only, because nodes at different hierarchical levels are not mutually independent.

## RESULTS

### Species and phylogenetic turnover

In Panama, species turnover ( $1 - \text{Jaccard}$ ) and phylogenetic turnover ( $\Pi_{ST}$ ) were highly correlated to spatial distance, as well as to difference in rainfall and difference in dry season length (Table 1). Partial Mantel tests indicated that spatial distance followed by difference in rainfall were the main drivers of species turnover, while phylogenetic turnover depended solely on the difference in rainfall (Table 1). In the Western Ghats, a similar pattern was found except that the difference in elevation also significantly affected species turnover and that the difference in dry season length was here the most important driver of both species turnover and phylogenetic turnover. Hence, for both datasets, spatial distance was no longer significant on phylogenetic turnover when the effect of the difference in rainfall has been factored out, a result in line with our expectation that dispersal limitation does not contribute to phylogenetic turnover at a regional scale. It should be noted that contrary to Mantel tests, partial Mantel tests tend to reject the null hypothesis too often. However, as they are too liberal, the absence of statistical significance can be considered as reliable.

$\Pi_{ST}$  was always significantly larger than zero, indicating spatial phylogenetic clustering (positive phylogenetic turnover), and the mean  $\Pi_{ST}$  was larger in the Western Ghats (mean  $\pm$  SD  $0.0051 \pm 0.0076$ ) than in the Panama Canal watershed (mean  $\pm$  SD  $0.0018 \pm 0.0027$ ). As illustrated in Fig. 1, although rainfall is a major driver of phylogenetic turnover, the mean  $\Pi_{ST}$  between plots receiving similar amounts of rainfall remains sta-



**Table 1** Species turnover (1 – Jaccard) and phylogenetic turnover ( $\Pi_{ST}$ ) between plots in the Panama Canal watershed and the Western Ghats according to geographic distance and environmental gradients (absolute difference in rainfall, dry season length, or elevation). Simple regression results are represented by correlation coefficients ( $r$ ) and their statistical significance according to the Mantel test. Multiple regression results are represented by partial correlation coefficient (pMantel  $r$ ) according to partial Mantel tests where all variables except the focal one are used as covariables.

	1 – Jaccard		$\Pi_{ST}$	
	Mantel $r$	pMantel $r$	Mantel $r$	pMantel $r$
Panama Canal				
ln(distance)	0.60***	0.40***	0.27***	0.04ns
Rainfall	0.55***	0.17***	0.39***	0.15**
Dry season length	0.50***	–0.06ns	0.33***	–0.02ns
Elevation	0.22**	0.04ns	0.16*	0.03ns
Western Ghats				
ln(distance)	0.44***	0.12*	0.23***	0.08ns
Rainfall	0.27***	0.31***	0.19*	0.14*
Dry season length	0.55***	0.34***	0.29**	0.21*
Elevation	0.34***	0.23**	0.02ns	–0.08ns

ns, not significant,  $P > 0.5$ ; \* $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.001$ .

tistically significant, indicating that difference in rainfall does not explain all of the phylogenetic turnover, so that other environmental gradients might contribute to the phylogenetic turnover. Similar results were obtained for the length of the dry season (results not shown).

At the regional scale,  $\Pi_{ST}$  increased from c. 0.001–0.003 to 0.005–0.008 when comparing pairs of plots receiving similar amount of rainfall (rainfall difference < 500 mm) with plots receiving contrasting amounts of rainfall (rainfall difference > 1000 mm in the Panama Canal or > 3500 mm in the Western Ghats; Table 2).  $\Pi_{ST}$  also increased from c. 0.001–0.003 to 0.008 when comparing, among the pairs of plots receiving a similar amount of rainfall, plots from the same continent with plots from different continents (Table 2). When both sharp ecological gradients and biogeographic barriers were combined,  $\Pi_{ST}$  reached on average 0.011 (for plots from different continents receiving contrasted amounts of rainfall, Table 2), indicating that biogeographic and environmental effects on phylogenetic turnover tend to be cumulative.

### Phylogenetic signal of species mesoclimatic niches

In Panama, the species niche trait values (i.e. Pearson's coefficient of correlation between local abundances and environmental variables) relative to gradients of rainfall, duration of dry season and elevation all showed positive autocorrelation between closely related species, indicating the presence of a phylogenetic signal (Fig. 2). In the Western Ghats, a phylogenetic niche signal was also clear for rainfall but it was less

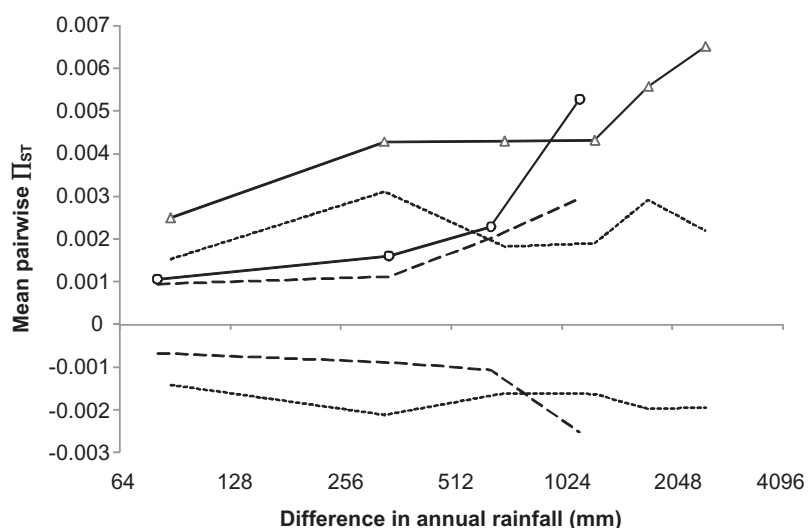
marked for the duration of the dry season and absent for elevation (Fig. 2).

A total of 73 nodes were shared between the phylogenetic trees of the Panama Canal and Western Ghats datasets, among which 27 correspond to shared Angiosperm Phylogeny Group (APG) families and eight to shared genera. The reconstruction of ancestral trait values revealed a marked correlation between node values of each dataset for the niche trait relative to the rainfall gradients ( $r = 0.61$ ; Fig. 3). Considering only the mutually independent family nodes, the correlation was statistically significant ( $r = 0.5$ ,  $P_{\text{val}} < 0.008$ ). Families showing shared adaptation patterns towards high rainfall were Clusiaceae, Olacaceae, Euphorbiaceae and Magnoliid families (Myristicaceae, Annonaceae, Lauraceae), while adaptation towards low rainfall was essentially found for Combretaceae. There were also a few families showing opposite trends, in particular Boraginaceae was more represented on the dry side in Panama and on the wet side in Western Ghats, but the family was represented by only two species in the Western Ghats dataset against nine species from two genera in the Panama Canal dataset. At the genus level, for the seven shared genera, it is noteworthy that they displayed similar trends in the two datasets, close to the regression line. Regarding major angiosperm clades, Rosids, Asterids and Magnoliids were not much differentiated from each other but all occurred on the wet side. The order Magnoliales was more characteristic with a clear adaptation to high rainfall while the order Rosales seems more adapted to lower rainfall, at least in Panama.

## DISCUSSION

### Spatial phylogenetic clustering occurs at the regional scale

The phylogenetic structure of our communities displayed spatial phylogenetic clustering ( $\Pi_{ST} > 0$ ). This pattern was found in most studies conducted at a deep taxonomic scale (here in angiosperm communities), at least in the presence of environmental gradients (e.g. Webb, 2000; Kembel & Hubbell, 2006; Hardy & Senterre, 2007; Parmentier & Hardy, 2009; reviewed in Vamوسي *et al.*, 2009). This probably reflects that there is a general trend for phylogenetic signal in niche traits (a positive correlation between niche trait distance and phylogenetic distance) although, in particular contexts, closely related species may display clear habitat differentiation associated with convergences among distant clades, potentially leading to phylogenetic overdispersion. In fact, studies reporting phylogenetic overdispersion ( $\Pi_{ST} < 0$ ) were usually conducted at a limited taxonomic scale, for instance within a genus (e.g. Cavender-Bares *et al.*, 2004). Here, the limited resolution of our phylogeny below the family level prevented us from testing whether phylogenetic overdispersion occurs at a shallow phylogenetic depth, a problem that should be solved in the future with detailed community-level phylogenetic trees based on DNA sequences.



**Figure 1** Phylogenetic turnover (mean pairwise  $\Pi_{ST}$ ) according to difference in annual rainfall between plots in the Western Ghats (triangles) and the Panama Canal watershed (circles). The dotted and dashed lines represent 95% confidence envelopes under the null hypothesis that there is no phylogenetic turnover, for the Western Ghats and Panama, respectively. In both regions, there is a significant phylogenetic turnover between plots that increases with the rainfall contrast.

**Table 2** Phylogenetic turnover (mean pairwise  $\Pi_{ST}$  between plots) in the angiosperm flora of rain forest tree communities in response to biogeography (within region versus between continents) and ecological gradients (for plots with similar versus contrasted environmental conditions).

Ecological contrast	Within region		Between continents
	Panama Canal	Western Ghats	
Weak (rainfall difference < 500 mm)	0.0013	0.0034	0.0081
Strong (1000 mm < rainfall difference < 3500 mm)	0.0051	0.0055	0.0092
Very strong (rainfall difference > 3500 mm)	–	0.0078	0.0110

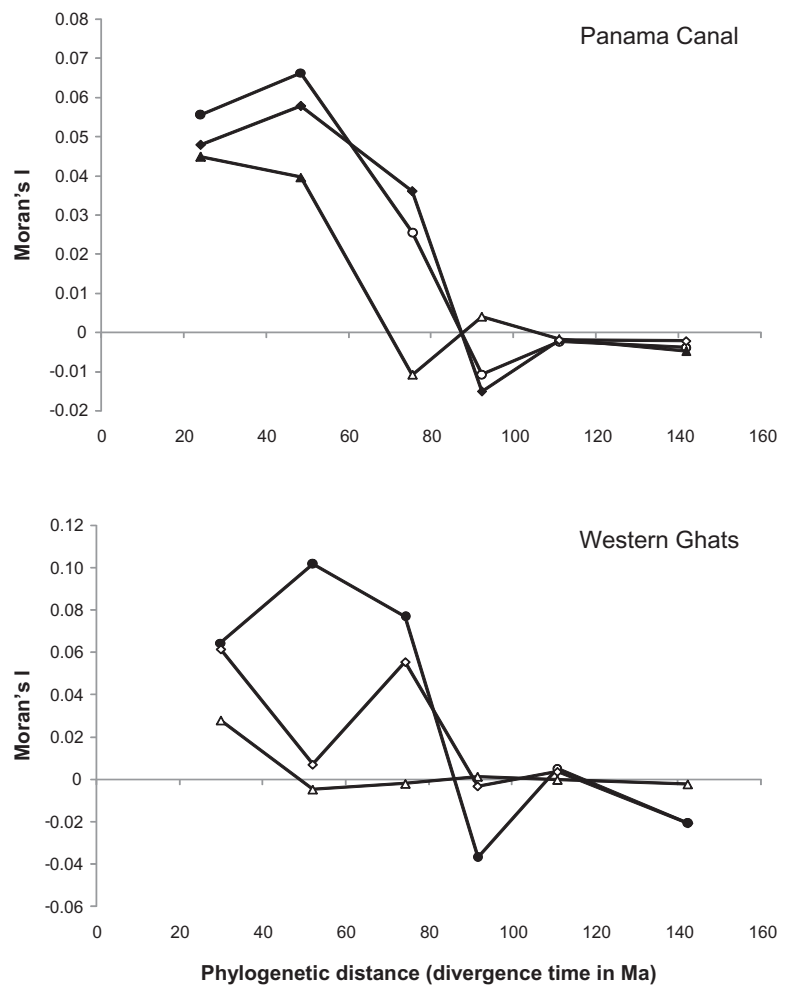
### Dispersal limitation and environmental filtering affect species and phylogenetic turnover differently

Species turnover as measured by the  $1 - \text{Jaccard index}$  of similarity and phylogenetic turnover as measured by pairwise  $\Pi_{ST}$  are based on independent information: the first one is based on species sharing between communities independently of species phylogeny while the second one depends on phylogenetic relationships among distinct species independently of species sharing. It should be noted that not all measures of phylogenetic turnover have this property: those considered by Swenson (2011), for example, are directly affected by species sharing while Ives & Helmus (2010) developed a metric that can be partitioned into phylogenetic and non-phylogenetic components. Nevertheless,  $\Pi_{ST}$  and the Jaccard index of similarity are not strictly speaking independent but are related in a triangular fashion: in the absence of species turnover there is no phylogenetic turnover while under complete species turnover (no shared species), phylogenetic turnover can be strong, absent or

even negative, making the two measures essentially independent of each other.

In our datasets, while species turnover was driven both by spatial distance and environmental gradients, phylogenetic turnover was only driven by environmental gradients. Though patterns in Panama and in India differed slightly. In Panama, species turnover between plots was mostly explained by geographical distance and then by rainfall difference, and phylogenetic turnover was only explained by rainfall difference. In the Western Ghats, species turnover was explained by geographic distance and by all environmental gradients, and phylogenetic turnover was explained by differences in rainfall and in dry season length, in agreement with the results reported by Swenson (2011) using other methods. These differences probably reflect the fact that the dataset for the Western Ghats covers a wider range of elevation (55–1050 m) and of dry season length (4–6 months) than the one for central Panama (50–410 m elevation and 3–4 months dry season), where the most striking environmental gradient was related to annual rainfall. These patterns confirm the results obtained on plant communities of inselbergs in Africa (Parmentier & Hardy, 2009), indicating that while species turnover reflects the action of environmental filtering and dispersal limitation, phylogenetic turnover (at least when measured using  $\Pi_{ST}$ ) reflects only the impact of environmental filtering. In Amazonian forest tree communities, Fine & Kembel (2011) reported that species turnover as well as phylogenetic turnover correlate both with spatial distance and edaphic gradient but they did not use partial Mantel tests to check whether phylogenetic turnover still correlates with spatial distance after factoring out environmental gradients.

$\Pi_{ST}$  depends on the mean phylogenetic distances between distinct species sampled within a community (MPDw) or among communities (MPDa):  $\Pi_{ST} = 1 - \text{MPDw}/\text{MPDa}$  (excluding intra-species comparisons). It can in theory range from  $-1$  to  $1$ . A  $\Pi_{ST}$  approaching  $1$  would be obtained when comparing two communities where each one is made up of closely related



**Figure 2** Phylogenetic signals represented by phylogenetic autocorrelograms of niche traits with respect to gradients of rainfall (circles), length of the dry season (diamond) and elevation (triangle) in the Panama Canal (above) and Western Ghats (below). Moran's  $I$  measures the mean niche trait similarity between species according to their divergence time (millions of years ago, Ma). Filled symbols indicate that the value departs significantly from the null hypothesis that there is no phylogenetic signal ( $P < 0.05$ ), open symbols indicate no significant phylogenetic signal.

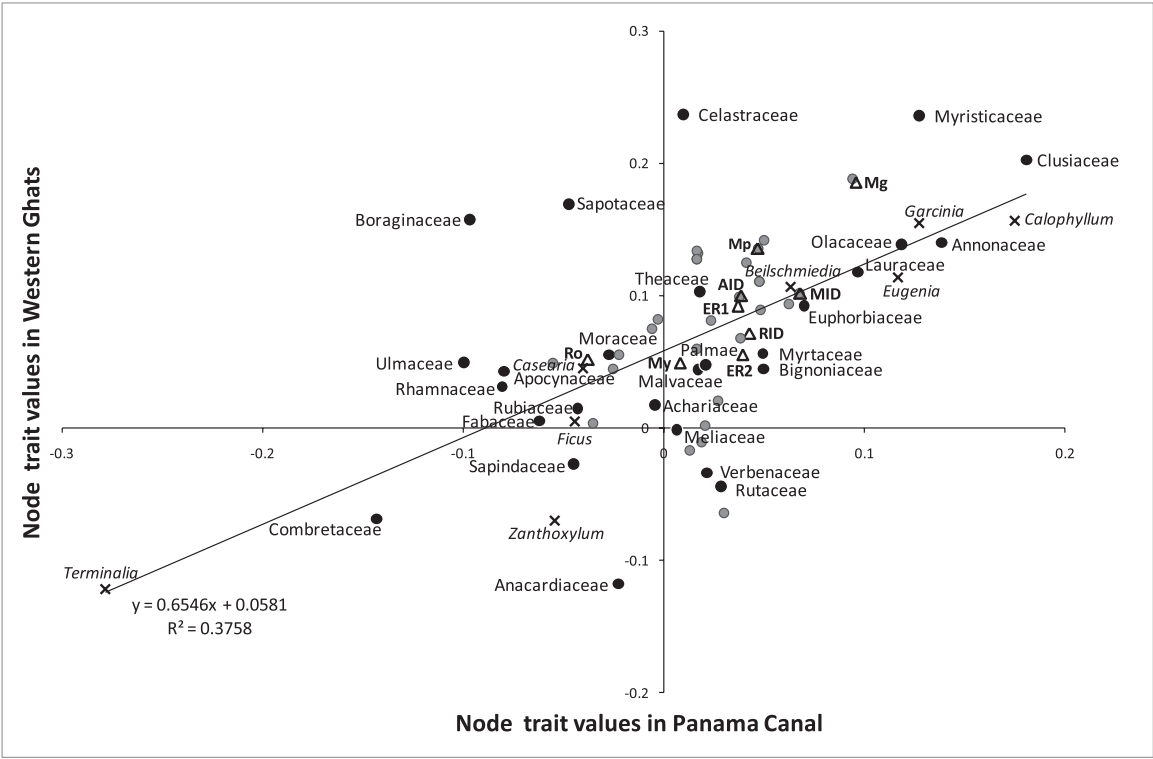
species that are distantly related to the species of the other community (for example, one community made only of oak species and one made only of pine species). A  $\Pi_{ST}$  approaching  $-1$  would be obtained when comparing two communities each made of two distantly related species but where each species has a closely related species in the other community (for example, one community with one oak and one pine species and one with another oak and another pine species). In the species-rich tropical tree communities where many different clades are represented, MPDw and MPDa are both large and usually fairly similar, so that  $\Pi_{ST}$  is close to 0. This means that most major clades can be represented in most environments by some species. Nevertheless, even slight deviation from zero can be detected when randomizing the phylogenetic tree: for the Panama dataset, values as small as 0.001 could be significantly different from zero (Fig. 1).

Phylogenetic turnover among plots situated in contrasted environmental conditions reached  $c. \Pi_{ST} = 0.01$  both in the Panama Canal watershed and the Western Ghats. This value is comparable to that found along a  $c. 1000$  m elevation gradient of forest tree communities from Central Africa (Hardy & Senterre, 2007) but it is much lower than the  $\Pi_{ST}$  of  $c. 0.05$  reported when comparing different plant formations occurring on inselbergs

(Parmentier & Hardy, 2009). This makes sense, because inselberg plant formations ranged from grasslands (dominated by Poaceae and Cyperaceae) to forests (dominated by Eudicotyledons) while the present study deals only with evergreen forest formations. The taxonomic scale is also very important to consider when comparing  $\Pi_{ST}$  values among studies, because phylogenetic turnover typically implies higher  $\Pi_{ST}$  values when lower taxonomic levels are considered. As an example, for our datasets, mean  $\Pi_{ST}$  values increased at least twofold when the analysis was performed at the level of a major clade of the angiosperms, like the Asterids or the Eurosids (Table 3).

### Phylogenetic turnover within a biome: impact of biogeography versus environmental filtering

The present study is the first to report phylogenetic turnover as measured by  $\Pi_{ST}$  among continents. Forest plots from central Panama and south India receiving similar amounts of annual rainfall showed a mean  $\Pi_{ST}$  of 0.008 while  $\Pi_{ST}$  approaches 0.011 when comparing plots receiving contrasting amounts of rainfall on different continents. Hence, the magnitude of the phylogenetic turnover across continents was comparable to the phylogenetic turnover along the ecological gradients considered at the



**Figure 3** Correlation between reconstructed niche trait values with respect to rainfall gradients for the nodes of the phylogenetic trees shared between the datasets for the Panama Canal watershed and the Western Ghats. Crosses show shared genera (written in *italics*), black dots show Angiosperm Phylogeny Group families, triangles show higher clades (Mg, Magnoliales; Mp, Malpighiales; My, Myrtales; Ro, Rosales; ER1, Eurosids 1; ER2, Eurosids 2; AID, Asterids; RID, Rosids; MID, Magnoliids) while grey dots represent other (unnamed) shared nodes. The regression line is based on the whole set of nodes.

**Table 3** Phylogenetic turnover (mean pairwise  $\Pi_{ST}$  between plots) at different phylogenetic depth within and among continents.

Phylogenetic depth	Within region		Between continents
	Panama Canal	Western Ghats	
Angiosperms	0.0018	0.0051	0.0090
Asterids	0.0119	0.0111	0.0266
Eurosids1	0.0087	0.0108	0.0284

regional scale. In addition, it seems that environmental gradients and biogeographic barriers combine cumulatively because we observed an increase in inter-continental phylogenetic turnover when comparing plots from more contrasting environments. Of course we cannot exclude that the inter-continental  $\Pi_{ST}$  for plots receiving similar amounts of rainfall is also affected by ecological gradients, because many environmental factors (elevation, dry season length but also soil factors) differ between the communities sampled in Panama and India. Our data thus at least imply that the phylogenetic turnover driven by environmental gradients within a plant formation can be as high as the phylogenetic turnover occurring among continents, at the scale

of angiosperms. This result is likely to stem from the deep phylogenetic depth considered, the root of our phylogenetic trees being 143 Myr old. During this period of time, major angiosperm lineages have had much time to disperse all over the world, and substantial inter-continental migration of tropical rain forest taxa might have occurred *c.* 50 Ma during the warm Eocene period (Donoghue, 2008). The pattern would probably be different at a lower taxonomic scale. Indeed, the major lineages of a botanical family have not necessarily dispersed widely among continents, so that the impact of biogeography on  $\Pi_{ST}$  might largely exceed the impact of environmental gradients. This can be illustrated with our datasets because the mean  $\Pi_{ST}$  between plots of different continents increases from 0.009 at the scale of angiosperms to 0.027 at the scale of the Asterid clade (Table 3).

**Mesoclimate niches: phylogenetic signals and inter-continental congruence**

A phylogenetic turnover driven by ecological gradients implies that there is a phylogenetic signal in the adaptation patterns of species with respect to these gradients. Quantifying these adaptive trends by the correlation coefficients between local species abundance and climatic variables, a phylogenetic signal was indeed observed in both datasets, at least with respect to the



rainfall gradient. On average, mesoclimatic niche similarity between species decreases with their divergence time up to c. 80 Ma, matching approximately the divergence between most APG families in the phylogenetic tree used. Hence, species from the same family tend to share similar adaptations towards the rainfall gradient.

Remarkably, the specific clade adaptations found towards the rainfall gradient were globally congruent between central Panama and the Western Ghats despite the absence of shared species. At the family level, niche phylogenetic signal was mostly driven by several families adapted to high rainfall (Annonaceae, Lauraceae, Myristicaceae, Clusiaceae, Euphorbiaceae) and one family adapted to low rainfall (Combretaceae). Annonaceae and Myristicaceae belong to the order Magnoliales which is sister to the order Laurales including Lauraceae, the whole belonging to the major Magnoliid clade. Hence, all these major clades display adaptation towards high rainfall according to both datasets. If regional niche conservatism was not extending on a large biogeographic scale (no inter-continental correlation between reconstructed clade niches), it would have suggested that interactions among species within a given biogeographic area played a prominent role in determining how species have adjusted their respective niches. Our results, however, indicate that the observed niche conservatism is deeply rooted in the origin of clades showing adaptive trends (phylogenetic signal up to c. 80 Ma) and would not result from recurrent reorganizations of species adaptations within each biogeographic context, giving support to the essay of Donoghue (2008). One cannot exclude that species competition at the regional scale might be involved in the maintenance of niche conservatism. Indeed, rapid niche evolution is typically observed when competition is relaxed in new empty ecosystems (e.g. adaptive radiations on islands; Emerson & Gillespie, 2008). Conversely, when competition is not relaxed because many potentially competing species occur (the typical case on continents), the limited opportunity for a species to adapt to an empty niche would favour niche conservatism. Previously, Crisp *et al.* (2009) demonstrated world-wide phylogenetic biome conservatism in plants, hence niche conservatism with respect to steep ecological gradients. Our results show that world-wide niche conservatism also occurs over moderate environmental gradients (i.e. not causing a biome shift) in tropical evergreen forest trees.

## CONCLUSION

This study confirms that phylogenetic turnover, when measured by  $\Pi_{ST}$ , is largely driven by climatic gradients in tropical tree communities, while species turnover is also influenced by dispersal limitation. It also shows that inter-continental biogeographic isolation causes a moderate increase in phylogenetic turnover, comparable to that resulting from a moderate climatic gradient, at least at the scale of angiosperms. Moreover, biogeographic and environmental filtering effects on phylogenetic turnover seem cumulative. This pattern results from a phylogenetic signal in species mesoclimatic niches whereby species from a same family are on average more similar in their climatic

requirements. Importantly, there is significant correlation between clade-wide adaptive trends observed on different continents, indicating that initial adaptations for particular climatic conditions tend to be well conserved within at least some major clades. This was already shown when considering highly contrasted environments (world-wide biome conservatism), while our results demonstrate that it also occurs within a biome along moderate ecological gradients.

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## BIOSKETCHES

The authors are interested in the ecological and evolutionary processes involved in the dynamics of biodiversity in tropical forest tree communities. They attempt to link processes and patterns using modelling and/or descriptive approaches. O.J.H. conducted the statistical analyses and wrote the first draft, B.R.R. collected the data from the Western Ghats, R.P., P.C. and F.M. conceived the project, contributed to data analyses and revised the text.

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