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Original research

Phylogenetic linkages between composition and structure of tree communities shed light on historical processes influencing tropical rainforest diversity

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Abstract

The separation of the Neotropics, Afrotropics and Madagascar has subjected their biotas to different histories. Based on current knowledge of these histories, we developed the following predictions about the phylogenetic structure and composition of rainforest tree communities: (1) isolation of Gondwanan biotas generated differences in phylogenetic composition between biogeographical regions; (2) greater angiosperm diversification in the Neotropics led to phylogenetic clustering in Amazonian communities; (3) major Cenozoic extinction events led to random phylogenetic structure in Afrotropical communities; (4) co-ccurrence of magnoliids tracking conserved habitat preferences and recently diversified eudicot lineages led to phylogenetic overdispersion near the Andes. Using abundance data of tropical rainforest tree species from 94 sites in the Neotropics, Afrotropics and Madagascar, we computed net relatedness index (NRI) to assess local phylogenetic clustering vs. overdispersion relative to regional species pools, and principal coordinates of phylogenetic structure (PCPS) to assess variation in phylogenetic composition across sites. Using PCPS, we observed significant differences in phylogenetic composition among biogeographical regions. Moreover, we identified lineages linked to shifts in phylogenetic structure (NRI) among sites across biogeographical regions. Most of Central Amazonian communities were phylogenetically random, although some communities presented significant phylogenetic clustering. We observed phylogenetic overdispersion mainly near the Andes, and widespread phylogenetic randomness in the Afrotropics. Evaluating the phylogenetic linkages between community structure and composition clarified distinct historical processes influencing community structure in tropical rainforests in different regions. The Gondwanan vicariance, with the subsequent isolation of biotas subject to different climatic and orographic histories, influenced the history of diversification of different clades in different regions. The dominance of regional

pools by some lineages and the co-occurrence of early- and late-diversified lineages in a region explain current variation in phylogenetic composition and structure of rainforest tree communities across the Neotropics, Afrotropics and Madagascar.

Introduction

Historical factors influence the formation of regional species pools (MacArthur 1972, Ricklefs 1987, Cracraft 1994), and, consequently, the structure of the local communities assembled from them (Parmentier and Hardy 2009, Leibold et al. 2010, Lessard et al. 2012a, Gerhold et al. 2015). Studies have inferred macroevolutionary processes structuring local communities by evaluating how phylogenetic patterns differ across biogeographical barriers (Graham et al. 2009, Kooyman et al. 2011, Kissling et al. 2012, Lessard et al. 2012b, Eiserhardt et al. 2013, Hawkins et al. 2014). Although these studies demonstrated that historical processes likely determine community structure, understanding the linkages between local phylogenetic structure and the variation in phylogenetic composition among regions remains a challenge. Commonly used measures of community phylogenetic structure enable the assessment of local phylogenetic clustering and overdispersion relative to a regional species pool (Webb et al. 2002), but give no information on which lineages are associated with phylogenetic clustering or overdispersion. For instance, two communities with the same phylogenetic structure value may have very different species composition (Graham et al. 2009). Hence, studies usually infer historical processes affecting phylogenetic structure by evaluating both compositional beta diversity and phylobetadiversity, which permits linking current phylogenetic structure to information on the macroevolution for certain lineages (Graham and Fine 2008, Graham et al. 2009). One way to link phylogenetic structure and composition is to measure both phylogenetic structure and phylobetadiversity using an approach that permits identification of the most common lineages across communities. While the net relatedness index (NRI; Webb et al. 2002) can be used to measure phylogenetic structure, the PCPS analysis (phylogenetic coordinates of phylogenetic structure; Duarte 2011, Duarte et al. 2012) can be used to assess phylobetadiversity. PCPS analysis synthesises phylobetadiversity into ordination vectors

(PCPS) representing gradients in phylogenetic composition across communities. By using PCPS, it is possible to identify the lineages linked to shifts in phylogenetic structure values (NRI) across biogeographical barriers, as those created by vicariance (see the methods for more information on PCPS). Observing how lineage composition differences among communities relate to phylogenetic co-occurrences may improve the inference of major macroevolutionary influences on current species co-occurrences (Gerhold et al. 2015).

In this study, we integrate NRI and PCPS approaches to test biogeographical hypotheses related to the fragmentation of Gondwana and its subsequent history. The Gondwanan vicariance started during the Cretaceous, ca. 112-106 Ma (Wilf et al. 2013), separating the Neotropical, Afrotropical, and Malagasy biotas. South America remained connected to Antarctica and Australia through the Early-Middle Eocene (Wilf et al. 2013). The Gondwanan breakup coincided with the early evolution of many extant lineages of angiosperms, and with the first appearance of the arboreal habit among angiosperms (Feild and Arens 2007). The major lineages of angiosperms, namely magnoliids, eudicots and monocots, appeared over a period of ca. 15 Ma (Aptian-Albian) from ca. 125 to 110 Ma (Feild and Arens 2007), so that the ancestors of these lineages should have been present in the early flora of the two new continents in formation. Among angiosperms, magnoliids form a major clade that diverged before monocots and eudicots (APG 2009). Magnoliids are considered “southern wet forest survivors” because they currently co-occur with other “ancient” clades (e.g. Araucariaceae, Podocarpaceae, Proteaceae) in forests that bear high compositional similarity with the Gondwanan rainforests they were part of during the Cretaceous (Kooyman et al. 2014). These Gondwana-like rainforests are currently found in the South American highlands (Segovia and Armesto 2015). Magnoliid species largely conserved traits of early angiosperms (from ca. 120 Ma) that limit water usage, which led to lower photosynthetic capacity compared to eudicots (Feild et al. 2002, Boyce et al. 2009, Brodribb and Feild 2010). These features force magnoliids to be mostly associated with tropical upland, shady and wet forests (Feild and Arens 2007), which suggests these plants track habitats across space and time (Duarte 2011; habitat tracking sensu Ackerly 2003).

The Gondwanan vicariance led to increasingly isolated biotas, subject to different climatic and orographic histories, which likely led to differences in net diversification (speciation minus extinction) of angiosperm clades between the Neotropics and Afrotropics (Gentry 1982, Parmentier et al. 2007, Ghazoul and Sheil 2010, Morley 2011). The separation of Neotropical and Afrotropical biotas increased during the Cenozoic (Morley 2011), when South America, Africa and Madagascar became totally separated from Antarctica and Australia (Wilf et al. 2013). A recent phylogeny based on molecular and fossil data points to a major diversification of angiosperm lineages after the Cretaceous-Paleogene (KPB) boundary (Silvestro et al. 2015). In the Neotropics, the persistence of a wet climate has maintained large areas of continuous rainforest across time, which propitiated the accumulation of angiosperm species due to high speciation (and low extinction) rates, especially monocots and eudicots (Gentry 1982, Colinvaux et al. 2000, Maslin et al. 2005, Morley 2011, Kissling et al. 2012, ter Steege et al. 2013). The accumulation of species in the Neotropics is consistent with the time-integrated species area effect (Fine and Ree 2006). Moreover, there is much stronger support for the role of major dry periods affecting floristic composition in the Afrotropics than in the Neotropics during the glacial ages of the late Cenozoic (Colinvaux et al. 2000, Parmentier et al. 2007, Ghazoul and Sheil 2010). These dry periods led to rainforest retraction, which caused major extinctions during the Cenozoic (Parmentier et al. 2007, Morley 2011). Moreover, these climatic fluctuations reduced habitat availability across time, which reduced speciation rates in the Afrotropics (Kissling et al. 2012).

Within region, the uplift of the Andes during the Cenozoic (from ca. 40 Ma) has driven recent diversification of many taxa (e.g. hummingbirds; Graham et al. 2009), including rapid diversification of angiosperm lineages (Gentry 1982, Richardson et al. 2001, Hughes and Eastwood 2006). The uplift of the Andes created a spatial configuration of habitats that promoted speciation, e.g. island-like habitats isolated by valleys of different environmental conditions (Hughes and Eastwood 2006). Given the preference of magnoliids for tropical upland forests (Feild and Arens 2007), mountain ranges such as the Andes are also likely to serve as refugia for magnoliid species tracking conserved habitat preferences. The net result of the effect of historical climatic and orographic differences between the Neotropics and Afrotropics was higher net diversification of angiosperms in the former than in the later (Gentry 1982, Parmentier et al. 2007).

Considering the major differences in angiosperm diversification between the Neotropics and Afrotropics, we expect to find major differences in phylogenetic composition between the Neotropics and Afrotropics (Hypothesis 1, Table 1). Moreover, given that magnoliids track conserved habitat preferences, we expect to observe magnoliids better represented in communities near mountain ranges such as the Andes (Hypothesis 1, Table 1). Considering the higher climatic stability and habitat availability during the Cenozoic and subsequent higher angiosperm diversification in the Neotropics, we expect to observe widespread phylogenetic clustering in the Central Amazon (Hypothesis 2, Table 1). Because of Cenozoic major extinction events likely have decreased net diversification in the Afrotropics, most of the divergences between extant lineages should be ancient, resulting in widespread random phylogenetic structure in Afrotropical rainforest communities (Hypothesis 3, Table 1). The co-occurrence of species belonging to recently-diversified lineages with species belonging to early-diversified lineages tracking ancestral habitats (i.e. magnoliids) have likely led to phylogenetic overdispersion in communities near the Andes (Hypothesis 4, Table 1).

Methods

Study sites

We gathered tree inventories for 115 sites from Neotropical and Afrotropical rainforests, i.e. Central American, Amazonian, Guineo-Congolian and Malagasy rainforests (not including Neotropical Atlantic rainforests): seven sites of the Tropical Ecology, Assessment and Monitoring Network (TEAM) (data sets available at http://www.teamnetwork.org), 74 Alwyn Gentry's forest sites (available at http://www.wlbcenter.org/gentry_data.htm), and 34 surveys published in the literature. TEAM's sites consisted in five to nine 1-ha plots per site. Alwyn Gentry's sites consisted of one 0.1 ha transect per site. The surveys obtained from the literature had variable sampling efforts. We compiled data from a total of 89 sites for the Neotropics, 23 sites for the Afrotropics, and three sites for Madagascar. We used the data from the 115 sites to build the pool of species of each biogeographic region. See Supplementary material Appendix 1 for the list of sites from surveys available from TEAM's and Gentry's data sets and published studies. Information on sampling design and data collection of the TEAM Network can be found in Supplementary material Appendix 1 and in TEAM Network (2010).

In this study, data on the identity and abundance of angiosperm species were pooled for each site (94 sites out of the 115 used for building the regional species pool). We obtained abundance data for 76 sites in the Neotropics, 15 sites in the Afrotropics, and three in Madagascar. To maintain consistency with TEAM's surveys and most of the surveys from published studies, we selected only the data from Gentry's transects for trees with diameter at breast height ≥10 cm. The majority of individuals were identified to the species level. Each individual identified to the genus level at a given site was regarded as a species specific to that site. Unidentified individuals in TEAM Network's sites (2.8% of the individuals) were excluded from the data matrix. We standardised the lists by removing non-arboreal species and correcting for nomenclatural synonyms using the online tool Taxonomic Name Resolution Service v3.2 (Boyle et al. 2013).

Given that the different sources had different sampling sizes, we tested for the effect of data source on the variation of NRI (Supplementary material Appendix 2). Even though different data sources had different sampling efforts, NRI did not significantly differ between data sources (see analyses in Supplementary material Appendix 2).

Phylogenetic tree

We built a phylogenetic tree from the megatree R20120829 (available at https://github.com/camwebb/tree-of-trees/blob/master/megatrees/R20120829.new), which is based on the phylogenetic backbone (mostly resolved at the "order level") proposed by APG III (APG 2009) and on relationships among families according to Stevens (2001). Considering that we were interested in deep relationships in the phylogenetic tree, we did not need to build a high-resolution tree. Then, we standardised the resolution of the megatree by removing infra-family phylogenetic relationships, keeping the resolution at the "family level" for the whole tree, with polytomies linking species within genus and genera within family. The tree branch lengths were adjusted through the BLADJ algorithm in Phylocom 4.2 software (Webb et al. 2008) following clade age estimates by Bell et al. (2010). Undated clades were evenly interpolated between dated clades. We used the module Phylomatic 2 in the software Phylocom

4.2 (Webb et al. 2008) to build a phylogeny with all the species present in our global species pool (6,056 species from the 115 compiled forest surveys), i.e. including the Neotropics, Afrotropics, and Madagascar. See the phylogeny in Supplementary material Appendix 3, Fig. A4. Finally, we calculated a matrix of phylogenetic distances (in millions of years) between pairs of terminal taxa for the entire phylogeny (containing 6,056 species).

Linking shifts in local phylogenetic structure to changes in phylogenetic composition across sites

For testing our hypotheses, we used two approaches. One approach is the net relatedness index (NRI; Webb et al. 2002), which measures phylogenetic structure in values representing clustering vs. overdispersion relative to a species pool. The other approach is the phylogenetic coordinates of phylogenetic structure (PCPS; Duarte 2011), which synthesises phylobetadiversity into ordination vectors representing changes in phylogenetic composition across communities. Using PCPS, we identified lineages linked to shifts in phylogenetic structure values (NRI) across biogeographical regions. Both of the methods are briefly explained next.

We evaluated phylogenetic structure (clustering vs. overdispersion) of local communities relative to regional species pool using the net relatedness index (NRI; Webb et al. 2002), which is the standardised effect size of mean pairwise phylogenetic distances among co-occurring taxa in a community. Significant positive values of NRI indicate that taxa are more related than expected by chance (phylogenetic clustering), while significant negative values indicate that taxa are less related than expected by chance (phylogenetic overdispersion). Communities presenting NRI values that do not differ from the null expectation of phylogenetic structure are interpreted as phylogenetically random. We used the null model phylogeny.pool, which controls for species richness and draws species without replacement from the phylogeny with equal probability of being included in the null communities (Kembel et al. 2010). We computed NRI values for each site using species pools defined by biogeographical region (Neotropics, Afrotropics or Madagascar). We did not use a global species pool comprising all the communities across all the three biogeographical regions for two reasons. First, the Neotropics had tree species richness three to five times higher than the Afrotropics. Second, our compilation was asymmetric, with more sites in the Neotropics (89) than in the Afrotropics (23) and Madagascar (3). This precluded us from properly interpreting differences between biogeographical regions regarding changes in NRI values when the size of the species pool increased from a regional to a global scale. We calculated NRI values by weighting species abundances. We computed NRI as -1 x ses.mpd using the package Picante v. 1.6.2 (Kembel et al. 2010) in the statistical software R (R Core Team 2015).

PCPS are ordination vectors expressing orthogonal gradients in phylogenetic composition across sites (Duarte 2011, Duarte et al. 2012, 2014a) and can be used to identify lineages that better represent different parts of environmental or biogeographical gradients (Brum et al. 2013, Duarte et al. 2014a). PCPS vectors were extracted by principal coordinates analysis (PCoA) on matrix **P** of phylogeny-weighted species composition (Duarte 2011) for each 1-ha and 400-m^2 subplot across all sites. In PCPS, lineage commonness across sites is evaluated using correlation of species with PCPS vectors (Duarte 2011). Labelling species according to their clades enables identification of the lineages better representing different sites. Shifts in phylogenetic structure likely reflect the variation in phylogenetic composition across communities. Then, subsequently correlating PCPS scores with NRI values enable identification of the lineages related to phylogenetic clustering or phylogenetic overdispersion.

The PCPS with the highest eigenvalue describes major changes in phylogenetic composition between sites related to the split of deep tree nodes (e.g. nodes splitting magnoliids from eudicots); as the eigenvalues of other PCPS vectors decrease, changes in phylogenetic composition related to splits of shallower nodes appear (Duarte et al. 2014a).

We opted to use species abundances rather than species occurrences in the community matrix of species per site, because the latter generated a strong arch effect (Legendre and Legendre 2012) on PCPS ordination, which would jeopardise inferences about phylogenetic composition across communities and regions. Moreover, abundances are better descriptors of species performance at the local scale than occurrences are. Our sampling units describe local communities of a particular habitat where species co-occur, differently from lists of species at coarser spatial grains such as 110 km x 110 km cells, for which occurrences would maybe be more appropriate. We computed PCPS using the package PCPS v. 1.0.1 (Debastiani and Duarte 2014) in the software R. For details on the calculation of matrix **P** see Pillar and Duarte (2010). See Duarte et al. (2014) for a flow chart of the phylogenetic fuzzy-weighting method, and Duarte et al. (2012) for a flow chart of the PCPS analysis.

We used a coarse-resolution phylogenetic tree because our historical hypotheses deal with deep relationships in the phylogenetic tree. NRI is little affected by loss of resolution terminally in the phylogeny, especially in phylogenies with a great number of species (Swenson 2009), as ours. Moreover, the lack of phylogenetic resolution is more likely to generate false negative than false positive results in phylogenetic dispersion analyses (Swenson 2009). The PCPS vectors used (PCPS I and II) captured the deep relationships in the phylogenetic tree, which deals with a temporal scale consistent with our historical hypotheses. Furthermore, a recent study has shown that terminal lack of resolution in the phylogeny is not likely to affect the first and second PCPS vectors (Maestri et al. 2016).

In order to test whether the phylogenetic structure and composition of rainforest tree communities differed between the Neotropics, Afrotropics, and Madagascar, we compared NRI values between biogeographical regions and PCPS scores between biogeographical regions, respectively. We used ANOVA to test for the significance of these comparisons.

We used Pearson's correlation to test for the association between shifts in local phylogenetic structure (NRI values) and the variation in phylogenetic composition (PCPS scores) across sites. We used Dutilleul's correction (Dutilleul 1993) to account for the influence of spatial autocorrelation on the number of degrees of freedom. Spatial analyses were performed using SAM (Rangel et al. 2010).

Results

We compiled 6,056 species for 115 sites across the Neotropics, Afrotropics, and Madagascar. The Neotropics had the highest species richness (4,668), followed by the Afrotropics (1,095) and Madagascar (347). Considering the 94 sites with species abundances separately, we compiled 5,506 species – 4,346 species for the Neotropics, 857 species for the Afrotropics, and 347 for Madagascar. The actual species pool of the Amazon rainforest harbours between 16,000 and 25,000 tree species (ter Steege et al. 2013, Slik et al. 2015), while the Afrotropical rainforest has between 4,500 and 6,000 tree species (Slik et al. 2015). Then, our global species pool would represent approximately 19-30% of the actual pool of tree species of the rainforests of the Neotropics, Afrotropics and Madagascar (not considering the Brazilian Atlantic forest). This sample is likely a good representation of the phylogenetic composition of trees in these biogeographic regions.

We identified major changes in phylogenetic composition correlated to shifts in phylogenetic structure across communities in different biogeographical regions (Fig. 1). Figure 2 provides maps of PCPS eigenvalues and NRI values to aid in the spatial interpretation of phylogenetic composition and structure patterns. The first PCPS eigenvector synthesised a gradient in phylogenetic composition across communities represented by major angiosperm lineages: magnoliids, monocots, and eudicots (see Supplementary material Appendix 3, Fig. A4 to locate clades in angiosperm phylogeny). Monocots were better represented in Andean and Western Amazonian communities (Fig. 1, 2a, c). Magnoliids were better represented in some of the Andean communities (Fig. 1, 2a, c). The second PCPS eigenvector described a gradient in phylogenetic composition characterised mostly by monocots being more represented in the Neotropics, while magnoliids and eudicots being well represented in the three biogeographic regions (Fig. 1, 2c). The phylogenetic composition differed between Neotropics and Afrotropics for both PCPS I and II (Fig. 2a-d).

Phylogenetic structure (NRI) values did not differ between biogeographical regions (Fig. 2f). Rather, phylogenetic structure varied within the Neotropics, with communities near the Andes showing phylogenetic overdispersion (Fig. 2e). Phylogenetic overdispersion was associated with communities near the Andes with high representation of magnoliids or monocots (Fig. 1), which mathematically means that there were more pairwise phylogenetic distances (for NRI calculation) being computed down to basal nodes when comparing eudicots to magnoliids or to monocots (see Supplementary material Appendix 3, Fig. A4 for angiosperm phylogeny). Values of NRI were significantly correlated with PCPS I ($r = 0.791$, $F_{30.2} = 50.35$, $P < .001$; see Supplementary material Appendix 4, Fig. A5). Negative PCPS I scores were related to negative NRI values (Fig 1, Fig. A5), which means that high representation of magnoliids, especially in the Andes, was related to phylogenetic overdispersion. Association of NRI values with PCPS II was also significant (r = 0.28, $F_{52.1}$ = 4.42, P = 0.04; Fig. A5), although their relationship was not linear. Negative PCPS II scores were related to negative NRI values (Fig 1, Fig. A5), which means that high representation of monocots near the Andes was related to phylogenetic overdispersion. Positive PCPS II scores were related to both negative and positive NRI values (Fig 1, Fig. A5), which means that high representation of magnoliids near the Andes was related to phylogenetic overdispersion, while high representation of eudicots in some Central Amazonian and some Afrotropical communities was related to phylogenetic clustering. Phylogenetic randomness predominated in Afrotropical and Malagasy, communities, and in part of Central Amazonian communities (Fig. 2e). It is important to note that random phylogenetic structure in Madagascar may be in part a result of the low number of sites we were able to compile for the region, given that small species pools may present less clustering than big species pools (Swenson et al. 2006).

In summary, we observed widespread phylogenetic overdispersion near the Andes associated with magnoliids and monocots, phylogenetic clustering in Central Amazon related to high representation of eudicots, and phylogenetic randomness in in Central Amazonian and Afrotropical communities (Fig. 1, 2).

Discussion

Linkages between phylogenetic structure and regional composition in Neotropical and Afrotropical rainforest tree communities

By evaluating the linkages between phylogenetic structure and phylobetadiversity in light of the Gondwanan biogeographical history, we were able to test our four hypotheses. As predicted, we identified major differences in phylogenetic composition with magnoliids better represented near mountain ranges (Andes). The variation in phylogenetic composition was accompanied by shifts in phylogenetic structure across biogeographical regions. Phylogenetic overdispersion was related to the high representation of magnoliids and monocots in communities near the Andes. The nodes that separate magnoliids and eudicots and monocots and eudicots are deep in the phylogeny, which increase phylogenetic diversity in places where magnoliids or monocots co-occur with eudicots (or the three lineages co-occur). Extant magnoliids are usually associated with upland, shady and wet habitats, (Feild and Arens 2007), which suggest magnoliids such as Lauraceae, Winteraceae and Annonaceae track this kind of habitats across space and time (Duarte 2011, Debastiani et al. 2015). Indeed, magnoliids have conserved traits that limit their establishment in open and drier habitats other than forest understoreys (Feild and Arens 2007). In addition, magnoliids appear to track ancestral-like habitats in Andean highlands (e.g. Drimys spp. that today occur in high elevations of the Andes; Colinvaux et al. 2000), which is consistent with the information that early-diverged lineages conserved austral Gondwanan niches in high latitudes and elevations of the Andes (Segovia and Armesto 2015). Besides providing refugia for lineages with conserved habitat preferences (e.g. magnoliids), the Andes appears to have promoted the recent diversification of many angiosperm lineages, especially of eudicots and monocots (Richardson et al. 2001, Kissling et al. 2012). Therefore, phylogenetic overdispersion in some of Andean communities is consistent with the co-occurrence of magnoliid species tracking conserved habitat preferences with eudicot species of lineages that diversified recently in the Andes. In a similar line, Diniz-Filho et al. (2007) argued that bird species accumulation in the Neotropics was the combined result of conservatism of ancestral tropical niches and recent diversification of lineages composed of small-ranged species in the Andes. The co-occurrence of eudicots and monocots is another feasible explanation for the phylogenetic overdispersion near the Andes, because monocots would increase phylogenetic diversity in presence of eudicots due to its deeper node in phylogeny. This result is consistent with recent finding that Western Amazonian tree communities tend to be phylogenetically overdispersed (Honorio Coronado et al. 2015).

Although most of the communities in the Central Amazon presented phylogenetic random values, we found support for our hypothesis of phylogenetic clustering in Central Amazon for some communities. This clustering is related to the dominance of eudicots in these communities, as elucidated by PCPS analysis. Dominance of eudicot species in local communities may be a reflection of the Amazonian pool of species, which is dominated by species of this clade. Eudicots underwent high diversification in the Amazon (Gentry 1982). Eudicot-dominated communities tend to be clustered because they are composed of many closely-related species, i.e. these communities have high phylogenetic redundancy. The Amazonian species pool is also well represented by monocot species, especially palms (Arecaceae) (Kissling et al. 2012). Previous studies observed phylogenetic clustering in Amazonian palm assemblages (Kissling et al. 2012, Eiserhardt et al. 2013). The likely reason why we did not find phylogenetic clustering associated with monocots is that we considered communities composed by not only monocots, but also by eudicots and magnoliids. Thus, we found monocots either related to phylogenetic overdispersion (in the Andes) or to phylogenetic randomness (in Central Amazon).

As hypothesised, we found phylogenetic randomness in Afrotropical communities, which is consistent with what was previously found for monocots in the region (Kissling et al. 2012). Phylogenetic randomness in the Afrotropics might be a result of major extinctions that occurred during the Cenozoic (Kissling et al. 2012).

Linking alpha phylogenetic structure with phylobetadiversity; what do we gain by identifying lineages responsible for observed patterns?

While many studies have assessed patterns of phylogenetic composition and species composition (phylobetadiversity and compositional beta diversity, respectively), this has not been enough to identify the lineages responsible for shifts in phylogenetic structure across regions. If historical biogeography inferences deeply rely on the information of how lineages evolved across space and time, it is essential to identify which lineages are responsible for differences in phylogenetic structure across biogeographical barriers to clarify the historical processes influencing current community structure. While species composition at the local scale may be ephemeral, lineage composition in regional species pools is likely to persist for millions of years (Gerhold et al. 2015). The knowledge on which lineage is linked to a given phylogenetic structure provides insight on the historical processes that were important for the formation of the regional species pool and, consequently, the structuring of local communities. For instance, we were able to relate the observed phylogenetic overdispersion near the Andes (as shown by NRI) to high representation of monocot and magnoliid species in the region (as shown by PCPS), which caused phylogenetic overdispersion when co-occurring with eudicots. By knowing that magnoliids tracked conserved habitat preferences, and that there was recent diversification of eudicot and monocot lineages during the uplift of the Andes, we were able to discuss the historical processes influencing phylogenetic structure of communities of the region. Therefore, integrating PCPS and NRI unifies phylogenetic structure and phylobetadiversity in a straightforward framework.

Conclusions

By linking phylogenetic structure with regional phylogenetic composition, we were able to identify how differences in lineage composition are related to phylogenetic co-occurrences at the local scale across communities in biogeographical regions that have been undergoing a major vicariance process during the past 100 Myr. By doing so, we were able to infer how macroevolutionary processes influenced current species co-occurrences. We observed both Mesozoic and Cenozoic imprints on the phylobetadiversity and phylogenetic structure of rainforest tree communities in the Neotropics and Afrotropics. Our results suggest that Gondwanan vicariance and the uplift of mountain ranges and their subsequent effect on angiosperm diversification explain current variation in phylogenetic composition and structure of rainforest tree communities across the Neotropics, Afrotropics and Madagascar. By identifying the linkages between lineage composition and phylogenetic structure across sites in the Neotropics, Afrotropics and Madagascar, we hope to contribute to the discussion on the historical and ecological processes that shaped the structure of rainforest tree communities in these regions with different biogeographical histories.

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Supplementary material (Appendix EXXXXX at <www.oikosoffice.lu.se/appendix>). Appendix 1–4.

Table 1. Hypotheses of the study, showing the predictions about the influence of historical factors on the structuring of rainforest tree communities in the Neotropics, Afrotropics, and Madagascar.

	Historical processes	Predictions about phylogenetic composition and structure	References
Hypothesis 1	The breakup of Gondwana led to increasing isolation of biotas. The biogeographic regions were completely separated in the Cenozoic, when great differences in diversification rates between regions occurred due to different climatic and orographic histories.	Major differences in phylogenetic composition between biogeographical regions, with eudicots well represented throughout study sites and magnoliids better represented near mountain ranges.	Ghazoul and Sheil 2010, Morley 2011, Wilf et al. 2013, Duarte et al. 2014b, Silvestro et al. 2015
Hypothesis 2	High speciation and low extinction rates of eudicots due to persistence of large areas of rainforest through the Cenozoic led to a regional species pool dominated by this clade in the Neotropics, especially for Central Amazonian communities.	Eudicot species would be more likely to be drawn from the regional species pool during community assembly, leading to widespread phylogenetic clustering in Central Amazonian communities.	Gentry 1982, Fine and Ree 2006
Hypothesis 3	Major extinction events during the Cenozoic resulted in a regional lineage pool with a lower number of recently-diverged lineages in the Afrotropics.	The low number of recently-diverged lineages in the regional species pool would lead to random phylogenetic structure in Afrotropical communities.	Parmentier et al. 2007, Kissling et al. 2012
Hypothesis 4	At a regional scale the uplift of the Andes promoted recent diversification of eudicots, as well as gave rise to montane, moist and shady habitats, similar to those that existed in Gondwana. Magnoliids generally show conserved preferences for these Gondwana-like habitats, and seem to have tracked them northwards coming from southern Andes and Patagonia. Then, magnoliids tracking conserved habitat preferences met eudicot lineages that diversified during the Cenozoic in northern Andes.	The node splitting magnoliids to other angiosperms, including eudicots, is deep in the phylogeny. Thus, the co-occurrence of magnoliids tracking conserved habitat preferences with recently-diverged eudicots increase phylogenetic diversity, leading to phylogenetic overdispersion in northern Andean communities.	Feild and Arens 2007, Graham 2009, Wilf et al. 2013, Segovia and Armesto 2015

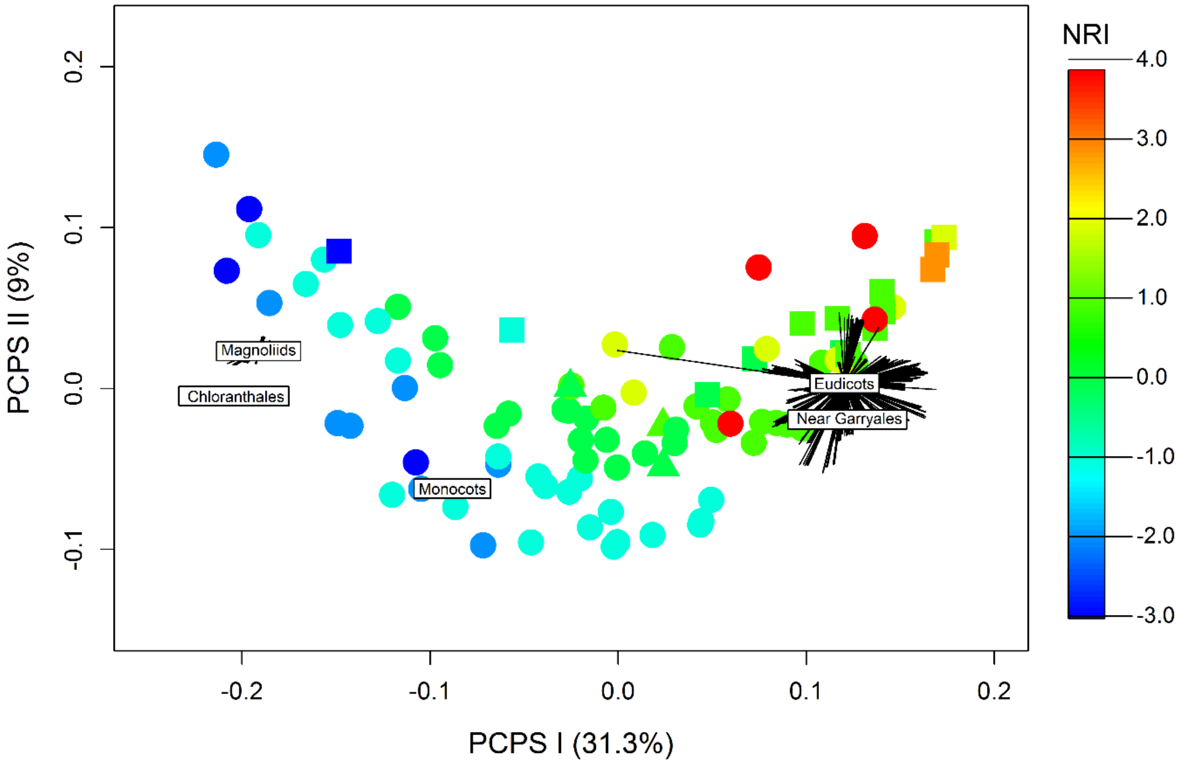

Figure 1. Scatter diagram of the two main ordination vectors representing gradients in phylogenetic composition of angiosperm trees across Neotropical, Afrotropical and Malagasy rainforest communities. Ordination vectors were computed using principal coordinates of phylogenetic structure (PCPS) approach (Duarte 2011). Phylogenetic structure was assessed using net relatedness index (NRI; Webb et al. 2002) computed according to regional species pools (Afrotropics, square; Neotropics, circle; and Madagascar, triangle). High positive values indicate phylogenetic clustering (reddish colours), values near zero indicate random phylogenetic structure (greenish colours) and high negative values indicate phylogenetic overdispersion (bluish colours). For the geographical location of sites, see Fig. 2.

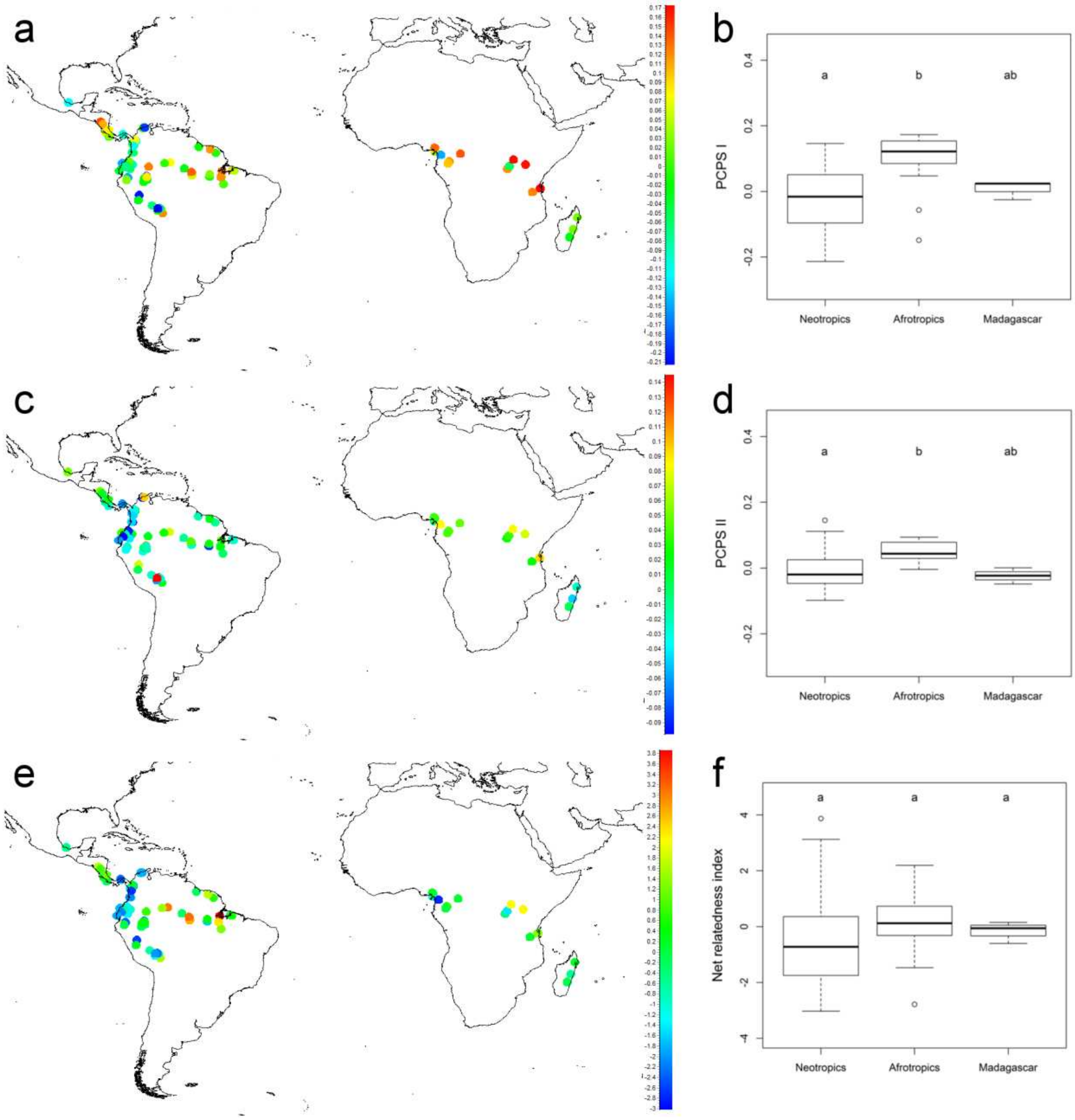

Figure 2. Spatial variation in phylogenetic composition (a, c) and structure (e) of angiosperm trees across Neotropical, Afrotropical and Malagasy rainforest communities. Phylogenetic composition and structure were assessed using principal coordinates of phylogenetic structure (PCPS) and net relatedness index, respectively. Phylogenetic composition differed between Neotropics and Afrotropics for the two main PCPS vectors (b, d). Phylogenetic structure did not differ between biogeographical regions (f), but presented an apparent gradient from Andes to Amazon in the Neotropics. Different letters over the boxplots represent significant comparisons under $P < 0.001$ for ANOVA and Tukey tests. The variation in phylogenetic structure (NRI) values (e) is represented by the same colours used in Fig. 1.