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

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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: (Hypothesis 1) isolation of Gondwanan biotas generated differences in phylogenetic composition among biogeographical regions; (H2) major Cenozoic extinction events led to lack of phylogenetic structure in Afrotropical and Malagasy communities; (H3) greater angiosperm diversification in the Neotropics led to greater phylogenetic clustering there than elsewhere; (H4) phylogenetic overdispersion is expected near the Andes due to the co-occurrence of magnoliids tracking conserved habitat preferences and recently diversified eudicot lineages. Using abundance data of tropical rainforest tree species from 94 communities in the Neotropics, Afrotropics and Madagascar, we computed net relatedness index (NRI) to assess local phylogenetic structure, i.e. phylogenetic clustering *vs.* overdispersion relative to regional species pools, and principal coordinates of phylogenetic structure (PCPS) to assess variation in phylogenetic composition across communities. We observed significant differences in phylogenetic composition among biogeographical regions (agreement with H1). Overall phylogenetic structure did not differ among biogeographical regions, but results indicated variation from Andes to Amazon. We found widespread phylogenetic randomness in most Afrotropical and all Malagasy communities (agreement with H2). Most of Central Amazonian communities were phylogenetically random, although some communities presented phylogenetic clustering (partial agreement with H3). We observed phylogenetic overdispersion near the Andes (agreement with H4). We identified lineages linked to shifts in local phylogenetic structure among communities. We were able to identify how differences in lineage composition are related to local phylogenetic co-

occurrences across biogeographical regions that have been undergoing different climatic and orographic histories during the past 100 Myr. We observed imprints of history following Gondwana breakup on phylobetadiversity and local phylogenetic structure of rainforest tree communities in 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 and habitats (Graham et al. 2009, Kooyman et al. 2011, Fine and Kembel 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 (Duarte 2011). For instance, two communities with the same phylogenetic structure measured using a given metric may have very different species composition (Graham et al. 2009). Hence, studies usually infer historical processes affecting phylogenetic structure by evaluating both taxonomic beta diversity (differences in species composition among communities) and phylobetadiversity (differences in lineage composition among communities), which links current phylogenetic structure and macroevolutionary processes for certain lineages (Graham and Fine 2008, Graham et al. 2009). One way to link phylogenetic structure and composition is to use both the net relatedness index (NRI; Webb et al. 2002) as a measure of local phylogenetic structure and PCPS analysis (phylogenetic coordinates of phylogenetic structure; Duarte 2011, Duarte et al. 2012) to measure phylobetadiversity and identify the most common lineages in sets of communities. PCPS analysis synthesises phylobetadiversity into ordination vectors (PCPS) representing variation in phylogenetic composition across communities. Thus, 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 this approach). 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 compute NRI and PCPS values across the Neotropics, Afrotropics and Madargascar and intregrate them to test biogeographical hypotheses related to the fragmentation of Gondwana and onward 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 newly developing continents.

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. Proteaceae) in forests that are similar in composition to the Gondwanan rainforests they were part of during the Cretaceous

(Kooyman et al. 2014). Today, these Gondwana-like rainforests are found in the South American highlands (Segovia and Armesto 2015). Magnoliid species usually bear conserved traits of early angiosperms (from ca. 120 Ma) that limit water usage, which led to overall lower photosynthetic capacity compared to eudicots (Feild et al. 2002, Boyce et al. 2009, Brodribb and Feild 2010). Habitat (and biome) tracking (*sensu* Ackerly 2003) is a major tendency among plants due to phylogenetic niche conservatism (Crisp et al. 2009), because, under major changes of regional conditions, plants more often move to other places with similar conditions than quickly adapt to the changing environment (Donoghue 2008). Thus magnoliids today are 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, Debastiani et al. 2015).

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, Afrotropics and Madagascar (Gentry 1982, Parmentier et al. 2007, Vences et al. 2009, Ghazoul and Sheil 2010, Morley 2011). The separation of Gondwanan landmasses and their 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 implies 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 promoted high speciation (and low extinction) rates, especially of 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). By contrast, the role of major dry periods affecting floristic composition during the glacial ages of the late Cenozoic was much greater in the Afrotropics than in the Neotropics (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 across the Afrotropics (Parmentier et al. 2007, Morley 2011). These climatic fluctuations reduced habitat availability across time, which reduced speciation rates in the Afrotropics compared to the Neotropics (Kissling et al. 2012). Similarly, major climatic flutuations affected the diversification of the insular Malagasy flora (Vences et al. 2009), where time-integrated species-area effect might have been even more intense than in the Afrotropics considering the even smaller availability of rainforest area through time.

Within the Neotropics, the uplift of the Andes during the Cenozoic (from ca. 40 Ma) influenced the recent diversification of many taxa (e.g. hummingbirds; Graham et al. 2009), including the rapid diversification of many angiosperm lineages (Gentry 1982, Richardson et al. 2001, Hughes and Eastwood 2006) by creating a spatial configuration of habitats that promoted speciation, such as island-like habitats isolated by valleys of different environmental conditions (Hughes and Eastwood 2006). Furthermore, 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 habitat preferences, thus reducing extinction rates. The net result of the effect of historical climatic and orographic differences between the Neotropics, Afrotropics and Madagascar was higher net diversification of angiosperms in the Neotropics (Gentry 1982, Parmentier et al. 2007).

Considering the higher angiosperm diversification rates in the Neotropics compared to the Afrotropics and Madagascar and their distinct biogeographical histories, we expect to find major differences in phylogenetic composition among these regions (Hypothesis 1, Table 1). Because of Cenozoic major extinction events likely have decreased net diversification in the Afrotropics and Madagascar, there should be widespread random phylogenetic structure in Afrotropical and Malagasy rainforest communities (Hypothesis 2, 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 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 compiled tree inventories for 115 sites from Neotropical (not including Atlantic rainforests), Afrotropical and Malagasy rainforests, i.e. Central American, Amazonian, Andean, Guineo-Congolian and Malagasy 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 sites from 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 data from these 115 sites to build the pool of species of each biogeographic region (See Supplementary material Appendix 1 for the list of sites).

The inclusion criterion of species was diameter at breast height (DBH) ≥5 cm in Gentry's surveys and DBH ≥10 cm in most remaining surveys (Table A1 in Supplementary material Appendix 1). We selected only the data for trees with DBH ≥5 cm from Gentry's transects, because Gentry's sites had the smallest sampling sizes and DBH ≥5 cm is more inclusive than greater stem diameters. We standardised the data by removing non-arboreal species, conifers and ferns from the surveys.

In this study, data on the identity and abundance of angiosperm tree species were pooled for each site. Among the 115 sites used for building the regional species pool, we obtained abundance data for 94 sites (76 in the Neotropics, 15 in the Afrotropics, and three in Madagascar). Each of these 94 sites was used as a sampling unit in data analyses, and we will refer to them as "communities" throughout the article. The majority of species (95.5%) were identified at least to the genus level, which enabled us to use them in the phylogenetic analyses. Each individual identified to the genus level at a given community was regarded as a species specific to that community. Species not identified at least to the genus level (4.5%) were excluded from the data matrix. We corrected species identities for nomenclatural synonyms using the online tool Taxonomic Name Resolution Service v3.2 (Boyle et al. 2013).

Given that the different sources (TEAM Network, Gentry forest transects and surveys from the literature) had different sampling sizes and inclusion criteria of tree individuals (DBH), we tested for the effect of data source on the variation of NRI (see analyses in Supplementary material Appendix 2). NRI did not significantly differ among data sources (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 (well resolved for deep phylogenetic relationships such as orders) 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 tree species from the 115 compiled forest surveys), i.e. including the Neotropics, Afrotropics, and Madagascar (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.

We removed conifer species from our data set because we were interested in angiosperm tree phylogenetic patterns. Moreover, only four out of the 6,059 species were gymnosperms. These four species comprised 224 individuals in four out of the 94 communities with species abundance, or 0.19% of the total of individuals recorded in the 94 communities. In terms of proportion these plants would not be important for revealing alpha and beta phylogenetic patterns across rainforest tree communities. Nonetheless, given the age of the deep node separating gymnosperms from angioperms, their inclusion would likely be sufficient for obscuring most of the patterns we discuss here.

In regard to non-arboreal species, such as herbs and lianas, most of the studies used did not record them. Therefore, although it would be interesting to include such plants in the analyses, we were not able to do so. Moreover, the inclusion of herbaceous and other non-woody species are unlikely to affect local phylogenetic structure and phylobetadiversity results, because these life forms evolved multiple times in different lineages of the major angiosperm clades, i.e. magnoliids, monocots and eudicots (Fitzjohn et al. 2014). Therefore, these plants would be likely represented in many of the lineages that are already represented in our data set, thereby not changing major observed patterns.

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

For testing our hypotheses, we used two approaches. One approach is the net relatedness index (NRI), which measures phylogenetic structure in values representing clustering vs. overdispersion relative to a species pool (Webb et al. 2002). The other approach is the phylogenetic coordinates of phylogenetic structure (PCPS), which synthesises phylobetadiversity into ordination vectors representing changes in phylogenetic composition across communities (Pillar and Duarte 2010, Duarte 2011). Using PCPS, we identified lineages linked to shifts in phylogenetic structure values (NRI) across biogeographical regions. Both 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) given a regional species pool. Communities presenting NRI values that do not differ from the null expectation of phylogenetic structure are interpreted as being phylogenetically random relative to the regional species pool. 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 community using species pools defined by biogeographical region (Neotropics, Afrotropics or Madagascar). 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).

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 or Madagascar. Second, our compilation was asymmetric, with more communities in the Neotropics (89) than in the Afrotropics (23) and Madagascar (3). This precluded us from properly interpreting differences among biogeographical regions regarding changes in NRI values when the size of the species pool increased from a regional to a global scale.

PCPS are ordination vectors expressing orthogonal gradients in phylogenetic composition across communities (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 (Pillar and Duarte 2010, Duarte 2011) for each community. In PCPS, lineage commonness across communities 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 communities. Shifts in local 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 among communities related to the split of deep tree nodes (e.g. nodes splitting magnoliids from eudicots and monocots 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 matrix of species per community, because the latter generated a strong arch effect (Legendre and Legendre 2012) on PCPS ordination, which would limit inferences about phylogenetic composition across communities and regions. Moreover, abundances are better descriptors of species performance at the local scale than mere occurrence. 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** of phylogeny-weighted species composition 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 did not 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 among biogeographical regions and PCPS scores among biogeographical regions, respectively. We used ANOVA to test for the significance of these comparisons. Pearson's correlation was used to test for the relationship between shifts in local phylogenetic structure (NRI values) and the variation in phylogenetic composition (PCPS scores) across communities, and Dutilleul's correction (Dutilleul 1993) was used 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

The 115 sites across the Neotropics, Afrotropics, and Madagascar contained 6,056 species. The Neotropics had the highest species richness (4,668), followed by the Afrotropics (1,095) and Madagascar (347). Considering the 94 communities with species abundances separately, these contained 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 >10 cm diameter (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 biogeographical 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 among the three biogeographical regions (Fig. 2f). Rather, phylogenetic structure varied within the Neotropics, with communities near the Andes showing phylogenetic overdispersion and Central Amazonian communities showing phylogenetic randomness or clustering (Fig. 2e). Phylogenetic overdispersion was associated with communities near the Andes with high representation of magnoliids or monocots (Fig. 1). Eleven out of 32 Andean communities presented significant phylogenetic overdispersion. Mathematically this 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 associated with negative NRI values (Fig 1, Fig. A5), which means that high representation of magnoliids or monocots, especially in the Andes, was related to phylogenetic overdispersion. The relationship between NRI values and 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 associated with 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 in turn were associated with 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. Six out of 44 Central Amazonian communities and two out of 15 Afrotropical communities presented significant phylogenetic clustering. Phylogenetic randomness predominated in Afrotropical and Malagasy communities, and in most Central Amazonian communities (Fig. 2e).

In summary, we observed (i) major changes in phylogenetic composition correlated to shifts in phylogenetic structure across communities in different biogeographical regions (agreement with H1), (ii) widespread phylogenetic randomness in Afrotropical and Malagasy communities (agreement with H2), (iii) phylogenetic clustering in some Central Amazonian communities related to high representation of eudicots (partial agreement with H3), and (iv) widespread phylogenetic overdispersion near the Andes associated with the co-occurrence of eudicots with magnoliids (agreement with H4) or monocots.

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 bear 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 show 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 the 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 plausible explanation for the phylogenetic overdispersion near the Andes, because monocots, similarly to magnoliids, would increase phylogenetic diversity in presence of eudicots due to the deep node splitting these clades in the 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 (38 out of 44 communities), we found support for our hypothesis of phylogenetic clustering in Central Amazon for six 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 likely reflects the Amazonian pool of species, which is dominated by species of this clade. Eudicots underwent high diversification in the Amazon (Gentry 1982), which may have been promoted by the time-integrated species-area effect

(Fine and Ree 2006). 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.

As hypothesised, we found phylogenetic randomness in Afrotropical and Malagasy communities, which is consistent with what was previously found for Afrotropical monocot communities (Kissling et al. 2012). Phylogenetic randomness in the Afrotropics and Madagascar might be a result of major extinctions that occurred during the Cenozoic (Vences et al. 2009, Kissling et al. 2012). Although we presented results for just three Malagasy communities, our results for Madagascar are probably unbiased. NRI is a measure of local phylogenetic structure relative to regional species pool. We built a species pool for Madagascar with species from three communities. Swenson (2009) showed that small pool sizes are likely to bias results towards phylogenetic clustering or overdispersion rather than towards randomness. Therefore, the results of phylogenetic randomness in Madagascar are likely reliable.

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

While many studies have assessed patterns of local phylogenetic structure, phylobetadiversity and/or taxonomic beta diversity, this has not been enough to identify the lineages responsible for shifts in local phylogenetic structure across regions or habitats (Kooyman et al. 2011, Fine and Kembel 2011, Kissling et al. 2012, Eiserhardt et al. 2013, Hawkins et al. 2014). 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 local 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 species of these clades co-occurred 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 local phylogenetic structure and phylobetadiversity in a relatively straightforward framework.

Conclusions

By linking local 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 historical imprints on the phylobetadiversity and local phylogenetic structure of rainforest tree communities in the Neotropics and Afrotropics. Our results suggest that Gondwanan vicariance, uplift of mountain ranges and their subsequent effect on angiosperm diversification and habitat tracking explain current variation in phylogenetic composition and structure of rainforest tree communities across regions. By identifying the linkages between lineage composition and phylogenetic structure across communities 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 communities 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	Major extinction events during the Cenozoic resulted in regional lineage pools with low redundancy of recently-diverged lineages in the Afrotropics and Madagascar.	The low number of recently-diverged lineages and a more balanced regional species pool would lead to random phylogenetic structure in Afrotropical and Malagasy communities.	Parmentier et al. 2007, Vences et al. 2009, Kissling et al. 2012
Hypothesis 3	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.	Species from rich recently-diversified eudicot lineages 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 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. Today magnoliids tracking conserved habitat preferences co-occur with eudicot lineages that diversified during the Cenozoic in northern Andes.	The node splitting magnoliids from 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

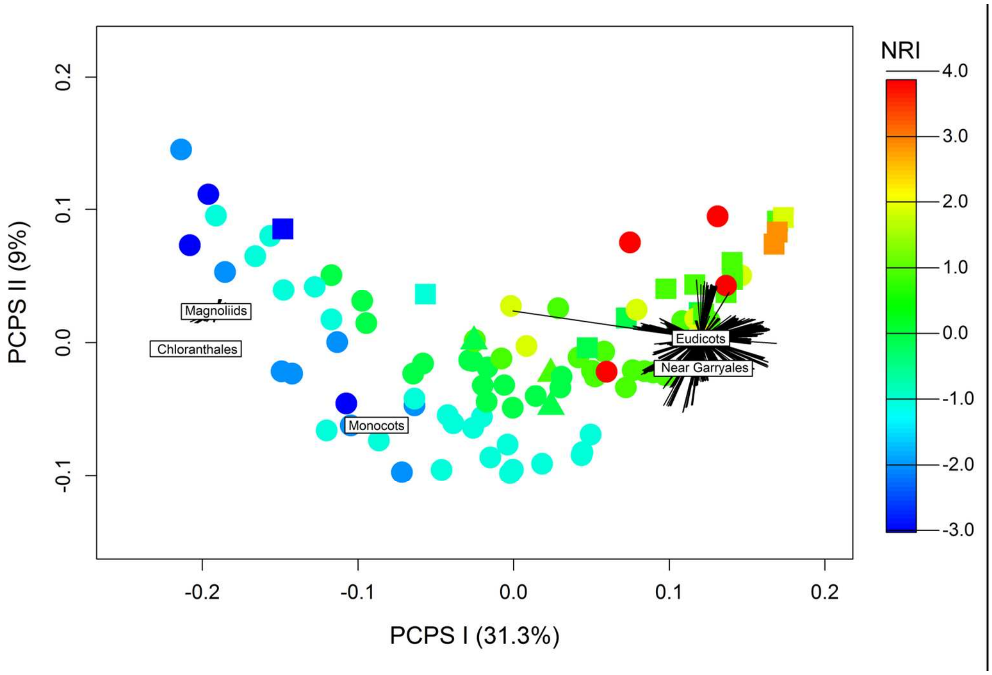

Figure 1. Scatter diagram of the two main ordination vectors representing variation in phylogenetic composition of angiosperm trees across Neotropical, Afrotropical and Malagasy rainforest communities. Ordination vectors were computed using principal coordinates of phylogenetic structure (PCPS) approach (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.
152x101mm (300 x 300 DPI)

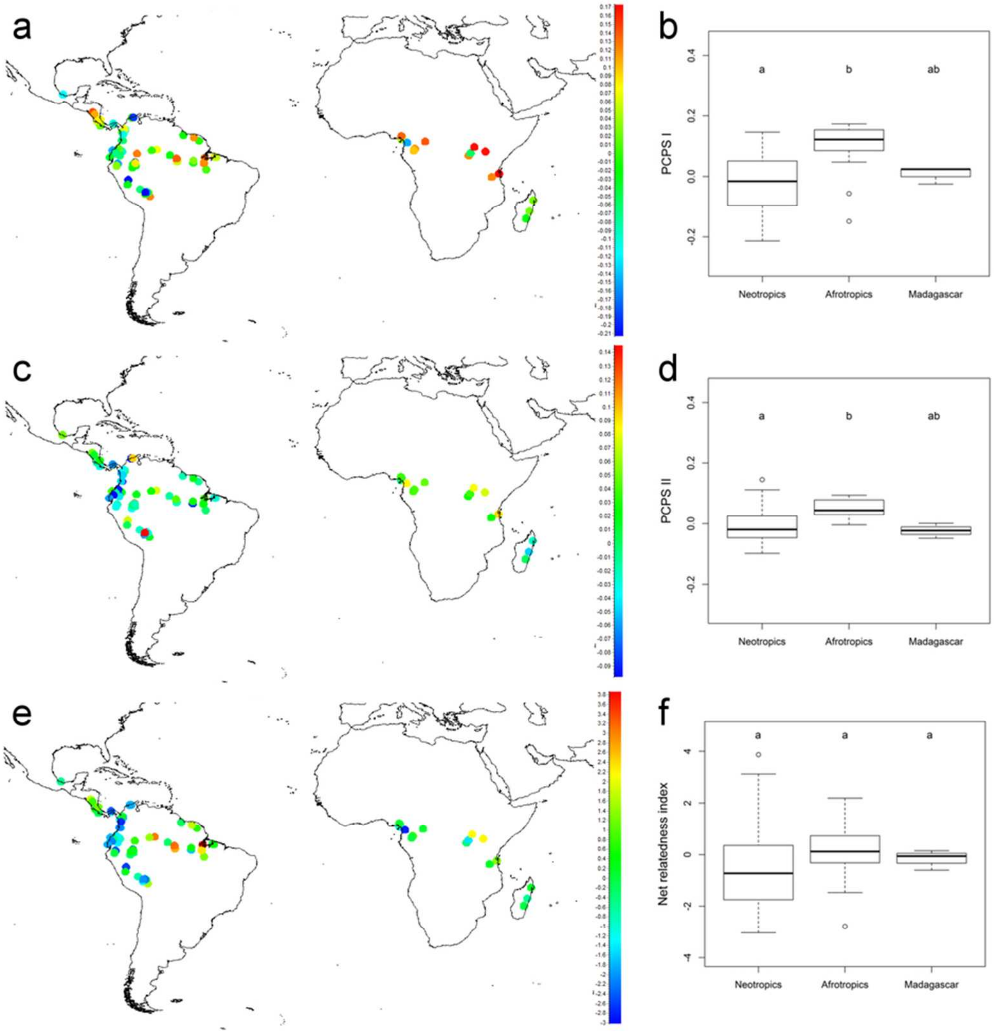

Figure 2. Spatial variation in phylogenetic composition (a, c) and structure (e) of angiosperm trees across Neotropical, Afrotropical and Malagasy rainforest communities. Phylogenetic composition and structure were assessed using principal coordinates of phylogenetic structure (PCPS) and net relatedness index, respectively. Phylogenetic composition differed between Neotropics and Afrotropics for the two main PCPS vectors (b, d). Local phylogenetic structure did not differ among biogeographical regions (f), but varied 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.
80x82mm (300 x 300 DPI)

Supplementary material for

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

M. B. Carlucci et al.

Appendix 1. Lists of TEAM Network's sites (7), Gentry's sites (74), published studies (34 sites from 32 studies) used to compile rainforest tree species pools for Neotropics, Afrotropics and Madagascar. TEAM data sets are available at http://www.teamnetwork.org. Gentry's transect data is available at http://www.mobot.org/mobot/research/gentry/welcome.shtml.

(a) TEAM's sites used: NEOTROPICS - Volcán Barva (La Selva Biological Station and Braulio Carrillo National Park, Costa Rica), Manaus (three different field stations near the city of Manaus, Brazil) and Caxiuanã (Caxiuanã National Forest, Brazil); AFROTROPICS - Korup (Korup National Park, Cameroon), Bwindi (Bwindi Impenetrable National Park, Uganda), Udzungwa (Udzungwa Mountains National Park, Tanzania); MADAGASCAR - Ranomafana (Ranomafana National Park, Madagascar).

We selected seven sites containing information of tree composition and abundance in tropical rainforests. For each site, we used the inventory data that ranged between Aug 2010 and May 2011. The TEAM Network sampling design for trees consists of tropical rainforest sites with five to seven 1-ha plots (100 x 100 m), each subdivided in 25 subplots of 400 m^2 (20 x 20 m), where trees with diameter at breast height ≥10 cm were recorded. Plots were placed in closed-canopy moist forest habitats. Each of the selected sites was composed by six plots of 1 ha, except for Korup and Volcán Barva, which were composed by five and nine plots, respectively. The data from all these plots were gathered using a defined, shared and therefore comparable method, which follows quality controls, such as including late successional forests with little anthropogenic impact. Further information can be found in TEAM Network (2010) and at http://www.teamnetwork.org.

(b) Alwyn Gentry's sites (codes in parentheses): AFROTROPICS – Banyong (Afr1), Belinga (Afr6), Makokou 1 (Afr7), Makokou 2 (Afr8), Mount Cameroun (Afr3), Ndakan (Afr4), Pande Forest Reserve (Afr17), Pugu Forest Reserve (Afr18); MADAGASCAR – Nosy Mangabe (Afr13), Perinet Forestry Station (Afr14); NEOTROPICS - Allpahuayo (SAm89), Alter de Chao (SAm20), Alto de Cuevas (SAm33), Alto de Mirador (SAm35), Alto Madidi (SAm10), Alto Madidi – Ridge Top (SAm11), Anchicayá (SAm36), Antado (SAm37), Araracuara (SAm39), Araracuara - High Campina (SAm38), Bajo Calima (SAm40), Belém-Mocambo (SAm29), Berbice River (SAm87), Bosque de la Cueva (SAm41), Bosque Nacional von Humboldt (SAm90), Cabeza de Mono (SAm91), Candamo (SAm108), Carajas (SAm23), Carara National Park (CAm6), Centinela (SAm70), Cerro de la Neblina 1 (SAm124), Cerro de la Neblina 2 (SAm125), Cerro El Picacho (CAm24), Cerro Olumo (CAm23), Cochacashu (SAm96), Constancia (SAm97),Cuangos (SAm71),Curundu (CAm25), Cuzco Amazónico (SAm99), Dureno (SAm72), Fila de Bilsa (SAm68), Huamaní (SAm75), Indiana (SAm101), Jatun Sacha (SAm76), Jenaro Herrera (SAm102), La Planada (SAm54), Madden Forest (CAm26), Maquipucuna (SAm78), Miazi (SAm79), Mishana - Tahuampa (SAm104), Mishana Old Floodplain (SAm105), Mishana White Sand (SAm106), Murrí (SAm59), Osa-Sirena (CAm8), Pampas del Heath (SAm109), Pipeline Road (CAm27), Quebrada Sucusari (SAm112), Rancho Quemado (CAm7), Río Manso (SAm61), Río

Nangaritza (SAm82), Río Palenque 1 (SAm83), Río Palenque 2 (SAm84), Río Távara (SAm110), San Sebastían (SAm85), Saul (SAm86), Shiringamazú (SAm111), Tambopata Alluvial (SAm114), Tambopata Lateritic (SAm116), Tambopata Swamp Trail (SAm115), Tambopata Upland Sandy (SAm113), Tutunendo (SAm65), Yanamono 1 (SAm120), Yanamono 2 (SAm121), Yanamono Tahuampo (SAm119).

(c) Published studies:

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128 **Table A1.** Criteria of inclusion used in the different data sources.

Data source	DBH
Alarcon & Peixoto 2007	≥10 cm
Amaral et al. 2009	≥10 cm
Bongers et al. 1988	≥10 cm
Chapman et al 1997	≥10 cm
Espírito-Santo et al. 2005	≥10 cm
Fashing & Gathua 2004	≥15 cm
Gentry_Allpahua	≥5 cm
Gentry_Alterdoc	≥5 cm
Gentry_Altocuevas	≥5 cm
Gentry_Altodemi	≥5 cm
Gentry_Anchicay	≥5 cm
Gentry_Antado	≥5 cm
Gentry_Araracua	≥5 cm
Gentry_Arcating	≥5 cm
Gentry_Banyong	≥5 cm
Gentry_Belem	≥5 cm
Gentry_Belinga	≥5 cm
Gentry_Berbicer	≥5 cm
Gentry_Bilsa	≥5 cm
Gentry_Bosqcueva	≥5 cm
Gentry_Cabezade	≥5 cm
Gentry_Calima	≥5 cm
Gentry_Candamo	≥5 cm
Gentry_Carajas	≥5 cm
Gentry_Carara	≥5 cm
Gentry_Centinel	≥5 cm
Gentry_Ceroneb1	≥5 cm
Gentry_Ceroneb2	≥5 cm
Gentry_Cerroelp	≥5 cm
Gentry_Cerroolu	≥5 cm
Gentry_Cochacas	≥5 cm
Gentry_Constanc	≥5 cm
Gentry_Cuangos	≥5 cm
Gentry_Curundu	≥5 cm
Gentry_Cuzcoama	≥5 cm
Gentry_Dureno	≥5 cm
Gentry_Huamani	≥5 cm
Gentry_Humboldt	≥5 cm
Gentry_Indiana	≥5 cm
Gentry_Jatunsac	≥5 cm
Gentry_Jenarohe	≥5 cm
Gentry_Laplanad	≥5 cm

Gentry_Madden	≥5 cm
Gentry_Madidi	≥5 cm
Gentry_Madidiri	≥5 cm
Gentry_Makokou1	≥5 cm
Gentry_Makokou2	≥5 cm
Gentry_Maquipuc	≥5 cm
Gentry_Miazi	≥5 cm
Gentry_Mishnfl	≥5 cm
Gentry_Mishws	≥5 cm
Gentry_Mtcam	≥5 cm
Gentry_Murri	≥5 cm
Gentry_Nangarit	≥5 cm
Gentry_Ndakani	≥5 cm
Gentry_Nosymang	≥5 cm
Gentry_Osasiren	≥5 cm
Gentry_Pande	≥5 cm
Gentry_Perinet	≥5 cm
Gentry_Pipeline	≥5 cm
Gentry_Pugu	≥5 cm
Gentry_Ranchoqu	≥5 cm
Gentry_Rioheath	≥5 cm
Gentry_Riomanso	≥5 cm
Gentry_Riopal1	≥5 cm
Gentry_Riopal2	≥5 cm
Gentry_Riotavar	≥5 cm
Gentry_Sansebas	≥5 cm
Gentry_Saul	≥5 cm
Gentry_Shiringa	≥5 cm
Gentry_Sucusari	≥5 cm
Gentry_Tahuampa	≥5 cm
Gentry_Tamblat2	≥5 cm
Gentry_Tambo	≥5 cm
Gentry_Tamboall	≥5 cm
Gentry_Tambupl	≥5 cm
Gentry_Tutunend	≥5 cm
Gentry_Yanam1	≥5 cm
Gentry_Yanam2	≥5 cm
Gentry_Yanamtah	≥5 cm
Salomão et al. 2007	≥5cm
Sheil et al. 2000	≥10cm
Silva et al. 2008	≥20cm
Stropp et al. 2011	≥10cm
TEAM_Bwindi	≥10 cm
TEAM_Caxiuanã	≥10 cm
TEAM_Korup	≥10 cm

TEAM_Manaus	≥10 cm
TEAM_Ranomafana	≥10 cm
TEAM_Udzungwa	≥10 cm
TEAM_Volcán Barva	≥10 cm
ter Steege et al. 2007	≥10cm
van Gemergen et al. 2003	≥10cm
Webb & Peralta 1998	≥10cm

Appendix 2. Analyses of the influence of data source on phylogenetic structure patterns.

Considering that our data came from different sources with different sampling sizes and inclusion criteria (minimum stem diameter), we tested for the influence of data source on net relatedness index (NRI), our measure of phylogenetic structure. Among the data sources used, the sites sampled by Alwyn Gentry had the smallest sampling size, with each site having one transect with 0.1 ha. TEAM Network's sites in turn had 5 to 9 ha sampled, while the surveys from the literature had variable sampling effort (but mostly 1 ha). See Table A1 in Supplementary material Appendix 1. Thus, one could wonder about the effect of small sampling effort in Gentry's sites over NRI.

In order to test for this possible sampling effect, we compared NRI values between data sources. For this, we used a two-way ANOVA, in which the factors were Source (Gentry vs. TEAM vs. Literature) and Andes (sites in the Andes vs. sites in other regions). Since the design was unbalanced, we used an ANOVA with randomization tests (Pillar and Orlóci 1996) to test for significance of the contrasts between groups of each factor. Analyses were performed using the software MULTIV v. 3.1 by V. Pillar (available at http://ecoqua.ecologia.ufrgs.br/software.html).

Gentry's sites had lower NRI values than TEAM's sites and surveys from the literature (Table A2; Fig. A1). Moreover, Andes sites had lower NRI values than other sites (Table A2; Fig. A2).

Given that all data on Andean sites came from Gentry's database, we were not able to decouple the effect of data source from biogeographic causation using only the data from Andean sites. Thus, we compared NRI values between Gentry's non-Andean sites and non-Andean sites from other data sources. If Gentry's sites are not biased toward low NRI values, then there should be no difference in NRI between Gentry's non-Andean sites and all other non-Andean sites.

Indeed, there were no significant differences in NRI between non-Andean sites from different data sources (Table A3; Fig. A3). Hence, Gentry's sites in general presented lower NRI values than other data sources probably because of Andes, which typically had low NRI values (see Results in the main text). Therefore, we conclude that Gentry's sites are unbiased and can be used together with TEAM Network’s sites and the surveys from the literature in the analyses.

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Table A2. Results of the two-way ANOVA with randomization tests, comparing NRI values between Andean and non-Andean sites and between sites from different data sources.

Source of variation	Sum of squares (*Q*)	$P(Qb_{null} \geq Qb)$
Factor Andes		
Andean sites vs. other sites	40.721	0.002
Factor Source		
Between groups	30.391	0.034
Contrasts:		
Gentry vs. Literature	17.188	0.048
Gentry vs. TEAM	16.656	0.036
Literature vs. TEAM	0.61308	0.672
Andes vs. Source *	-18.8	0.973
Between groups	52.312	0.001
Within groups	158.17	
Total	210.48	

*Note that the interaction between Andes and Source does not contain all the combinations of levels, because all Andean sites came from Gentry's database.

Table A3. Results of the one-way ANOVA with randomization tests, comparing NRI values between non-Andean sites from different data sources.

Source of variation	Sum of squares (Q)	$P(Qb_{null} \geq Qb)$
Factor Source		
Between groups	11.591	0.084
Contrasts		
Gentry vs. Literature	5.9116	0.096
Gentry vs. TEAM	7.7806	0.061
Literature vs. TEAM	0.61308	0.669
Within groups	129.01	
Total	140.6	

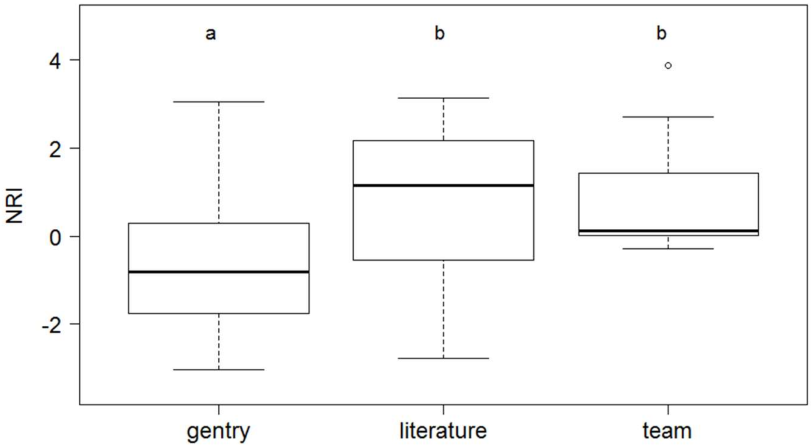

Figure A1. Comparison of NRI values between different sources of data: Gentry's transects, surveys from the literature, and TEAM Network's plots. Different letter above boxes mean significant differences between data sources (*P* < 0.05).

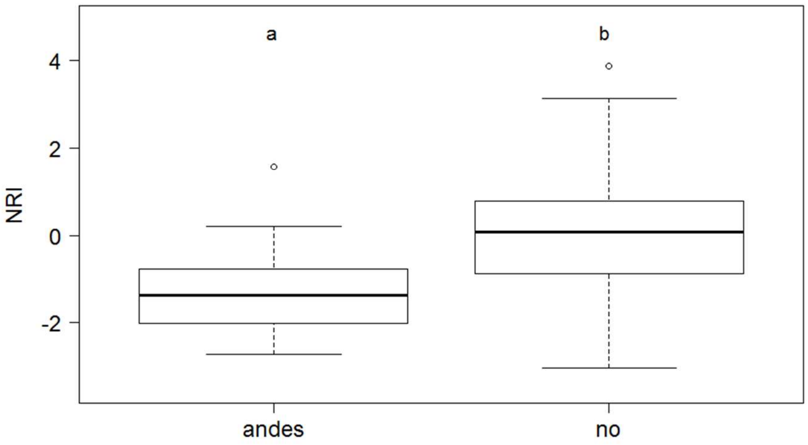

Figure A2. Comparison of NRI values between groups of sites in Andes and in other regions. Different letter above boxes mean significant differences between data sources ($P < 0.05$).

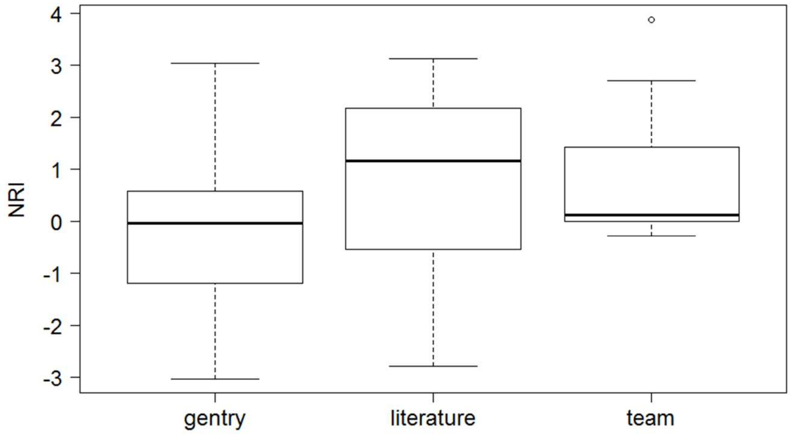

Figure A3. Comparison of NRI values between non-Andean sites from different data sources. NRI did not differ between groups.

Appendix 3. Figure of the phylogenetic tree.

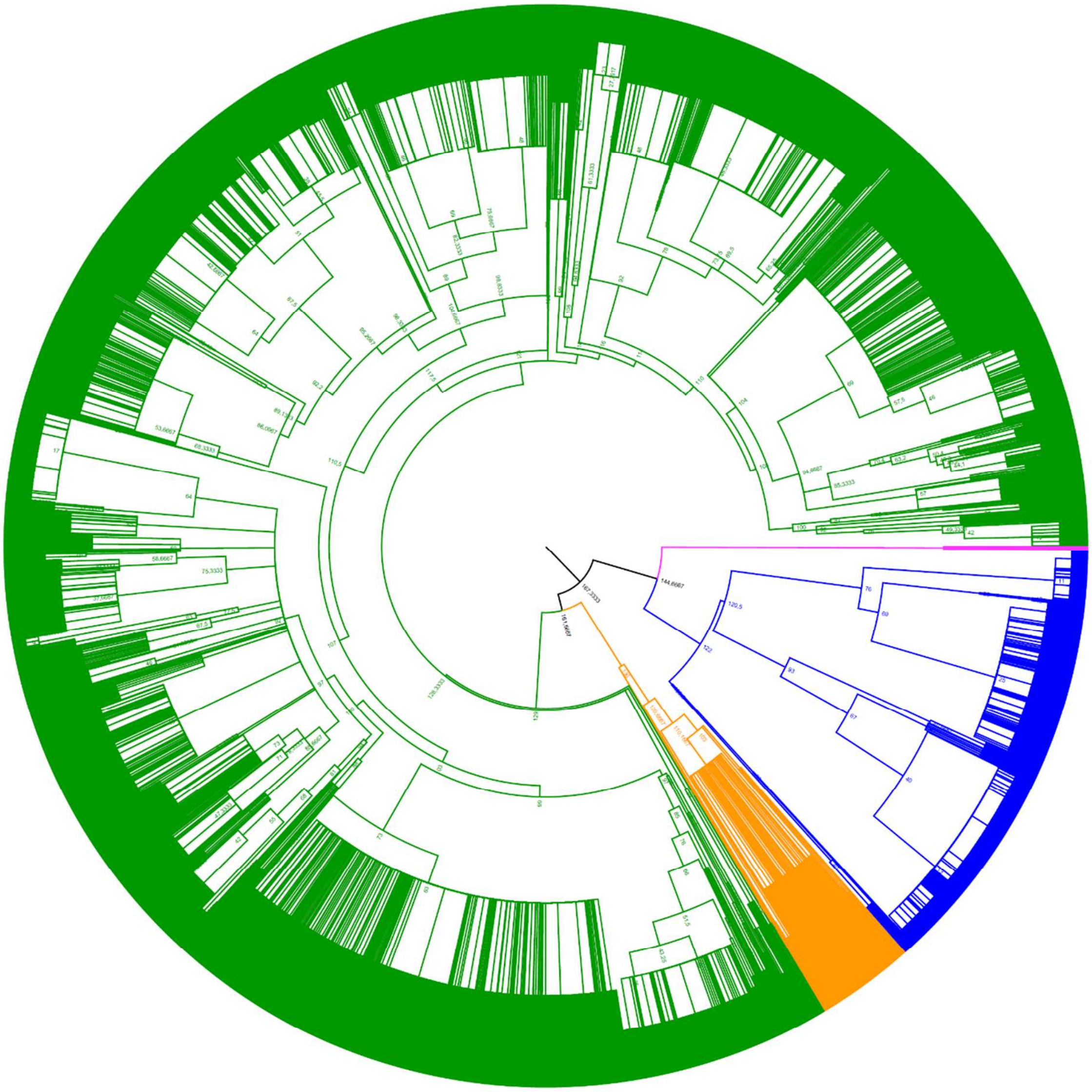

Figure A4. Phylogenetic tree for 6,056 rainforest tree species occurring in 115 Neotropical, Afrotropical and Malagasy communities (including the 94 with species abundance data and 21 with only species occurrence data). Pink, Chloranthales; Blue, magnoliids; orange, monocots; Green, eudicots.

Appendix 4. Correlation between PCPS (principal coordinates of phylogenetic structure) and NRI (net relatedness index).

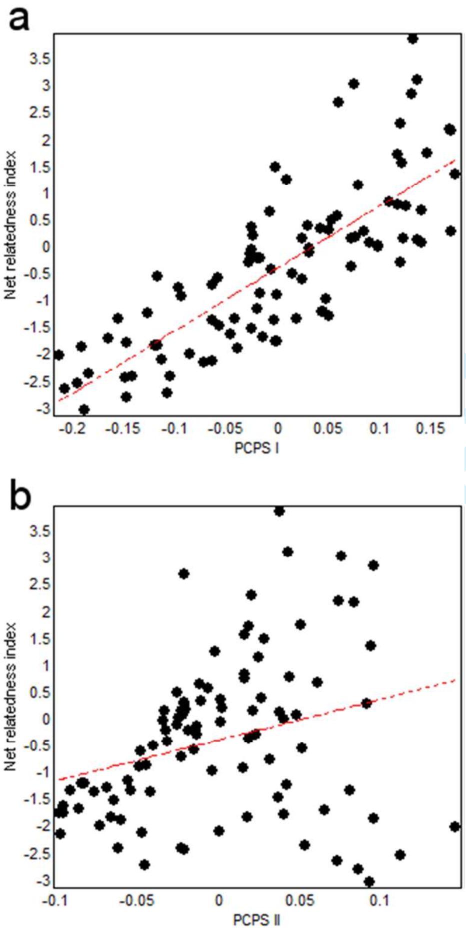

Figure A5. Scatter plot between phylogenetic composition and local phylogenetic structure of tropical rainforest tree communities (n= 94), measured using PCPS and NRI, respectively. Pearson's correlation was significant for the comparisons of NRI with both main phylogenetic composition vectors: (a) PCPS I *vs*. NRI, $r = 0.791$, $F_{30.2} = 50.35$, $P < .001$; (b) PCPS II *vs*. NRI, $r = 0.28$, $F_{52.1} = 4.42$, $P = 0.04$. Correlation statistics and significance were obtained after accounting for the influence of spatial autocorrelation on the number of degrees of freedom by using Dutilleul's correction (Dutilleul 1993).

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