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BIODIVERSITY RESEARCH

Phylogenetic diversity of Amazonian tree communities

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ABSTRACT

Aim To examine variation in the phylogenetic diversity (PD) of tree communities across geographical and environmental gradients in Amazonia.

Location Two hundred and eighty-three *c.* 1 ha forest inventory plots from across Amazonia.

Methods We evaluated PD as the total phylogenetic branch length across species in each plot (PDss), the mean pairwise phylogenetic distance between species (MPD), the mean nearest taxon distance (MNTD) and their equivalents standardized for species richness (ses.PDss, ses.MPD, ses.MNTD). We compared PD of tree communities growing (1) on substrates of varying geological age; and (2) in environments with varying ecophysiological barriers to growth and survival.

Results PDss is strongly positively correlated with species richness (SR), whereas MNTD has a negative correlation. Communities on geologically young- and intermediate-aged substrates (western and central Amazonia respectively) have the highest SR, and therefore the highest PDss and the lowest MNTD. We find that the youngest and oldest substrates (the latter on the Brazilian and Guiana Shields) have the highest ses.PDss and ses.MNTD. MPD and ses.MPD are strongly correlated with how evenly taxa are distributed among the three principal angiosperm clades and are both highest in western Amazonia. Meanwhile, seasonally dry tropical forest (SDTF) and forests on white sands have low PD, as evaluated by any metric.

Main conclusions High ses.PDss and ses.MNTD reflect greater lineage diversity in communities. We suggest that high ses.PDss and ses.MNTD in western

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Amazonia results from its favourable, easy-to-colonize environment, whereas high values in the Brazilian and Guianan Shields may be due to accumulation of lineages over a longer period of time. White-sand forests and SDTF are dominated by close relatives from fewer lineages, perhaps reflecting ecophysiological barriers that are difficult to surmount evolutionarily. Because MPD and ses.MPD do not reflect lineage diversity *per se*, we suggest that PDss, ses.PDss and ses.MNTD may be the most useful diversity metrics for setting large-scale conservation priorities.

Keywords

Amazon basin, Eudicots, Magnoliids, Monocots, phylogenetic diversity, species richness.

INTRODUCTION

A central task of biology is to quantify biodiversity and how it varies geographically (Myers *et al.*, 2000). Elucidating and understanding the patterns of diversity is particularly important within the tropics, because of their high species richness and the pressing need to develop and apply effective conservation strategies in the face of massive habitat alteration. While the species diversity of specific areas can be measured using different indices (e.g. species richness, Fisher's alpha), these ecological metrics may fail to account for the evolutionary, or lineage, diversity of communities. As a result, some authors have advocated developing and implementing metrics, such as phylogenetic diversity, which quantify the lineage diversity of communities (Vane-Wright *et al.*, 1991; Faith, 1992).

Phylogenetic diversity (PD) is generally estimated as the total branch length of a phylogeny representing the species in a community (PDss; Faith, 1992). Alternative metrics to represent the evolutionary diversity in communities are available, such as the mean phylogenetic distance between all species and the mean phylogenetic distance between each species and its closest relative (MPD and MNTD respectively; Webb *et al.*, 2002; Helmus *et al.*, 2007; Cadotte *et al.*, 2010). All these metrics are often correlated with species richness (SR; the total number of species in a community), and thus SR can sometimes be used as a proxy for PD (Polasky *et al.*, 2001; Rodrigues & Gaston, 2002). However, some areas contain significantly greater or less PD than expected given their SR (Sechrest *et al.*, 2002; Forest *et al.*, 2007), and null model approaches have been developed to estimate PD while controlling for variation in SR (Kembel *et al.*, 2010). These standardized metrics may add complementary information about the evolutionary history and conservation significance of sites (Winter *et al.*, 2013). The availability of these recently developed PD metrics, in conjunction with the advent of standardized floristic sampling across Amazonia (Malhi *et al.*, 2002; Phillips & Miller, 2002) and a robust angiosperm phylogeny (Bremer *et al.*, 2009), now make it possible to examine how PD varies at large spatial scales across the world's most species-rich forest (Gentry, 1988; ter Steege *et al.*, 2013; see also Chave *et al.*, 2007).

Previous research has shown tree species diversity in 1 ha plots across the Amazon to be highest in its western and central regions and lowest in the east, on the Guianan and Brazilian shields (ter Steege *et al.*, 2003). Because PD is correlated with SR, we would expect that PD is greatest in the western and central Amazon, but this has yet to be thoroughly tested (although see Chave *et al.*, 2007). In addition, numerous factors may drive spatial variation in PD and whether communities show greater or less PD than expected given their SR. For example based on variation in substrate age, one might hypothesize that tree communities on the Guiana and Brazilian Shields, which overlay substrates of ancient Pre-Cambrian origin (Quesada *et al.*, 2011), might have higher PD than expected given their relatively low SR. This high PD would reflect accumulated lineage diversity over tens of millions of years, with many deep phylogenetic branches separating species from these older diversification events (Swenson, 2009). In contrast, tree communities of western Amazonia overlying Pliocene and Pleistocene sediments from the Andes (Hoorn *et al.*, 2010; Quesada *et al.*, 2011) might be expected to show lower PD than expected given their high SR because of the dominance of recent evolutionary radiations of certain clades within which phylogenetic branches are short (Richardson *et al.*, 2001; Erkens *et al.*, 2007).

Soil fertility and precipitation seasonality also vary across Amazonia. Overall, the relatively young soils of western Amazonia are fertile in comparison with the highly weathered soils of central and eastern Amazonia and the Guianan and Brazilian Shields, whereas the poorest soils are found beneath white-sand forests that occur sporadically in small to large patches throughout the northern part of the basin (Quesada *et al.*, 2011). In addition, the dry season varies from being essentially absent in the north-west to lasting 5–6 months in the south-east and some northern areas (Sombroek, 2001), where moist forests give way to savannas and seasonally dry tropical forest (SDTF). Some of these environmental conditions may represent ecophysiological barriers that few lineages have been able to overcome (Anacker & Harrison, 2012; Miller *et al.*, 2013). Thus, an additional hypothesis to the one above, based on substrate age, is that tree communities in areas of the Amazon with greater ecophysiological barriers to growth (i.e. potentially more stressful environments) will show the lowest phylogenetic diversity (Qian *et al.*, 2013).

We used a network of 283 forest inventory plots (RAINFOR; Malhi *et al.*, 2002) to quantify the PD of tree communities and examine its spatial and environmental variation across Amazonia. We rarefied all plots to the same number of individuals, and then calculated (1) the total phylogenetic branch length of all species occurring in each plot, PD *sensu stricto* (PDss; Faith, 1992), (2) the mean pairwise phylogenetic distance between species (MPD; Webb, 2000; Webb *et al.*, 2002), and (3) the mean nearest taxon distance (MNTD; Webb, 2000). We also calculated standardized versions of these metrics that account for variation in SR. We then tested the hypothesis, based on substrate age, that tree communities in the Guiana and Brazilian Shields will show the greatest PD, whereas those in the western Amazon will show lower PD. And while our sample size outside of typical terra firme and floodplain moist forest is limited, we conducted a preliminary test of the hypothesis that tree communities in potentially more stressful environments, namely white sands, savannas, and SDTFs, will show the lowest PD. By examining the phylogenetic diversity of tree communities throughout Amazonia, we aim to provide insights into its biogeographical history and to inform the setting of conservation priorities.

METHODS

Tree community plot data

In this study, we used a total of 283 inventory plots of the RAINFOR forest plot network curated at ForestPlots.net (see Table S1 in Supporting Information). Plots are generally one hectare in size (mean ± SD = 1.1 ± 0.6 ha) and with all trees ≥ 10 cm diameter at breast height (DBH) sampled. We restricted analyses to old-growth forest plots and excluded plots with limited species identifications. Each plot was treated as a community and classified into three main biomes (Fig. 1): tropical moist forest, TMF (n = 265 plots), seasonally dry tropical forest, SDTF (n = 13), and savanna, S (n = 5). Fourteen plots were from the northern Andes (Colombia and Venezuela), outside the Amazon basin, but were included because of their close phytogeographical connection to Amazonia. SDTF plots are located from Bolivia to Venezuela, whereas savanna plots are only from Brazil and are separated by a maximum of 250 km.

The 265 tropical moist forest plots were further classified by the maximum age of the underlying geological formation. The Guiana and Brazilian Shields represent the oldest geological formations in Amazonia (TMF.o: > 500 Ma), followed by formations of central and eastern Amazonia (TMF.i: 20–100 Ma) located between the Shields, whereas areas near to the Andes (western Amazonia and northern Andes) are dominated by younger sediments (TMF.y: < 20 Ma; Quesada *et al.*, 2011) deposited mainly during the Pliocene and the Pleistocene (Hoorn *et al.*, 2010) (Fig. 1). All TMF plots were also classified by forest type: montane forest, flooded forest, terra firme forest, and white-sand forest. Terra firme and flooded forests were sampled for each substrate age category, whereas montane forests were only sampled in western Amazonia on young substrates and white-sand forests were not sampled on substrates of intermediate age (see Table S1).

In total, the initial dataset included 183,908 individual trees sampled in Bolivia, Brazil, Colombia, Ecuador, French Guiana, Guyana, Peru, Surinam and Venezuela. To ensure a standardized nomenclature across plots based on the APG-III classification (Bremer *et al.*, 2009), the Taxonomic Name Resolution Service version 3.0 was used (http://tnrs.iplantcollaborative.org; accessed on 01/03/2013). Tree ferns and gymnosperms only occur in significant numbers in montane plots, and they are exceedingly rare in lowland forest, which is the focus of this study. These very rare species represent 0.018% of all individual trees in our lowland plots and are essentially stochastically sampled in any given 1 ha plot (tree ferns and gymnosperms were found in a total of nine and two lowland plots respectively). Given this stochasticity and the strong effect of tree ferns and gymnosperms on phylogenetic diversity metrics (they are subtended by very long phylogenetic branches; Faith *et al.*, 2004; Kembel & Hubbell, 2006; Chave *et al.*, 2007), we excluded them from phylogenetic diversity calculations. We also excluded all individuals not identified to a named species (13.6% of individuals). To determine if unidentified individuals could be biasing results, we assessed the correlation between the PD metrics and the proportion of unidentified individuals in each plot.

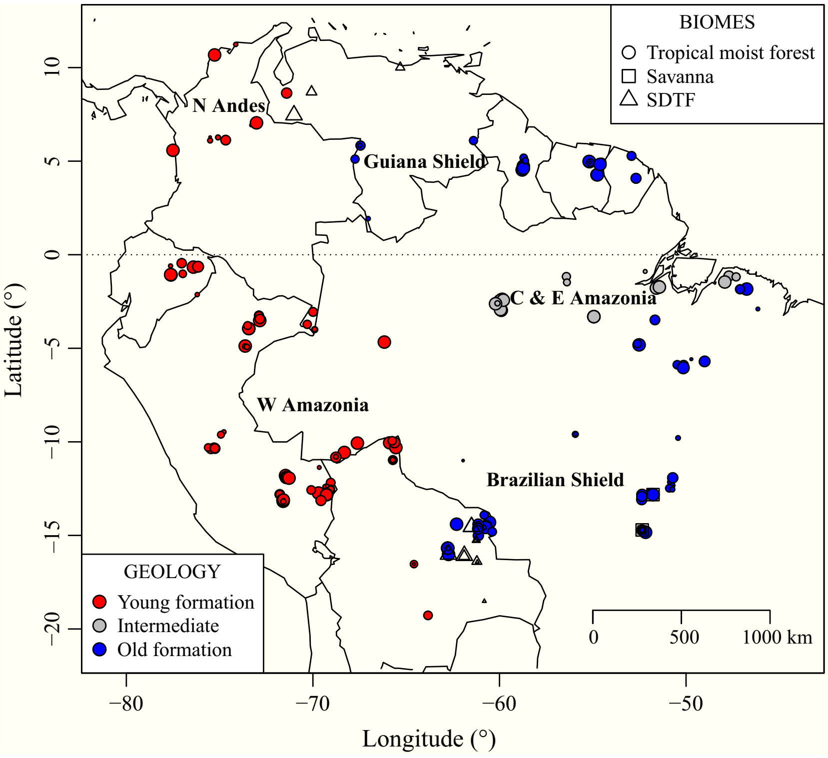

Figure 1 Location of 283 permanent RAINFOR plots classified by geological formation and biome in South America. Circle size represents species richness per plot (9 to 99 species for 249 rarefied individuals). Geographical regions used in the text are indicated in bold.

The final dataset contained a total of 157,340 individuals, belonging to 3868 species, 732 genera and 126 families of angiosperms.

Phylogenetic trees

A phylogenetic tree of the whole species pool (see Fig. S1) was generated using Phylomatic in PHYLOCOM version 4.2 (Webb *et al.*, 2008). This tool provides a phylogenetic hypothesis for the relationships among taxa by matching the list of species with up-to-date family and genus names, and tip labels of a provided megatree (Webb & Donoghue, 2005). In this case, the topology of R20120829.new provided at http://phylodiversity.net/phylomatic/ was used. An ultrametric phylogeny including branch length in millions of years (Ma) was obtained using bladj in PHYLOCOM. This command fixes the root node (angiosperms, 179 Ma) and other nodes to specified ages based on Wikström *et al.* (2001). Inconsistencies in syntax between internal node labels of the phylogeny and the ages file were modified manually to ensure a better performance of the node calibration using bladj (Gastauer & Meira-Neto, 2013). To determine if PD metrics are affected by phylogenetic resolution, we compared our results generated using the PHYLOCOM phylogeny with those using a phylogeny of Amazonian tree genera generated from DNA sequences of *rbc*L and *mat*K plastid genes (K. G. Dexter & J. Chave, unpublished data). Full details of the temporally-calibrated, ultrametric phylogeny construction can be found in the Supporting information.

Phylogenetic diversity metrics

We used the PHYLOCOM phylogeny, which includes all genera in our dataset, to calculate six metrics that evaluate the evolutionary history present in communities: (1) the total phylogenetic branch length of all species occurring in a given community, i.e. phylogenetic diversity *sensu stricto* (PDss; Faith, 1992); (2) mean pairwise phylogenetic distance between species in terms of branch length (MPD; Webb, 2000; Webb *et al.*, 2002); (3) mean nearest taxon distance (MNTD; Webb, 2000; Webb *et al.*, 2002) and (4, 5 & 6) their equivalents, standardized for species richness (ses.PDss, ses.MPD, and ses.MNTD). For each community, these standardizations were accomplished by randomly drawing the same number of species from the phylogeny as present in the community, repeating this 1000 times, calculating PDss, MPD and MNTD for each randomization, taking the difference between the observed value of PDss, MPD, and MNTD and the mean of the random values, and dividing these differences by the standard deviation across the randomizations. These derived metrics therefore represent standardized effect sizes (ses) and are designated as such ses.MPD and ses.MNTD are equivalent to the inverse of the NRI and NTI indices of Webb (2000). We consider the total phylogenetic branch length (PDss) in communities (Faith, 1992; Forest *et al.*, 2007) and its deviation from expectation given species richness (ses.PDss) to be the most straightforward measures of evolutionary diversity in communities with respect to conservation prioritization. Lastly, we included the MPD, MNTD, ses.MPD, and ses.MNTD metrics of PD because of their history of use in the literature (e.g. Forest *et al.*, 2007; Gonzalez *et al.*, 2010; Fine & Kembel, 2011); MPD measures phylogenetic structure at deep nodes and MNTD at shallow nodes (Webb, 2000).

Data assessment and analysis

To minimize the effects of variation in sampling effort (i.e. plot size) and tree density, we used a rarefaction procedure that standardized all plots to 249 individuals, which was the lowest observed number of individual trees (≥ 10 cm DBH) among all plots. Values for PDss, MPD, MNTD, ses.PDss, ses.MPD, ses.MNTD and SR (the total number of species) for each rarefied community were calculated using the package *picante* (Kembel *et al.*, 2010) in the R STATISTICAL SOFTWARE version 2.15.1. PD metrics can also be sensitive to the most basal clades in a phylogeny (Swenson, 2009), so we classified taxa into one of the three major angiosperm clades (Magnoliids including Chloranthales, Monocots, and Eudicots), and the percentage of species in each clade was calculated. The mean across 100 rarefactions of the PD metrics, SR, and the proportion of major clades were used in subsequent analyses.

The values of PDss, MPD, MNTD, ses.PDss, ses.MPD and ses.MNTD were compared among communities growing on substrates of different geologic ages and forest types using *F*-tests and Tukey tests. We additionally compared all communities in potentially more stressful environments (white-sand forests, savannas and SDTF) vs. all in potentially less stressful environments (terra firme and montane forests) using a *t* test. Flooded forests were excluded from the analysis of stressful habitats because intensity and length of flooding is known to vary among plots, but we lack precise information on this. We also assessed the correlation of PD metrics with SR, the proportions of species in major clades, and the latitude and longitude of plots.

We assessed if there was any bias to the phylogenetic diversity metrics with respect to unidentified individuals by examining the correlation between percentage of unidentified individuals in plots and the various PD metrics. We also re-analysed a subset of the data (n = 117 plots each with >500 trees), rarefying the plots to 500 individuals per sampling unit, in order to test the effect of sample size in the rarefaction procedure on estimating phylogenetic diversity. Finally, we re-analysed a subset of the data (n = 257 plots), including plots that have more than 80% of species and individuals sampled in the sequenced-based genus-level phylogeny, in order to test the effect of phylogenetic resolution on estimating phylogenetic diversity. The random resolution of species-level relationships within genera in the genus-level phylogeny was repeated for each set of rarefied communities.

RESULTS

Species richness and major angiosperm clades

Terra firme moist forests of intermediate and young geological formations have the highest species richness (SR), with an average of 88 and 72 species respectively (for 249 rarefied individuals; Table 1). Flooded moist forest communities in western and central Amazonia had greater SR than flooded and terra firme forests on the Guiana and Brazilian Shields, whereas the lowest SR was found in white-sand forests of the Guiana Shield and Andean montane forests (Table 1). SDTF and savannas show intermediate values of SR, resembling values of forest types on old geological formations.

On average, 85.8% of species per plot belong to Eudicots, 11.1% to Magnoliids and 3.1% to Monocots. Early diverging clades such as Magnoliids and Monocots tend to have a higher percentage of species on young geological formations than on intermediate and old formations, whereas Eudicots show the opposite pattern (Table 1). SDTF shows the lowest percentage of Magnoliid and Monocot species, and the greatest of Eudicots, but the abundance of these clades in savannas is more similar to the values typical of the moist forest plots.

Phylogenetic diversity metrics

Species richness strongly correlates with PDss ($r = 0.98$, $P < 0.001$; Fig. 2a) and MNTD ($r = -0.89$, $P < 0.001$; Fig. 2c), following a power relationship ($\text{PDss} = 230.6{*}\text{SR}^{0.7}$, $r^2 = 0.96$; $\text{MNTD} = 361.3{*}\text{SR}^{-0.4}$, $r^2 = 0.79$, both $P < 0.001$), which was a better fit than a linear relationship for both metrics ($\text{PDss} = 1160.0 + 37.1{*}\text{SR}$, $r^2 = 0.92$; $\text{MNTD} = 121.0–0.6{*}\text{SR}$, $r^2 = 0.71$, both $P < 0.001$). A much weaker correlation was observed between species richness and MPD ($r = 0.38$, $P < 0.001$; see Fig. S2). In contrast, the percentage of species in Magnoliids + Monocots (i.e. = 1−Eudicots) correlates strongly with MPD ($r = 0.88$, $P < 0.001$; Fig. 2b), which is driven mostly by variation in the relative abundance of Magnoliids ($r = 0.88$, $P < 0.001$) rather than Monocots ($r = 0.27$, $P < 0.001$). These correlations reflect the fact that communities with more Magnoliids and Monocots have a more even distribution of species across the three major angiosperm clades (see Fig. S3); a perfectly even split (1/3 in each clade) would give the highest value for MPD. The correlations of the percentages of species in major clades with PDss ($r_{1-\text{Eudicots}} = 0.52$, $r_{\text{Magnoliids}} = 0.48$, $r_{\text{Monocots}} = 0.26$, all $P < 0.001$) and MNTD ($r_{1-\text{Eudicots}} = 0.39$, $r_{\text{Magnoliids}} = 0.40$, $r_{\text{Monocots}} = 0.10$, all $P < 0.001$) were weaker (see Fig. S2). Both MPD and MNTD were strongly correlated with their standardized equivalents (MPD and ses.MPD: $r = 0.94$,

Table 1 Community composition and diversity across forest types, showing proportional representation of major clades and mean values of species richness (SR) and phylogenetic diversity. Phylogenetic diversity *sensu stricto* (PDss), mean pairwise phylogenetic distance between species (MPD) and mean nearest taxon distance (MNTD) are given in millions of years (Ma), whereas ses.PDss, ses.MPD and ses.MNTD are standardized metrics without units

Biome (max. geological age)	Forest type	No. of plots	Sample area (ha)	ID to spp (%)*	Species (mean, %) Magnoliids	Monocots	Eudicots	Mean diversity values SR	PDss (Ma)	MPD (Ma)	MNTD (Ma)	ses. PDss	ses. MPD	ses. MNTD
Tropical moist forest (< 20 Ma)	Flooded	12	17	86	16	6	78	72	3963	260	74	−1.24	0.48	−0.99
	Montane	16	16	80	12	1	87	29	2180	255	105	−0.41	0.03	−0.47
	Terra firme	86	95	85	14	5	81	78	4148	256	74	−1.42	0.15	−1.10
	White sand	4	4	83	10	5	85	42	2839	254	106	0.06	−0.12	−0.07
Tropical moist forest (20–100 Ma)	Flooded	2	2	73	9	0	90	72	3478	242	62	−3.44	−1.59	−2.69
	Terra firme	39	54	85	12	1	87	88	4200	248	64	−2.86	−0.90	−2.11
Tropical moist forest (> 500 Ma)	Flooded	17	16	89	5	2	93	34	2368	238	111	−0.59	−1.22	−0.23
	Terra firme	85	94	87	10	3	87	56	3310	247	85	−1.07	−0.91	−0.79
	White sand	4	4	87	7	0	93	22	1608	233	97	−1.90	−1.41	−1.53
Savanna	Savanna	5	4	100	5	2	93	47	3105	239	88	−0.28	−1.56	−0.63
SDTF	Dry forest	13	14	96	2	3	95	34	2195	224	89	−2.12	−2.42	−1.30
Total		283	320	86	11	3	86	63	3510	249	81	−1.41	−0.57	−1.06

*The mean proportion of individuals identified to species.

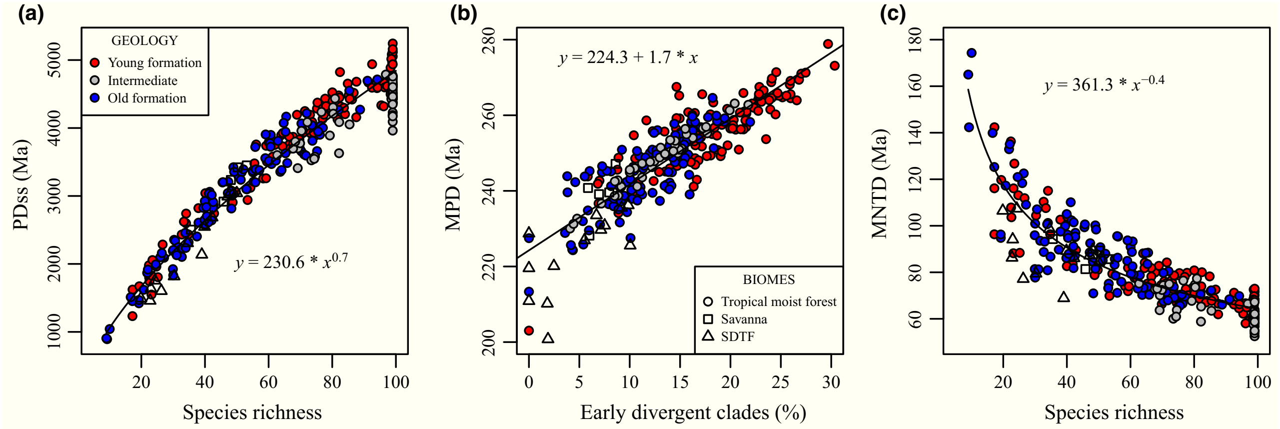

Figure 2 Relationship between (a) phylogenetic diversity *sensu stricto* and species richness, between (b) mean pairwise phylogenetic distance between species and the proportion of species of Magnoliids and Monocots (= 1−Eudicots), and between c) mean nearest taxon distance and species richness. Tropical moist forest biome is classified based on maximum age of geological formations (young: < 20 Ma; intermediate: 20–100 Ma, old: > 500 Ma; Quesada *et al.*, 2011).

$P < 0.001$; MNTD and ses.MNTD: $r = 0.71$, $P < 0.01$; see Fig. S2), and show similar results with respect to the plot groupings we considered (e.g. substrate age, forest type). We therefore present results for only ses.MPD and ses.MNTD below. Interestingly, ses.PDss and ses.MNTD are strongly positively correlated with each other ($r = 0.95$, $P < 0.001$; see Fig. S2), whereas neither shows a strong relationship with ses.MPD (ses.PDss and ses.MPD: $r = 0.23$, $P < 0.001$; ses.MNTD and ses.MPD: $r = 0.09$, $P = 0.14$; see Fig. S2).

Geographical and environmental patterns

All of the PD metrics show non-random spatial distributions across Amazonia (Fig. 3a–d). While PDss shows weak relationships with both latitude and longitude ($r_{\mathrm{Latitude}} = 0.14$, $P < 0.05$; $r_{\mathrm{Longitude}} = -0.16$, $P < 0.05$) and ses.PDss and ses.MNTD show weak latitudinal gradients (ses.PDss: $r_{\mathrm{Latitude}} = -0.18$, $P < 0.01$; ses.MNTD: $r_{\mathrm{Latitude}} = -0.17$, $P < 0.01$), ses.MPD shows a strong longitudinal gradient decreasing from west to east ($r_{\mathrm{Longitude}} = -0.52$, $P < 0.001$). PDss was greatest in communities on young and intermediate-aged geological formations (Fig. 3e), whereas ses.PDss and ses.MNTD were greatest in communities on young and old geological formations (Fig. 3f,h). ses.MPD was greatest in young geological formations (Fig. 3g). These spatial patterns are conserved across the different forest types within the moist forest biome (e.g. terra firme, floodplain) (see Table 1).

Among the moist forest communities, montane and white-sand forests have the lowest PDss values and high values for ses.PDss, ses.MPD and ses.MNTD, at least in western Amazonia. In contrast to this, flooded and terra firme forests in central Amazonia have high PDss and the lowest values for ses.PDss, ses.MPD and ses.MNTD (Table 1). For all metrics, PD values of savannas were similar to moist forest communities, whereas SDTF consistently showed lower PD (Fig. 3e–h). Overall, PDss and ses.MPD were significantly lower in potentially more stressful habitats, i.e. savanna, SDTF and white-sand forest (mean ± 95% confidence interval: 2379 ± 305 Ma and −1.75 ± 0.40 respectively), than potentially less stressful habitats (3702 ± 118 Ma and −0.44 ± 0.14; $t_{\mathrm{PDss}} = 8.28$, d.f. = 34, $P < 0.001$ and $t_{\mathrm{ses.MPD}} = 6.27$, d.f. = 32, $P < 0.001$), whereas ses.PDss and ses.MNTD were not significantly different between the two (ses.PDss: −1.39 ± 0.50 vs. −1.47 ± 0.17, $t_{\mathrm{ses.PDss}} = -0.28$, d.f. = 31, $P = 0.78$; and ses.MNTD: −1.02 ± 0.35 vs. −1.11 ± 0.13, $t_{\mathrm{ses.MNTD}} = -0.51$, d.f. = 33, $P = 0.61$).

PDss ($r^2 = 0.002$, $P = 0.20$), ses.MPD ($r^2 = 0.004$, $P = 0.15$), and ses.MNTD ($r^2 = 0.007$, $P = 0.08$) showed no relationship with the percentage of unidentified individuals excluded per plot, whereas ses.PDss ($r^2 = 0.013$, $P < 0.05$) shows a very weak relationship (see Fig. S4). In addition, for plots with sufficient sample size to assess, we found a strong 1 : 1 relationship between phylogenetic diversity metrics (PDss, ses.PDss, ses.MPD, and ses.MNTD) calculated with rarefactions of 500 vs. 249 individuals (see Fig. S5). We also found that the patterns of PD metrics across Amazonia were qualitatively identical when using the sequenced-based genus-level phylogeny vs. the PHYLOCOM phylogeny (see Figs S6 & S7).

DISCUSSION

Our study has revealed a highly non-random spatial and environmental distribution of phylogenetic diversity (PD) across tree communities of Amazonia, by whichever metric it is evaluated, with some areas and environments holding significantly more, or less, phylogenetic diversity than others (Fig. 3). Phylogenetic diversity *sensu stricto* (PDss) and the mean nearest taxon distance (MNTD) in the Amazon correlate strongly with species richness (SR; Fig. 2a,c) following positive and negative trends, respectively. Therefore, diverse communities on young- and intermediate-aged substrates

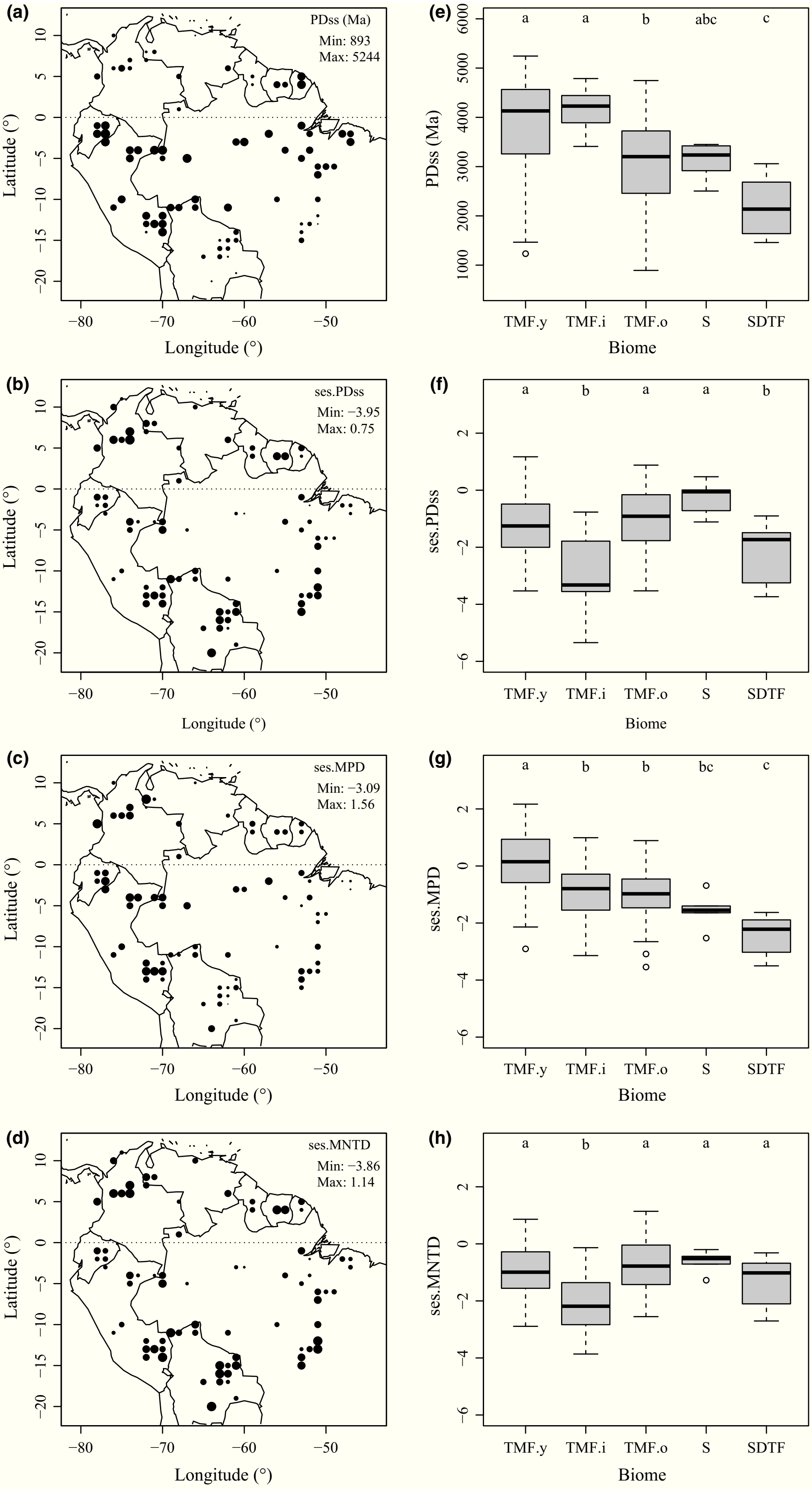
(a)
PDss (Ma)
Min: 893
Max: 5244
Latitude (°)
Longitude (°)
10
5
0
−5
−10
−15
−20
−80
−70
−60
−50
(e)
a
a
b
abc
c
PDss (Ma)
1000
2000
3000
4000
5000
6000
TMF.y
TMF.i
TMF.o
S
SDTF
Biome
(b)
ses.PDss
Min: −3.95
Max: 0.75
Latitude (°)
Longitude (°)
(f)
a
b
a
a
b
ses.PDss
2
0
−2
−4
−6
TMF.y
TMF.i
TMF.o
S
SDTF
Biome
(c)
ses.MPD
Min: −3.09
Max: 1.56
Latitude (°)
Longitude (°)
(g)
a
b
b
bc
c
ses.MPD
TMF.y
TMF.i
TMF.o
S
SDTF
Biome
(d)
ses.MNTD
Min: −3.86
Max: 1.14
Latitude (°)
Longitude (°)
(h)
a
b
a
a
a
ses.MNTD
TMF.y
TMF.i
TMF.o
S
SDTF
Biome

Figure 3 Variation in phylogenetic diversity, as evaluated by several metrics, across Amazonia. The results for phylogenetic diversity *sensu stricto* (PDss), its equivalent standardized for variation in species richness (ses.PDss), and the standardized measures of mean pairwise phylogenetic distance between species (ses.MPD) and mean nearest taxon distance (ses.MNTD) are shown in different rows. (a–d) The maps show the spatial distribution of values for each metric, with the size of circles corresponding to their values. If there were multiple plots in a given one-degree grid, the mean value is shown. (e–h) The tropical moist forest biome is classified based on maximum age of geological formations (TMF.y: < 20 Ma; TMF.i: 20–100 Ma, TMF.o: > 500 Ma), whereas savanna and seasonally dry tropical forest are indicated as S and SDTF respectively. Letters in boxplots indicate significant difference among mean values (Tukey's HSD; $P < 0.05$).

(western and central Amazonia respectively) have the highest PDss and the lowest MNTD values. Once variation in SR is controlled for, we found that the youngest and oldest substrates (the latter on the Brazilian and Guiana Shields) have the highest ses.PDss and ses.MNTD. The lowest values of ses.PDss and ses.MNTD were found in potentially more stressful environments, in particular white-sand forest and SDTF.

We also found that the mean pairwise phylogenetic distance between species (MPD) and its standardized equivalent, ses.MPD, depend primarily on how evenly taxa are distributed among the three major angiosperm clades (Magnoliids, Monocots and Eudicots), which is shown by the strong positive correlation between their values and the proportion of taxa in plots that are Magnoliids and Monocots (the two rarer clades; Fig. 2b). Thus, communities in western Amazonia, that have many Magnoliids and Monocots present, have the greatest MPD and ses.MPD values. While it is important to have a measure of how evenly distributed taxa are across the major clades of a phylogeny, MPD and ses.MPD do not seem to reflect lineage diversity *per se*. Moreover, ses.PDss and ses.MNTD were strongly positively correlated, giving similar patterns across geological substrates environments. We therefore focus below primarily on patterns with respect to PDss and ses.PDss.

Has the greatest phylogenetic diversity been accumulated in communities overlaying old geological formations?

Communities on old geological substrates in the Brazilian and Guianan Shields showed lower PDss than communities on young or intermediately aged geological substrates (Fig. 3e), which is unsurprising given their lower species richness. The communities on old geological substrates did show a higher median ses.PDss (Fig. 3f), but the distribution of ses.PDss values overlapped broadly with those for communities on the youngest substrate. The same pattern was found for ses.MNTD. Thus, our prediction that PD would be positively correlated with substrate age was falsified. However, we suggest that different processes may explain the high ses.PDss values observed in different communities across Amazonia. The high ses.PDss and ses.MNTD found in the Guiana and Brazilian Shields may very well be explained by their long-term geological history and the accumulation of lineages over many millions of years.

To understand the rejection of the hypothesis that geologically older substrates show the greatest PD, we need to consider why tree communities of western Amazonia show such high ses.PDss and ses.MNTD. That communities of western Amazonia show high PDss is unsurprising, as PDss is strongly correlated with SR, and SR is substantially higher in the western Amazon (ter Steege *et al.*, 2003). However, much of this species diversity is due to recently radiated species-rich genera (Gentry, 1982) such as *Inga* (Richardson *et al.*, 2001) and *Guatteria* (Erkens *et al.*, 2007), and short phylogenetic branches such as those within these genera do not greatly increase PD (Swenson, 2009). Moreover, low MNTD would be explained by the presence of short phylogenetic branches separating the nearest taxa in these diverse communities. However, another exceptional aspect of western Amazonian tree communities is that they are occupied by lineages from the entirety of the angiosperm phylogeny, which leads these communities to have high ses.PDss, and apparently also high ses.MNTD. One explanation might be related to the potentially high phylogenetic diversity found in the adjacent Andes, which provides a proximate resource to 'invade' western Amazonia (see also Chave *et al.*, 2007). Another explanation might be related to the particular environmental and ecological conditions (relatively fertile and aseasonal environments) in the west, which may be easier to invade by multiple lineages with diverse evolutionary backgrounds. Moreover, the ability of diverse lineages to establish in the western and southern Amazon may also be related to the high rates of disturbance and turnover in the region (Quesada *et al.*, 2012; Marimon *et al.*, 2013; Baker *et al.*, 2014). Thus, in the same way that more fertile, dynamic, and disturbed tropical forests have more open nutrient-cycles on ecological time-scales (Vitousek & Sanford, 1986), they also appear to be more open to repeated establishment of plant lineages on evolutionary time-scales.

Do environments with more potential ecophysiological barriers to growth show the lowest PD in their tree communities?

We expected that environments with potentially more stressful ecological conditions, namely marked seasonality of precipitation and/or low soil fertility, would have the lowest phylogenetic diversity, because these may represent ecophysiological barriers that are difficult for many lineages to surmount evolutionarily (Anacker & Harrison, 2012; Miller *et al.*, 2013; Qian *et al.*, 2013). Both savannas and SDTF have a pronounced dry season, but they show contrasting patterns of PD. While PD metrics of savannas were similar to those of nearby communities in tropical moist forest, SDTF generally has low PD (Fig. 3e–h). Savannas and tropical moist forest communities may share similar lineages across the angiosperm phylogeny, a pattern which supports previous studies that suggested that Brazilian savannas are formed by the numerous independent colonizations of lineages from nearby biomes around 4–10 Ma (Simon *et al.*, 2009; Simon & Pennington, 2012). Conversely, the low PD values shown for SDTF communities suggest that fewer clades have succeeded in colonizing SDTF, and that consequently, SDTF is occupied by closer relatives. However, our conclusions must be taken as preliminary given the low sample size and limited geographical extent of our savanna and SDTF plots.

Previous studies have indicated strong habitat specialization in white-sand communities as indicated by the high number of individuals that represent white-sand specialist species (Fine *et al.*, 2010), and by the distinct ecophysiology and defences against herbivores that these species have evolved in order to live on such poor soils (Fine *et al.*, 2004). Therefore, we also expected that white-sand forests would have a high frequency of closely related species and low phylogenetic diversity. But while our results showed that both white-sand communities of the Guiana Shield and the western Amazon have low PDss, only those communities in the Guyana Shield have low ses.PDss values compared to neighbouring terra firme or flooded forest. We found higher values of ses.PDss in the small patches of white-sand forests of western Amazonia than in the Guiana Shield, suggesting a greater influence of the regional pool (i.e. species present in the surrounding phylogenetically diverse terra firme forest entering white-sand patches) than in the larger, more contiguous white-sand patches of the Guiana Shield.

Conservation priorities

Conservation planning based upon species richness (SR) gives the same value to communities with equal SR regardless of the total phylogenetic diversity of the species that they contain (e.g. Forest *et al.*, 2007). But if we are to preserve the full spectrum of lineage diversity and the evolutionary processes that led to the exceptional biodiversity of Amazonian communities, regional conservation planning must incorporate phylogenetic information.

In this study, we showed that while PDss is strongly correlated with SR (see also Forest *et al.*, 2007; Cadotte *et al.*, 2012), communities can vary greatly in their deviation from expected PD given SR, as measured by ses.PDss. While communities in the central and western Amazon have the greatest tree species richness in the basin (ter Steege *et al.*, 2003), the central Amazon shows much lower phylogenetic diversity than expected given its species richness (ses.PDss) compared to the western Amazon (Fig. 3e), thus suggesting that the western Amazon basin may hold a higher value for conservation of lineage diversity.

In addition, we found that the mean pairwise phylogenetic distance between species (MPD) is not strongly correlated with species richness, which could suggest that it is a better metric of phylogenetic diversity than PDss. However, we found that MPD and its standardized equivalent (ses.MPD) are strongly dependent on how evenly divided the species in a tree community are among the three major angiosperm clades (Magnoliids, Monocots and Eudicots; Fig. 2b). While this division is certainly interesting from an ecological and evolutionary perspective, we suggest that MPD and ses.MPD may not be the most useful metrics of phylogenetic diversity for conservation prioritization. Meanwhile, MNTD shows a strong inverse relationship with SR, and ses.MNTD essentially conveys the same information as ses.PDss (i.e. they are strongly positively correlated). Thus, we suggest that, PDss and ses.PDss may provide the most straightforward, interpretable means to evaluate lineage diversity in communities. While PDss is strongly correlated with SR and could perhaps be inferred from it, a phylogeny is clearly necessary to calculate ses.PDss and determine whether communities show more or less lineage diversity than expected given their species richness. An urgent priority for conservation should be to develop bigger community phylogenies that include all lineages, greater numbers of species within lineages, and greater phylogenetic resolution. Such phylogenies would allow evolutionary information to be properly incorporated into conservation decisions.

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REFERENCES

Anacker, B.L. & Harrison, S.P. (2012) Historical and ecological controls on phylogenetic diversity in Californian plant communities. *The American Naturalist*, **180**, 257–269.

Baker, T.R., Pennington, R.T., Magallon, S. *et al.* (2014) Fast demographic traits promote high diversification rates of Amazonian trees. *Ecology Letters*, **17**, 527–536.

Bremer, B., Bremer, K., Chase, M.W., Fay, M.F., Reveal, J.L., Soltis, D.E., Soltis, P.S., Stevens, P.F., Anderberg, A.A., Moore, M.J., Olmstead, R.G., Rudall, P.J., Sytsma, K.J., Tank, D.C., Wurdack, K., Xiang, J.Q.Y., Zmarzty, S. & Angiosperm Phylogeny, G. (2009) An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. *Botanical Journal of the Linnean Society*, **161**, 105–121.

Cadotte, M.W., Jonathan Davies, T., Regetz, J., Kembel, S.W., Cleland, E. & Oakley, T.H. (2010) Phylogenetic diversity metrics for ecological communities: integrating species richness, abundance and evolutionary history. *Ecology Letters*, **13**, 96–105.

Cadotte, M.W., Dinnage, R. & Tilman, D. (2012) Phylogenetic diversity promotes ecosystem stability. *Ecology*, **93**, S223–S233.

Chave, J., Chust, G. & Thebaud, C. (2007) The importance of phylogenetic structure in biodiversity studies. *Scaling biodioversity* (ed.by D. Storch, P.L. Marquet and J.H. Brown), pp. 150–167. Cambridge University Press, Cambridge, UK.

Erkens, R.H.J., Chatrou, L.W., Maas, J.W., van der Niet, T. & Savolainen, V. (2007) A rapid diversification of rainforest trees (*Guatteria*; Annonaceae) following dispersal from Central into South America. *Molecular Phylogenetics and Evolution*, **44**, 399–411.

Faith, D.P. (1992) Conservation evaluation and phylogenetic diversity. *Biological Conservation*, **61**, 1–10.

Faith, D.P., Reid, C.A.M. & Hunter, J. (2004) Integrating phylogenetic diversity, complementarity, and endemism for conservation assessment. *Conservation Biology*, **18**, 255–261.

Fine, P.V.A. & Kembel, S.W. (2011) Phylogenetic community structure and phylogenetic turnover across space and edaphic gradients in western Amazonian tree communities. *Ecography*, **34**, 552–565.

Fine, P.V.A., Mesones, I. & Coley, P.D. (2004) Herbivores promote habitat specialization by trees in Amazonian forests. *Science*, **305**, 663–665.

Fine, P.V.A., García-Villacorta, R., Pitman, N.C.A., Mesones, I. & Kembel, S.W. (2010) A floristic study of the white-sand forests of Peru. *Annals of the Missouri Botanical Garden*, **97**, 283–305.

Forest, F., Grenyer, R., Rouget, M., Davies, T.J., Cowling, R.M., Faith, D.P., Balmford, A., Manning, J.C., Proches, S., van der Bank, M., Reeves, G., Hedderson, T.A.J. & Savolainen, V. (2007) Preserving the evolutionary potential of floras in biodiversity hotspots. *Nature*, **445**, 757–760.

Gastauer, M. & Meira-Neto, J.A.A. (2013) Avoiding inaccuracies in tree calibration and phylogenetic community analysis using Phylocom 4.2. *Ecological Informatics*, **15**, 85–90.

Gentry, A.H. (1982) Neotropical floristic diversity: phytogeographical connections between Central and South-America, Pleistocene climatic fluctuations, or an accident of the Andean orogeny. *Annals of the Missouri Botanical Garden*, **69**, 557–593.

Gentry, A.H. (1988) Tree species richness of upper Amazonian forests. *Proceedings of the National Academy of Sciences USA*, **85**, 156–159.

Gonzalez, M.A., Roger, A., Courtois, E.A., Jabot, F., Norden, N., Paine, C.E.T., Baraloto, C., Thébaud, C. & Chave, J. (2010) Shifts in species and phylogenetic diversity between sapling and tree communities indicate negative density dependence in a lowland rain forest. *Journal of Ecology*, **98**, 137–146.

Helmus, M.R., Bland, T.J., Williams, C.K. & Ives, A.R. (2007) Phylogenetic measures of biodiversity. *The American Naturalist*, **169**, E68–E83.

Hoorn, C., Wesselingh, F.P., ter Steege, H., Bermudez, M.A., Mora, A., Sevink, J., Sanmartín, I., Sanchez-Meseguer, A., Anderson, C.L., Figueiredo, J.P., Jaramillo, C., Riff, D., Negri, F.R., Hooghiemstra, H., Lundberg, J., Stadler, T., Särkinen, T. & Antonelli, A. (2010) Amazonia through time: Andean uplift, climate change, landscape evolution, and biodiversity. *Science*, **330**, 927–931.

Kembel, S.W. & Hubbell, S.P. (2006) The phylogenetic structure of a Neotropical forest tree community. *Ecology*, **87**, S86–S99.

Kembel, S.W., Cowan, P.D., Helmus, M.R., Cornwell, W.K., Morlon, H., Ackerly, D.D., Blomberg, S.P. & Webb, C.O. (2010) Picante: R tools for integrating phylogenies and ecology. *Bioinformatics*, **26**, 1463–1464.

Malhi, Y., Phillips, O.L., Lloyd, J. *et al.* (2002) An international network to monitor the structure, composition and dynamics of Amazonian forests (RAINFOR). *Journal of Vegetation Science*, **13**, 439–450.

Marimon, B.S., Marimon-Junior, B.H., Feldpausch, T.R., Oliveira-Santos, C., Mews, H.A., Lopez-Gonzalez, G., Lloyd, J., Franczak, D.D., de Oliveira, E.A., Maracahipes, L., Miguel, A., Lenza, E. & Phillips, O.L. (2013) Disequilibrium and hyperdynamic tree turnover at the forest–cerrado transition zone in southern Amazonia. *Plant Ecology & Diversity*, **7**, 281–292.

Miller, E.T., Zanne, A.E. & Ricklefs, R.E. (2013) Niche conservatism constrains Australian honeyeater assemblages in stressful environments. *Ecology Letters*, **16**, 1186–1194.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B. & Kent, J. (2000) Biodiversity hotspots for conservation priorities. *Nature*, **403**, 853–858.

Phillips, O. & Miller, J. (2002) *Global patterns of plant diversity: Alwyn H. Gentry's forest transect data set*. Missouri Botanical Garden Press, St. Louis, MO.

Polasky, S., Csuti, B., Vossler, C.A. & Meyers, S.M. (2001) A comparison of taxonomic distinctness versus richness as criteria for setting conservation priorities for North American birds. *Biological Conservation*, **97**, 99–105.

Qian, H., Zhang, Y., Zhang, J. & Wang, X. (2013) Latitudinal gradients in phylogenetic relatedness of angiosperm trees in North America. *Global Ecology and Biogeography*, **22**, 1183–1191.

Quesada, C.A., Lloyd, J., Anderson, L.O., Fyllas, N.M., Schwarz, M. & Czimczik, C.I. (2011) Soils of Amazonia with particular reference to the RAINFOR sites. *Biogeosciences*, **8**, 1415–1440.

Quesada, C.A., Phillips, O.L., Schwarz, M. *et al.* (2012) Basin-wide variations in Amazon forest structure and function are mediated by both soils and climate. *Biogeosciences*, **9**, 2203–2246.

Richardson, J.E., Pennington, R.T., Pennington, T.D. & Hollingsworth, P.M. (2001) Rapid diversification of a species-rich genus of Neotropical rain forest trees. *Science*, **293**, 2242–2245.

Rodrigues, A.S.L. & Gaston, K.J. (2002) Maximising phylogenetic diversity in the selection of networks of conservation areas. *Biological Conservation*, **105**, 103–111.

Sechrest, W., Brooks, T.M., da Fonseca, G.A.B., Konstant, W.R., Mittermeier, R.A., Purvis, A., Rylands, A.B. & Gittleman, J.L. (2002) Hotspots and the conservation of evolutionary history. *Proceedings of the National Academy of Sciences USA*, **99**, 2067–2071.

Simon, M.F. & Pennington, R.T. (2012) Evidence for adaptation to fire regimes in the tropical savannas of the Brazilian cerrado. *International Journal of Plant Sciences*, **173**, 711–723.

Simon, M.F., Grether, R., de Queiroz, L.P., Skema, C., Pennington, R.T. & Hughes, C.E. (2009) Recent assembly of the Cerrado, a neotropical plant diversity hotspot, by *in situ* evolution of adaptations to fire. *Proceedings of the National Academy of Sciences USA*, **106**, 20359–20364.

Sombroek, W. (2001) Spatial and temporal patterns of Amazon rainfall: consequences for the planning of agricultural occupation and the protection of primary forests. *Ambio*, **30**, 388–396.

ter Steege, H., Pitman, N., Sabatier, D. *et al.* (2003) A spatial model of tree α-diversity and tree density for the Amazon. *Biodiversity and Conservation*, **12**, 2255–2277.

ter Steege, H., Pitman, N.C.A., Sabatier, D. *et al.* (2013) Hyperdominance in the Amazonian tree flora. *Science*, **342**, 1243092.

Swenson, N.G. (2009) Phylogenetic resolution and quantifying the phylogenetic diversity and dispersion of communities. *PLoS ONE*, **4**, e4390.

Vane-Wright, R.I., Humphries, C.J. & Williams, P.H. (1991) What to protect?—Systematics and the agony of choice. *Biological Conservation*, **55**, 235–254.

Vitousek, P.M. & Sanford, R. (1986) Nutrient cycling in moist tropical forest. *Annual Review of Ecology and Systematics*, **17**, 137–167.

Webb, C.O. (2000) Exploring the phylogenetic structure of ecological communities: an example for rain forest trees. *The American Naturalist*, **156**, 145–155.

Webb, C.O. & Donoghue, M.J. (2005) Phylomatic: tree assembly for applied phylogenetics. *Molecular Ecology Notes*, **5**, 181–183.

Webb, C.O., Ackerly, D.D., McPeek, M.A. & Donoghue, M.J. (2002) Phylogenies and community ecology. *Annual Review of Ecology and Systematics*, **33**, 475–505.

Webb, C.O., Ackerly, D.D. & Kembel, S.W. (2008) Phylocom: software for the analysis of phylogenetic community structure and trait evolution. *Bioinformatics*, **24**, 2098–2100.

Wikström, N., Savolainen, V. & Chase, M.W. (2001) Evolution of the angiosperms: calibrating the family tree. *Proceedings of the Royal Society B: Biological Sciences*, **268**, 2211–2220.

Winter, M., Devictor, V. & Schweiger, O. (2013) Phylogenetic diversity and nature conservation: where are we? *Trends in Ecology and Evolution*, **28**, 199–204.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1 Floristic tree inventories compiled from RAINFOR forest plot network.

Table S2 Fossil-based calibrations used in sequenced-based genus-level phylogeny.

Figure S1 Phylogenetic tree for the whole species pool for 283 floristic inventories compiled from RAINFOR dataset.

Figure S2 Relationships and correlation values among phylogenetic diversity metrics, species richness and the proportion of species of Magnoliids and Monocots.

Figure S3 Distributions of species across the three major angiosperm clades for tree communities with increasing values of MPD.

Figure S4 Relationships between phylogenetic diversity metrics and the percentage of unidentified individuals excluded for each plot.

Figure S5 Sensitivity analysis of phylogenetic diversity metrics for the tropical moist forest biome calculated using different number of individuals per plot.

Figure S6 Variation in phylogenetic diversity metrics across Amazonia, calculated using phylogenies resolved to genus and family level.

Figure S7 Sensitivity analysis of phylogenetic diversity metrics calculated using genus- and family-level phylogenies.

BIOSKETCH

Eurídice N. Honorio Coronado is a researcher at the Instituto de Investigaciones de la Amazonia Peruana, and her research focuses on tropical ecology. She is interested in understanding the ecological and historical processes determining tree species distribution and diversity in Amazonia. Most authors formed part of RAINFOR, an international network to understand changes in vegetation and biomass in Amazonia.

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SUPPORTING INFORMATION

Honorio Coronado *et al.* Phylogenetic diversity of Amazonian tree communities

Table S1. Floristic tree inventories (n = 283 plots) compiled from RAINFOR forest plot network (Lopez-Gonzalez *et al.*, 2009; 2011). Total number of angiosperm individuals, and proportion of individuals identified to species are provided. Regions: Brazilian Shield (BSh), central Amazonia (CA), eastern Amazonia (EA), Guiana Shield (GSh), Northern Andes (NSA), north-western Amazonia (NWA), and south-western Amazonia (SWA). Forest type: montane forest (at 1650 - 3000 m a.s.l.), flooded forest (affected by the flooding of rivers or with a high water table), lowland terra firme forest (in the interfluvial plain on clay or brown-sand soils), and white-sand forest (on white-sand soils).

Biome	Region	Forest type	Country	Plot code	Lat	Long	Area (ha)	Nº Ind.	ID (%)
Tr. moist forest	BSh	Flooded	Bolivia	HCC-11	-13.91	-60.82	1.0	582	67.4
Tr. moist forest	BSh	Flooded	Bolivia	HCC-12	-13.91	-60.82	1.0	725	66.9
Tr. moist forest	BSh	Flooded	Bolivia	LGB-01	-14.80	-60.39	1.0	656	76.4
Tr. moist forest	BSh	Flooded	Bolivia	LSL-01	-14.40	-61.14	1.0	501	82.6
Tr. moist forest	BSh	Flooded	Bolivia	LSL-02	-14.40	-61.14	1.0	631	81.3
Tr. moist forest	BSh	Flooded	Bolivia	NCR-01	-14.64	-61.16	1.0	566	75.1
Tr. moist forest	BSh	Flooded	Bolivia	NCR-02	-14.71	-61.15	1.0	590	75.3
Tr. moist forest	BSh	Flooded	Brazil	NXV-06	-14.72	-52.36	1.4	719	97.8
Tr. moist forest	BSh	Flooded	Brazil	PEA-01	-12.15	-50.83	0.4	330	100.0
Tr. moist forest	BSh	Flooded	Brazil	PEA-02	-12.32	-50.74	0.4	461	100.0
Tr. moist forest	BSh	Flooded	Brazil	PEA-03	-12.38	-50.89	1.0	1579	99.9
Tr. moist forest	BSh	Flooded	Brazil	PEA-04	-12.42	-50.71	1.0	1278	100.0
Tr. moist forest	BSh	Flooded	Brazil	PEA-05	-11.90	-50.75	1.0	966	99.8
Tr. moist forest	BSh	Flooded	Brazil	PEA-06	-11.92	-50.71	1.0	922	99.6
Tr. moist forest	BSh	Flooded	Brazil	PEA-07	-12.48	-50.90	1.0	472	100.0
Tr. moist forest	BSh	Flooded	Brazil	PEA-08	-12.54	-50.74	1.0	426	100.0
Tr. moist forest	BSh	Terra firme	Bolivia	BBC-01	-14.30	-60.53	1.0	532	81.0
Tr. moist forest	BSh	Terra firme	Bolivia	BBC-02	-14.30	-60.53	1.0	543	81.0
Tr. moist forest	BSh	Terra firme	Bolivia	CHO-01	-14.39	-61.15	1.0	729	86.0
Tr. moist forest	BSh	Terra firme	Bolivia	CHO-02	-14.34	-61.16	1.0	544	74.6
Tr. moist forest	BSh	Terra firme	Bolivia	HCC-21	-14.53	-60.74	1.0	529	90.9
Tr. moist forest	BSh	Terra firme	Bolivia	HCC-22	-14.53	-60.73	1.0	613	85.6
Tr. moist forest	BSh	Terra firme	Bolivia	HCC-23	-14.56	-60.75	1.0	712	86.5
Tr. moist forest	BSh	Terra firme	Bolivia	HCC-24	-14.57	-60.75	1.0	616	83.3
Tr. moist forest	BSh	Terra firme	Bolivia	KEN-01	-16.02	-62.73	1.0	450	99.8
Tr. moist forest	BSh	Terra firme	Bolivia	LCA-13	-15.68	-62.78	1.0	423	82.7
Tr. moist forest	BSh	Terra firme	Bolivia	LCA-16	-15.68	-62.78	1.0	385	74.5
Tr. moist forest	BSh	Terra firme	Bolivia	LCA-29	-15.68	-62.77	1.0	394	84.5
Tr. moist forest	BSh	Terra firme	Bolivia	LCA-30	-15.68	-62.77	1.0	417	85.9
Tr. moist forest	BSh	Terra firme	Bolivia	LFB-01	-14.58	-60.83	1.0	564	89.7
Tr. moist forest	BSh	Terra firme	Bolivia	LFB-02	-14.58	-60.83	1.0	536	92.0
Tr. moist forest	BSh	Terra firme	Bolivia	MVE-01	-15.01	-61.13	1.0	567	89.9
Tr. moist forest	BSh	Terra firme	Bolivia	SRQ-01	-14.40	-62.30	1.0	291	97.9
Tr. moist forest	BSh	Terra firme	Brazil	ALF-01	-9.60	-55.94	1.0	514	93.0
Tr. moist forest	BSh	Terra firme	Brazil	ALF-02	-9.58	-55.92	1.0	537	96.3

Biome	Region	Forest type	Country	Plot code	Lat	Long	Area (ha)	Nº Ind.	ID (%)
Tr. moist forest	BSh	Terra firme	Brazil	AMD-01	-1.83	-46.75	1.0	536	92.5
Tr. moist forest	BSh	Terra firme	Brazil	AMD-02	-1.83	-46.75	1.0	453	94.3
Tr. moist forest	BSh	Terra firme	Brazil	ARA-01	-4.82	-52.52	1.0	439	80.4
Tr. moist forest	BSh	Terra firme	Brazil	ASR-01	-4.76	-52.60	1.0	455	88.6
Tr. moist forest	BSh	Terra firme	Brazil	CAR-01	-5.58	-49.72	1.0	482	84.6
Tr. moist forest	BSh	Terra firme	Brazil	CPP-01	-1.84	-47.10	1.0	477	93.9
Tr. moist forest	BSh	Terra firme	Brazil	CPP-02	-1.84	-47.10	1.0	465	97.4
Tr. moist forest	BSh	Terra firme	Brazil	CRG-01	-5.90	-50.13	1.0	438	91.3
Tr. moist forest	BSh	Terra firme	Brazil	FLO-01	-12.81	-51.85	1.0	604	97.7
Tr. moist forest	BSh	Terra firme	Brazil	FLO-02	-12.76	-51.88	1.0	484	96.1
Tr. moist forest	BSh	Terra firme	Brazil	LFA-01	-5.85	-50.48	1.0	460	95.4
Tr. moist forest	BSh	Terra firme	Brazil	MCP-01	-5.88	-50.47	1.0	536	86.2
Tr. moist forest	BSh	Terra firme	Brazil	MRB-01	-5.73	-49.05	2.0	1035	97.2
Tr. moist forest	BSh	Terra firme	Brazil	MRB-02	-5.72	-49.03	2.0	1084	96.6
Tr. moist forest	BSh	Terra firme	Brazil	MRB-03	-5.70	-490.00	2.0	997	94.4
Tr. moist forest	BSh	Terra firme	Brazil	NXV-02	-14.70	-52.35	1.0	564	99.8
Tr. moist forest	BSh	Terra firme	Brazil	NXV-04	-14.70	-52.35	0.5	372	89.2
Tr. moist forest	BSh	Terra firme	Brazil	NXV-09	-14.69	-52.35	0.5	359	98.3
Tr. moist forest	BSh	Terra firme	Brazil	ODE-01	-3.48	-51.67	3.0	1413	70.8
Tr. moist forest	BSh	Terra firme	Brazil	RBR-01	-11.00	-61.95	1.0	560	85.2
Tr. moist forest	BSh	Terra firme	Brazil	RIA-01	-2.90	-46.15	4.0	1937	93.3
Tr. moist forest	BSh	Terra firme	Brazil	SAA-01	-9.79	-50.43	1.0	509	90.6
Tr. moist forest	BSh	Terra firme	Brazil	SMT-02	-12.82	-51.77	1.0	444	100.0
Tr. moist forest	BSh	Terra firme	Brazil	SNP-01	-6.04	-50.15	1.0	382	87.4
Tr. moist forest	BSh	Terra firme	Brazil	TAN-02	-13.09	-52.38	1.0	476	90.3
Tr. moist forest	BSh	Terra firme	Brazil	TAN-03	-12.82	-52.36	1.0	589	87.4
Tr. moist forest	BSh	Terra firme	Brazil	TAN-04	-12.92	-52.37	1.0	578	95.7
Tr. moist forest	BSh	Terra firme	Brazil	VCR-04	-14.83	-52.17	1.0	459	96.5
Tr. moist forest	CA	Terra firme	Brazil	BDF-01	-2.34	-60.10	2.0	1330	91.5
Tr. moist forest	CA	Terra firme	Brazil	BDF-03	-2.42	-59.85	1.0	592	83.3
Tr. moist forest	CA	Terra firme	Brazil	BDF-04	-2.43	-59.85	1.0	590	90.5
Tr. moist forest	CA	Terra firme	Brazil	BDF-05	-2.43	-59.85	1.0	652	91.7
Tr. moist forest	CA	Terra firme	Brazil	BDF-06	-2.41	-59.86	3.0	1896	90.5
Tr. moist forest	CA	Terra firme	Brazil	BDF-07	-2.40	-59.90	1.0	638	87.3
Tr. moist forest	CA	Terra firme	Brazil	BDF-08	-2.40	-59.90	1.0	592	86.0
Tr. moist forest	CA	Terra firme	Brazil	BDF-09	-2.40	-59.85	1.0	575	86.3
Tr. moist forest	CA	Terra firme	Brazil	BDF-10	-2.39	-59.86	2.0	1241	84.9
Tr. moist forest	CA	Terra firme	Brazil	BDF-11	-2.38	-59.85	3.0	1826	89.9
Tr. moist forest	CA	Terra firme	Brazil	BDF-12	-2.39	-59.85	2.0	1211	88.9
Tr. moist forest	CA	Terra firme	Brazil	BDF-13	-2.40	-59.91	9.0	5192	84.1
Tr. moist forest	CA	Terra firme	Brazil	BDF-14	-2.36	-59.97	1.0	685	90.7
Tr. moist forest	CA	Terra firme	Brazil	BNT-01	-2.64	-60.16	1.0	567	69.1
Tr. moist forest	CA	Terra firme	Brazil	BNT-04	-2.63	-60.15	1.0	612	70.1
Tr. moist forest	CA	Terra firme	Brazil	BNT-05	-2.63	-60.17	1.0	560	67.3
Tr. moist forest	CA	Terra firme	Brazil	BNT-07	-2.63	-60.17	1.0	643	65.6
Tr. moist forest	CA	Terra firme	Brazil	TEM-01	-2.97	-59.90	1.0	576	93.1
Tr. moist forest	CA	Terra firme	Brazil	TEM-02	-2.93	-59.95	1.0	599	92.8
Tr. moist forest	CA	Terra firme	Brazil	TEM-03	-2.41	-59.90	1.0	674	88.4
Tr. moist forest	CA	Terra firme	Brazil	TEM-04	-2.43	-59.79	1.0	581	90.2
Tr. moist forest	CA	Terra firme	Brazil	TEM-05	-2.62	-60.21	1.0	612	94.9
Tr. moist forest	CA	Terra firme	Brazil	TEM-06	-2.60	-60.11	1.0	693	91.2
Tr. moist forest	EA	Flooded	Brazil	TEC-01	-1.71	-51.46	1.0	501	70.1
Tr. moist forest	EA	Flooded	Brazil	TEC-06	-1.73	-51.43	1.0	456	75.2
Tr. moist forest	EA	Terra firme	Brazil	CAX-01	-1.74	-51.46	1.0	515	86.6
Tr. moist forest	EA	Terra firme	Brazil	CAX-02	-1.74	-51.46	1.0	523	74.4

Biome	Region	Forest type	Country	Plot code	Lat	Long	Area (ha)	Nº Ind.	ID (%)
Tr. moist forest	EA	Terra firme	Brazil	GMT-01	-1.11	-47.80	1.0	505	89.5
Tr. moist forest	EA	Terra firme	Brazil	JBU-01	-1.14	-47.70	1.0	456	91.2
Tr. moist forest	EA	Terra firme	Brazil	JRI-01	-0.89	-52.19	1.0	599	77.0
Tr. moist forest	EA	Terra firme	Brazil	PPB-01	-1.18	-47.32	1.0	415	94.9
Tr. moist forest	EA	Terra firme	Brazil	PPB-02	-1.18	-47.32	1.0	497	89.5
Tr. moist forest	EA	Terra firme	Brazil	PPB-03	-1.18	-47.32	1.0	440	97.3
Tr. moist forest	EA	Terra firme	Brazil	PTB-01	-1.17	-56.41	1.0	438	95.7
Tr. moist forest	EA	Terra firme	Brazil	PTB-02	-1.48	-56.39	1.0	502	97.4
Tr. moist forest	EA	Terra firme	Brazil	SRT-01	-1.46	-47.92	1.0	503	93.6
Tr. moist forest	EA	Terra firme	Brazil	TAP-01	-3.31	-54.94	1.0	561	77.2
Tr. moist forest	EA	Terra firme	Brazil	TAP-02	-3.31	-54.95	1.0	479	81.0
Tr. moist forest	EA	Terra firme	Brazil	TAP-03	-3.31	-54.94	1.0	525	77.0
Tr. moist forest	EA	Terra firme	Brazil	TEC-04	-1.75	-51.52	1.0	474	76.4
Tr. moist forest	EA	Terra firme	Brazil	TEC-05	-1.78	-51.59	1.0	510	67.3
Tr. moist forest	GSh	Flooded	Fr. Guiana	PAR-21	5.28	-52.92	1.0	590	87.6
Tr. moist forest	GSh	Terra firme	Fr. Guiana	NOU-02	4.09	-52.67	1.0	512	90.8
Tr. moist forest	GSh	Terra firme	Fr. Guiana	NOU-11	4.08	-52.68	1.0	524	94.1
Tr. moist forest	GSh	Terra firme	Fr. Guiana	NOU-12	4.08	-52.68	1.0	475	81.7
Tr. moist forest	GSh	Terra firme	Fr. Guiana	NOU-15	4.08	-52.68	1.0	482	83.8
Tr. moist forest	GSh	Terra firme	Fr. Guiana	NOU-17	4.08	-52.68	1.0	572	81.3
Tr. moist forest	GSh	Terra firme	Fr. Guiana	NOU-18	4.08	-52.68	1.0	567	81.8
Tr. moist forest	GSh	Terra firme	Fr. Guiana	PAR-20	5.28	-52.92	1.5	927	88.3
Tr. moist forest	GSh	Terra firme	Fr. Guiana	PAR-22	5.28	-52.92	1.5	968	82.2
Tr. moist forest	GSh	Terra firme	Fr. Guiana	PAR-23	5.28	-52.92	2.0	499	86.4
Tr. moist forest	GSh	Terra firme	Guyana	FMH-01	5.17	-58.69	1.0	455	95.8
Tr. moist forest	GSh	Terra firme	Guyana	FMH-02	5.17	-58.69	1.0	353	92.4
Tr. moist forest	GSh	Terra firme	Guyana	IWO-03	4.53	-58.78	1.0	563	75.0
Tr. moist forest	GSh	Terra firme	Guyana	IWO-11	4.62	-58.72	1.0	445	78.4
Tr. moist forest	GSh	Terra firme	Guyana	IWO-12	4.73	-58.72	1.0	450	77.1
Tr. moist forest	GSh	Terra firme	Guyana	IWO-22	4.62	-58.72	1.0	443	84.0
Tr. moist forest	GSh	Terra firme	Guyana	PIB-05	5.02	-58.62	1.0	470	86.8
Tr. moist forest	GSh	Terra firme	Guyana	PIB-06	5.01	-58.62	1.0	494	93.5
Tr. moist forest	GSh	Terra firme	Guyana	PIB-12	5.03	-58.60	1.0	407	84.5
Tr. moist forest	GSh	Terra firme	Suriname	BBS-04	4.97	-55.18	1.0	465	77.2
Tr. moist forest	GSh	Terra firme	Suriname	BBS-05	4.99	-55.20	1.0	515	82.7
Tr. moist forest	GSh	Terra firme	Suriname	BBS-07	4.92	-55.13	1.0	458	80.3
Tr. moist forest	GSh	Terra firme	Suriname	BBS-08	4.93	-55.14	1.0	555	75.7
Tr. moist forest	GSh	Terra firme	Suriname	LMS-04	4.25	-54.73	1.0	524	67.0
Tr. moist forest	GSh	Terra firme	Suriname	LMS-05	4.25	-54.73	1.0	981	76.8
Tr. moist forest	GSh	Terra firme	Suriname	LMS-06	4.26	-54.78	1.0	477	68.3
Tr. moist forest	GSh	Terra firme	Suriname	LMS-07	4.27	-54.78	1.0	476	74.2
Tr. moist forest	GSh	Terra firme	Suriname	LMS-08	4.27	-54.75	1.0	489	72.8
Tr. moist forest	GSh	Terra firme	Suriname	NMS-01	4.78	-54.62	1.0	475	69.1
Tr. moist forest	GSh	Terra firme	Suriname	NMS-03	4.82	-54.60	1.0	497	76.3
Tr. moist forest	GSh	Terra firme	Suriname	NMS-04	4.93	-54.52	1.0	739	78.3
Tr. moist forest	GSh	Terra firme	Suriname	NMS-05	4.93	-54.52	1.0	810	80.2
Tr. moist forest	GSh	Terra firme	Suriname	NMS-06	4.83	-54.61	1.0	607	68.7
Tr. moist forest	GSh	Terra firme	Venezuela	ELD-01	6.10	-61.39	1.0	576	94.6
Tr. moist forest	GSh	Terra firme	Venezuela	PTA-01	5.11	-67.74	1.0	500	89.6
Tr. moist forest	GSh	Terra firme	Venezuela	PTA-02	5.84	-67.45	1.0	436	95.4
Tr. moist forest	GSh	Terra firme	Venezuela	PTA-03	5.11	-67.74	1.0	593	94.4
Tr. moist forest	GSh	Terra firme	Venezuela	PTA-04	5.84	-67.49	1.0	407	87.0
Tr. moist forest	GSh	Terra firme	Venezuela	SCR-05	1.93	-67.04	1.0	681	93.1
Tr. moist forest	GSh	White sand	Guyana	FMH-03	5.18	-58.70	1.0	635	91.0
Tr. moist forest	GSh	White sand	Guyana	IWO-09	4.61	-58.73	1.0	675	70.2

Biome	Region	Forest type	Country	Plot code	Lat	Long	Area (ha)	Nº Ind.	ID (%)
Tr. moist forest	GSh	White sand	Guyana	IWO-21	4.63	-58.74	1.0	563	90.2
Tr. moist forest	GSh	White sand	Venezuela	SCR-04	1.93	-67.04	1.0	829	95.8
Tr. moist forest	NSA	Flooded	Colombia	AMA-02	5.58	-77.50	1.0	453	81.9
Tr. moist forest	NSA	Montane	Colombia	BET-01	6.92	-73.30	1.0	936	91.0
Tr. moist forest	NSA	Montane	Colombia	BET-02	6.92	-73.30	1.0	889	84.0
Tr. moist forest	NSA	Montane	Colombia	DIV-01	7.05	-73.02	1.0	824	76.9
Tr. moist forest	NSA	Montane	Colombia	MTV-01	6.28	-75.51	1.0	1050	92.8
Tr. moist forest	NSA	Montane	Colombia	SSE-01	6.10	-75.51	1.0	891	69.0
Tr. moist forest	NSA	Montane	Venezuela	SEU-03	8.64	-71.41	1.0	676	89.5
Tr. moist forest	NSA	Terra firme	Colombia	ECE-01	10.68	-75.27	1.0	352	95.2
Tr. moist forest	NSA	Terra firme	Colombia	KAL-01	11.24	-74.14	1.0	363	78.5
Tr. moist forest	NSA	Terra firme	Colombia	PTN-01	6.12	-74.67	1.0	540	66.1
Tr. moist forest	NSA	Terra firme	Colombia	SRF-01	6.27	-75.09	0.9	632	72.3
Tr. moist forest	NWA	Flooded	Colombia	ZAR-02	-4.00	-69.90	1.0	624	73.2
Tr. moist forest	NWA	Flooded	Ecuador	JAS-05	-1.06	-77.62	1.0	557	86.2
Tr. moist forest	NWA	Flooded	Ecuador	TIP-03	-0.64	-76.15	1.0	444	67.6
Tr. moist forest	NWA	Flooded	Peru	JEN-13	-4.92	-73.54	1.0	643	70.3
Tr. moist forest	NWA	Flooded	Peru	SUC-03	-3.25	-72.92	1.0	599	98.7
Tr. moist forest	NWA	Montane	Peru	PNY-01	-10.38	-75.47	1.0	580	87.4
Tr. moist forest	NWA	Montane	Peru	PNY-02	-10.30	-75.61	1.0	653	68.8
Tr. moist forest	NWA	Terra firme	Brazil	JAM-01	-4.67	-66.17	4.0	3118	82.4
Tr. moist forest	NWA	Terra firme	Colombia	AGP-01	-3.72	-70.31	1.0	625	93.8
Tr. moist forest	NWA	Terra firme	Colombia	AGP-02	-3.72	-70.30	1.0	584	90.1
Tr. moist forest	NWA	Terra firme	Colombia	LOR-01	-3.06	-69.99	1.0	604	88.2
Tr. moist forest	NWA	Terra firme	Colombia	LOR-02	-3.06	-69.99	1.0	578	87.2
Tr. moist forest	NWA	Terra firme	Colombia	ZAR-03	-3.99	-69.90	1.0	692	67.1
Tr. moist forest	NWA	Terra firme	Colombia	ZAR-04	-3.99	-69.91	1.0	652	68.3
Tr. moist forest	NWA	Terra firme	Ecuador	BOG-01	-0.70	-76.48	1.0	544	80.1
Tr. moist forest	NWA	Terra firme	Ecuador	BOG-02	-0.70	-76.47	1.0	614	78.5
Tr. moist forest	NWA	Terra firme	Ecuador	JAS-02	-1.07	-77.62	1.0	724	89.4
Tr. moist forest	NWA	Terra firme	Ecuador	JAS-03	-1.08	-77.61	1.0	648	91.0
Tr. moist forest	NWA	Terra firme	Ecuador	JAS-04	-1.07	-77.61	1.0	794	69.8
Tr. moist forest	NWA	Terra firme	Ecuador	JUY-01	-2.13	-76.20	1.0	620	65.5
Tr. moist forest	NWA	Terra firme	Ecuador	PAY-01	-0.45	-77.03	1.0	653	67.8
Tr. moist forest	NWA	Terra firme	Ecuador	SHI-01	-1.02	-76.98	1.0	628	94.1
Tr. moist forest	NWA	Terra firme	Ecuador	SUM-01	-0.60	-77.63	0.8	572	77.6
Tr. moist forest	NWA	Terra firme	Ecuador	TIP-01	-0.66	-76.40	1.0	566	78.4
Tr. moist forest	NWA	Terra firme	Ecuador	TIP-02	-0.63	-76.14	1.0	502	82.9
Tr. moist forest	NWA	Terra firme	Peru	ALP-01	-3.95	-73.43	1.0	612	92.3
Tr. moist forest	NWA	Terra firme	Peru	ALP-02	-3.95	-73.44	1.0	593	92.6
Tr. moist forest	NWA	Terra firme	Peru	CDM-01	-10.33	-75.30	1.0	520	72.5
Tr. moist forest	NWA	Terra firme	Peru	IND-01	-3.52	-72.85	1.0	488	71.1
Tr. moist forest	NWA	Terra firme	Peru	JEN-11	-4.88	-73.63	1.0	600	85.3
Tr. moist forest	NWA	Terra firme	Peru	MSH-01	-3.78	-73.50	1.0	813	92.4
Tr. moist forest	NWA	Terra firme	Peru	PNY-03	-10.31	-75.29	1.0	797	75.9
Tr. moist forest	NWA	Terra firme	Peru	PNY-04	-10.34	-75.25	1.0	542	83.0
Tr. moist forest	NWA	Terra firme	Peru	PNY-05	-10.35	-75.25	1.0	573	88.7
Tr. moist forest	NWA	Terra firme	Peru	PNY-06	-10.36	-75.25	1.0	481	82.3
Tr. moist forest	NWA	Terra firme	Peru	PNY-07	-10.35	-75.26	1.0	536	84.0
Tr. moist forest	NWA	Terra firme	Peru	RCS-01	-9.47	-74.77	1.0	639	66.4
Tr. moist forest	NWA	Terra firme	Peru	RCS-05	-9.62	-74.93	1.0	595	89.1
Tr. moist forest	NWA	Terra firme	Peru	SUC-01	-3.25	-72.91	1.0	594	92.9
Tr. moist forest	NWA	Terra firme	Peru	SUC-02	-3.25	-72.90	1.0	591	94.9
Tr. moist forest	NWA	Terra firme	Peru	SUC-04	-3.25	-72.89	1.0	614	93.2
Tr. moist forest	NWA	Terra firme	Peru	SUC-05	-3.26	-72.89	1.0	561	90.6

Biome	Region	Forest type	Country	Plot code	Lat	Long	Area (ha)	Nº Ind.	ID (%)
Tr. moist forest	NWA	Terra firme	Peru	YAN-01	-3.43	-72.84	1.0	567	95.8
Tr. moist forest	NWA	Terra firme	Peru	YAN-02	-3.43	-72.84	1.0	599	94.0
Tr. moist forest	NWA	White sand	Colombia	ZAR-01	-4.01	-69.91	1.0	872	73.6
Tr. moist forest	NWA	White sand	Peru	ALP-30	-3.95	-73.43	1.0	504	93.5
Tr. moist forest	NWA	White sand	Peru	ALP-40	-3.94	-73.44	1.0	1209	73.6
Tr. moist forest	NWA	White sand	Peru	JEN-12	-4.90	-73.63	1.0	744	91.3
Tr. moist forest	SWA	Flooded	Peru	AGJ-01	-11.89	-71.36	2.0	1314	93.6
Tr. moist forest	SWA	Flooded	Peru	LAS-02	-12.57	-70.09	1.0	596	86.9
Tr. moist forest	SWA	Flooded	Peru	MNU-01	-11.89	-71.41	2.3	1305	93.7
Tr. moist forest	SWA	Flooded	Peru	MNU-05	-11.88	-71.41	2.0	1252	93.2
Tr. moist forest	SWA	Flooded	Peru	MNU-06	-11.89	-71.40	2.3	1155	95.1
Tr. moist forest	SWA	Flooded	Peru	TAM-03	-12.84	-69.28	1.0	650	95.4
Tr. moist forest	SWA	Montane	Peru	ESP-01	-13.18	-71.59	1.0	709	82.1
Tr. moist forest	SWA	Montane	Peru	TRU-01	-13.11	-71.61	1.0	647	79.1
Tr. moist forest	SWA	Montane	Peru	TRU-02	-13.11	-71.60	1.0	743	77.4
Tr. moist forest	SWA	Montane	Peru	TRU-03	-13.11	-71.60	1.0	561	75.4
Tr. moist forest	SWA	Montane	Peru	TRU-04	-13.11	-71.59	1.0	888	70.8
Tr. moist forest	SWA	Montane	Peru	TRU-05	-13.09	-71.57	1.0	1001	82.1
Tr. moist forest	SWA	Montane	Peru	TRU-06	-13.08	-71.57	1.0	862	73.4
Tr. moist forest	SWA	Montane	Peru	WAY-01	-13.19	-71.59	1.0	1100	88.1
Tr. moist forest	SWA	Terra firme	Bolivia	BEE-01	-16.53	-64.58	1.0	574	87.1
Tr. moist forest	SWA	Terra firme	Bolivia	BEE-05	-16.53	-64.58	1.0	544	94.7
Tr. moist forest	SWA	Terra firme	Bolivia	MBT-01	-10.07	-65.89	1.0	451	82.5
Tr. moist forest	SWA	Terra firme	Bolivia	MBT-02	-10.05	-65.89	1.0	403	73.0
Tr. moist forest	SWA	Terra firme	Bolivia	MBT-04	-10.31	-65.55	1.0	493	69.6
Tr. moist forest	SWA	Terra firme	Bolivia	MBT-05	-10.03	-65.63	1.0	456	74.3
Tr. moist forest	SWA	Terra firme	Bolivia	MBT-07	-9.91	-65.74	1.0	485	75.3
Tr. moist forest	SWA	Terra firme	Bolivia	MBT-08	-9.94	-65.75	1.0	442	74.4
Tr. moist forest	SWA	Terra firme	Bolivia	MTG-01	-19.27	-63.83	1.0	535	82.6
Tr. moist forest	SWA	Terra firme	Bolivia	RET-05	-10.97	-65.72	1.0	597	83.9
Tr. moist forest	SWA	Terra firme	Bolivia	RET-06	-10.97	-65.72	1.0	524	87.0
Tr. moist forest	SWA	Terra firme	Bolivia	RET-08	-10.97	-65.72	1.0	526	89.2
Tr. moist forest	SWA	Terra firme	Bolivia	RET-09	-10.97	-65.72	1.0	474	90.5
Tr. moist forest	SWA	Terra firme	Brazil	DOI-01	-10.57	-68.32	1.0	479	77.7
Tr. moist forest	SWA	Terra firme	Brazil	FEC-01	-10.07	-67.62	1.0	521	70.2
Tr. moist forest	SWA	Terra firme	Brazil	POR-01	-10.82	-68.77	1.0	558	79.9
Tr. moist forest	SWA	Terra firme	Brazil	POR-02	-10.80	-68.77	1.0	535	75.9
Tr. moist forest	SWA	Terra firme	Peru	ALM-01	-11.80	-71.47	2.0	1226	89.5
Tr. moist forest	SWA	Terra firme	Peru	BAR-01	-11.90	-71.42	1.0	473	92.8
Tr. moist forest	SWA	Terra firme	Peru	CAG-01	-12.18	-69.05	1.1	663	92.8
Tr. moist forest	SWA	Terra firme	Peru	CAL-01	-12.80	-71.78	1.0	630	72.4
Tr. moist forest	SWA	Terra firme	Peru	CAL-02	-12.81	-71.78	1.0	848	71.1
Tr. moist forest	SWA	Terra firme	Peru	CBP-01	-12.39	-69.31	0.9	537	97.0
Tr. moist forest	SWA	Terra firme	Peru	CJC-04	-12.66	-69.08	0.7	562	93.4
Tr. moist forest	SWA	Terra firme	Peru	CLT-01	-12.82	-69.35	0.9	581	94.3
Tr. moist forest	SWA	Terra firme	Peru	CUZ-01	-12.54	-69.06	1.0	516	98.6
Tr. moist forest	SWA	Terra firme	Peru	CUZ-02	-12.54	-69.06	1.0	553	98.2
Tr. moist forest	SWA	Terra firme	Peru	CUZ-03	-12.53	-69.05	1.0	497	97.0
Tr. moist forest	SWA	Terra firme	Peru	CUZ-04	-12.54	-69.05	1.0	558	94.1
Tr. moist forest	SWA	Terra firme	Peru	INF-01	-12.73	-69.70	1.3	810	82.3
Tr. moist forest	SWA	Terra firme	Peru	MNU-03	-11.90	-71.40	2.0	1281	93.6
Tr. moist forest	SWA	Terra firme	Peru	MNU-04	-11.90	-71.40	2.0	1196	92.9
Tr. moist forest	SWA	Terra firme	Peru	MNU-08	-12.00	-71.24	2.0	1153	96.2
Tr. moist forest	SWA	Terra firme	Peru	MNU-09	-12.04	-71.21	2.0	971	97.4
Tr. moist forest	SWA	Terra firme	Peru	PAK-01	-11.94	-71.28	1.0	575	89.6

Biome	Region	Forest type	Country	Plot code	Lat	Long	Area (ha)	Nº Ind.	ID (%)
Tr. moist forest	SWA	Terra firme	Peru	RPA-01	-12.39	-69.36	1.0	494	76.9
Tr. moist forest	SWA	Terra firme	Peru	RPI-01	-12.36	-69.23	1.0	552	86.4
Tr. moist forest	SWA	Terra firme	Peru	RTH-01	-11.37	-69.66	1.0	525	93.1
Tr. moist forest	SWA	Terra firme	Peru	TAM-01	-12.84	-69.29	1.0	566	95.6
Tr. moist forest	SWA	Terra firme	Peru	TAM-02	-12.83	-69.29	1.0	600	93.0
Tr. moist forest	SWA	Terra firme	Peru	TAM-05	-12.83	-69.27	1.0	532	93.6
Tr. moist forest	SWA	Terra firme	Peru	TAM-06	-12.84	-69.30	1.0	544	93.6
Tr. moist forest	SWA	Terra firme	Peru	TAM-07	-12.83	-69.26	1.0	549	89.3
Tr. moist forest	SWA	Terra firme	Peru	TAM-08	-12.83	-69.27	1.0	532	93.0
Tr. moist forest	SWA	Terra firme	Peru	TMP-01	-13.13	-69.57	2.3	1306	81.5
Savanna	BSh	Savanna	Brazil	LET-01	-14.71	-52.35	1.0	375	100.0
Savanna	BSh	Savanna	Brazil	NXV-01	-14.71	-52.35	1.0	341	99.7
Savanna	BSh	Savanna	Brazil	NXV-03	-14.71	-52.35	0.5	320	99.7
Savanna	BSh	Savanna	Brazil	NXV-05	-14.71	-52.35	0.5	439	99.3
Savanna	BSh	Savanna	Brazil	SMT-01	-12.82	-51.77	1.0	380	99.5
SDTF	BSh	Dry forest	Bolivia	ACU-01	-15.25	-61.25	1.0	479	95.4
SDTF	BSh	Dry forest	Bolivia	ACU-02	-15.25	-61.24	1.0	406	90.6
SDTF	BSh	Dry forest	Bolivia	ALV-01	-16.12	-61.89	1.0	479	98.5
SDTF	BSh	Dry forest	Bolivia	ALV-02	-16.08	-61.89	1.0	423	98.3
SDTF	BSh	Dry forest	Bolivia	CRP-01	-14.54	-61.50	1.0	456	95.8
SDTF	BSh	Dry forest	Bolivia	CRP-02	-14.54	-61.50	1.0	464	92.7
SDTF	BSh	Dry forest	Bolivia	KEN-02	-16.02	-62.73	1.0	396	98.7
SDTF	BSh	Dry forest	Bolivia	OTT-01	-16.39	-61.21	1.0	422	95.7
SDTF	BSh	Dry forest	Bolivia	OTT-03	-16.42	-61.19	1.0	252	98.8
SDTF	SWA	Dry forest	Bolivia	TUC-01	-18.52	-60.81	1.0	758	98.5
SDTF	NSA	Dry forest	Venezuela	BAC-01	7.46	-71.01	1.5	432	95.1
SDTF	NSA	Dry forest	Venezuela	CAI-01	8.70	-70.07	1.5	424	94.1
SDTF	NSA	Dry forest	Venezuela	CLA-03	10.01	-65.32	0.5	302	98.3

DNA sequence-based genus-level phylogeny construction

In order to determine if PD metrics are affected by phylogenetic resolution, we compared our results generated using the PHYLOCOM phylogeny with those using a phylogeny of Amazonian tree genera generated from DNA sequences of *rbc*L and *mat*K plastid genes (Dexter & Chave, unpublished data). These regions were chosen as they are alignable across all angiosperms, and many sequences were already available for many genera because they represent the two markers selected for DNA barcoding in plants (Hollingsworth *et al.*, 2009). The details of DNA extraction, PCR, and DNA sequencing protocols can be found in Gonzalez *et al.* (2009). We generated new *rbc*L sequence data for 276 genera and *mat*K data for 122 genera. This was supplemented with *rbc*L data for 340 genera and *mat*K data for 327 genera from GenBank. All genera (n=616) were represented with an *rbcL* sequence. We included sequences of *Amborella trichopoda* (Amborellaceae) and *Nymphaea alba* (Nymphaeaceae) as outgroups.

We estimated an initial tree using maximum likelihood analysis with separate partitions for *rbc*L and *mat*K in RAxML v7.0.3 (Stamatakis, 2014), on the CIPRES web server (www.phylo.org). This initial tree was used as a starting point for simultaneous topology and divergence time estimation in the software package BEAST v1.54 (Drummond & Rambaut, 2007). We implemented a relaxed log-normal molecular clock and a Yule pure-birth model of speciation. We conducted one initial run of 10^6 generations without any constraints on node ages to generate an ultrametric starting tree for subsequent analyses with fossil-based constraints. In total, we constrained 24 internal nodes using log-normal prior distributions with a median value equal to the fossil age estimate, a standard deviation equal to 5% of the age estimate, and a hard age minimum equal to 80% of the age estimate (see Table S2 for nodes and full prior distribution parameters). This prior distribution represents uncertainty in both fossil age estimates and in their correspondence to the true appearance of lineages that is proportional to the age of the fossil. The constraints selected were taken from (Magallon & Castillo, 2009; Smith *et al.*, 2010). We placed no constraint on the root age of the tree. We conducted several initial runs of 10^6 generations to optimize operator settings before conducting two final runs of 10^8 generations. We assessed the two final runs for convergence and then combined their posterior distribution of trees after a burn-in of 10^7 generations for each run. In the combined distribution, most parameter values including the prior, likelihood, posterior, and node age estimates had effective sample sizes greater than 200. We generated the ‘best’ tree by calculating the majority-rule consensus tree of all compatible clades and assigned branch-lengths and divergence times to the tree that correspond to the mean values across the posterior distribution of trees (using TreeAnnotator v1.5.4; Drummond & Rambaut, 2007).

We converted the genus-level phylogeny into a species-level phylogeny by generating a random phylogeny via a birth-death process ($b = 1.0$, $d = 0.9$) with n tips for each genus where n corresponds to the number of species in our dataset for a given genus. Species were assigned to the tips in their respective genera randomly. The final phylogeny includes 3,467 species (89.6 % of species in the whole tree community dataset), 487 genera (66.5 % of total number of genera), and 103 families (81.7 % of total number of families).

Table S2. Fossil-based calibrations for prior ages of clades in the simultaneous analysis of topology and divergence times (BEAST v1.54; Drummond & Rambaut, 2007).

Clade	Crown/Stem	Offset	Mean	Standard deviation
Apocynaceae	Stem	29.8	7.7	0.27
Brassicaceae	Stem	71.4	22.7	0.65
Caryophyllales	Crown	66.8	20.2	0.62
Core Eudicots	Stem	100	45.7	1.1
Cunoniaceae	Stem	66.8	20.2	0.62
Ericales	Crown	73	22.6	0.66
Fabales	Crown	48	13.5	0.48
Fagales	Stem	76.8	24.2	0.68
Lamiales	Crown	35.4	9.5	0.35
Laurales	Crown	84.6	27.5	0.72
Magnoliales	Stem	89.6	29.7	0.75
Malpighiales	Crown	71.2	22	0.65
Malvales	Crown	55.8	16.1	0.54
Myrtales	Crown	70.4	21.6	0.64
Santalales	Crown	41.6	11.3	0.41
Sapindales	Crown	52	14.8	0.51
Solanales	Crown	35.4	9.5	0.35
Ulmaceae	Crown	27.2	7	0.23
Anacardiaceae	Stem	52.8	15.1	0.52
Annonaceae	Stem	56	16.2	0.54
Arecaceae	Crown	52	14.8	0.51
Chrysobalanus	Stem	26.4	6.8	0.22
Combretaceae	Stem	59.2	17.4	0.57
Moraceae	Stem	59.2	17.4	0.57
Sapotaceae	Stem	52.8	15.1	0.52

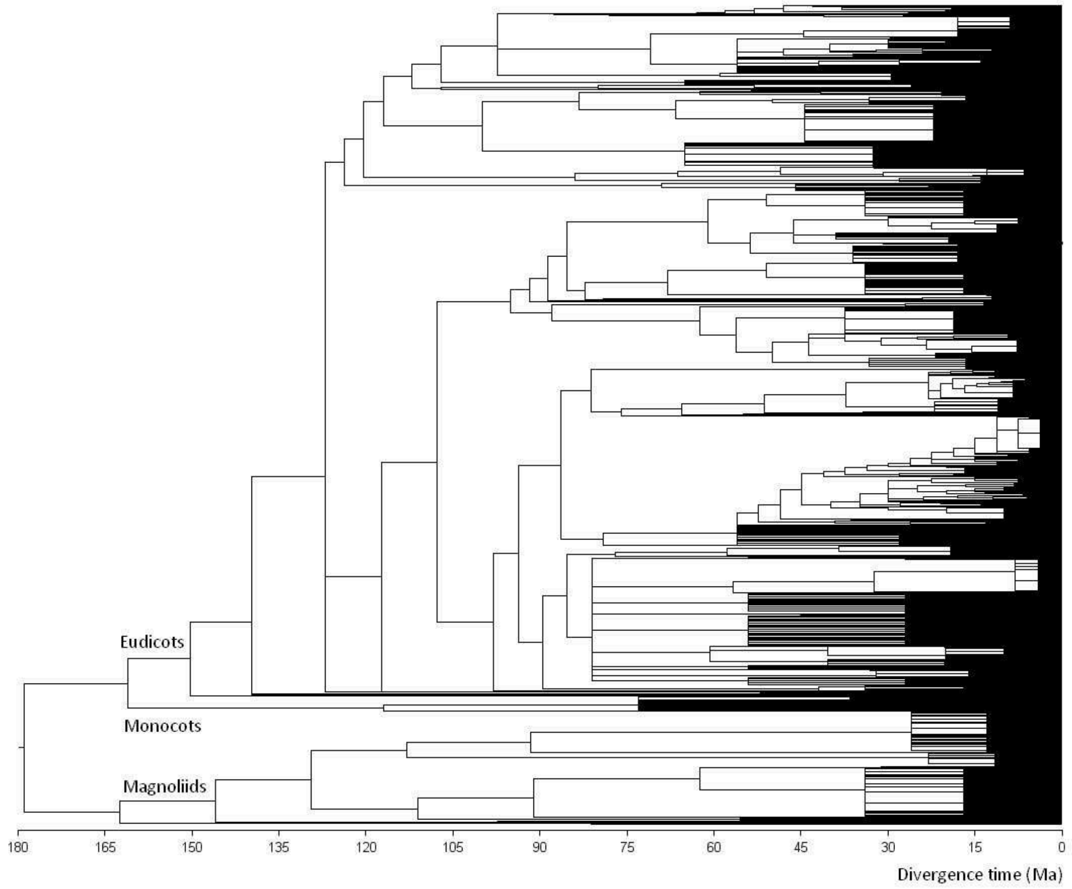

Figure S1. Phylogenetic tree for the whole species pool for 283 floristic inventories compiled from RAINFOR dataset and produced in PHYLOCOM. This phylogeny reflects the most current understanding of the phylogenetic relationship among families for angiosperms (Bremer *et al.*, 2009), but the resolution among genera or species is poor, i.e. lower taxa are represented as polytomies in the phylogeny, for example, with identical node age for congeneric species.

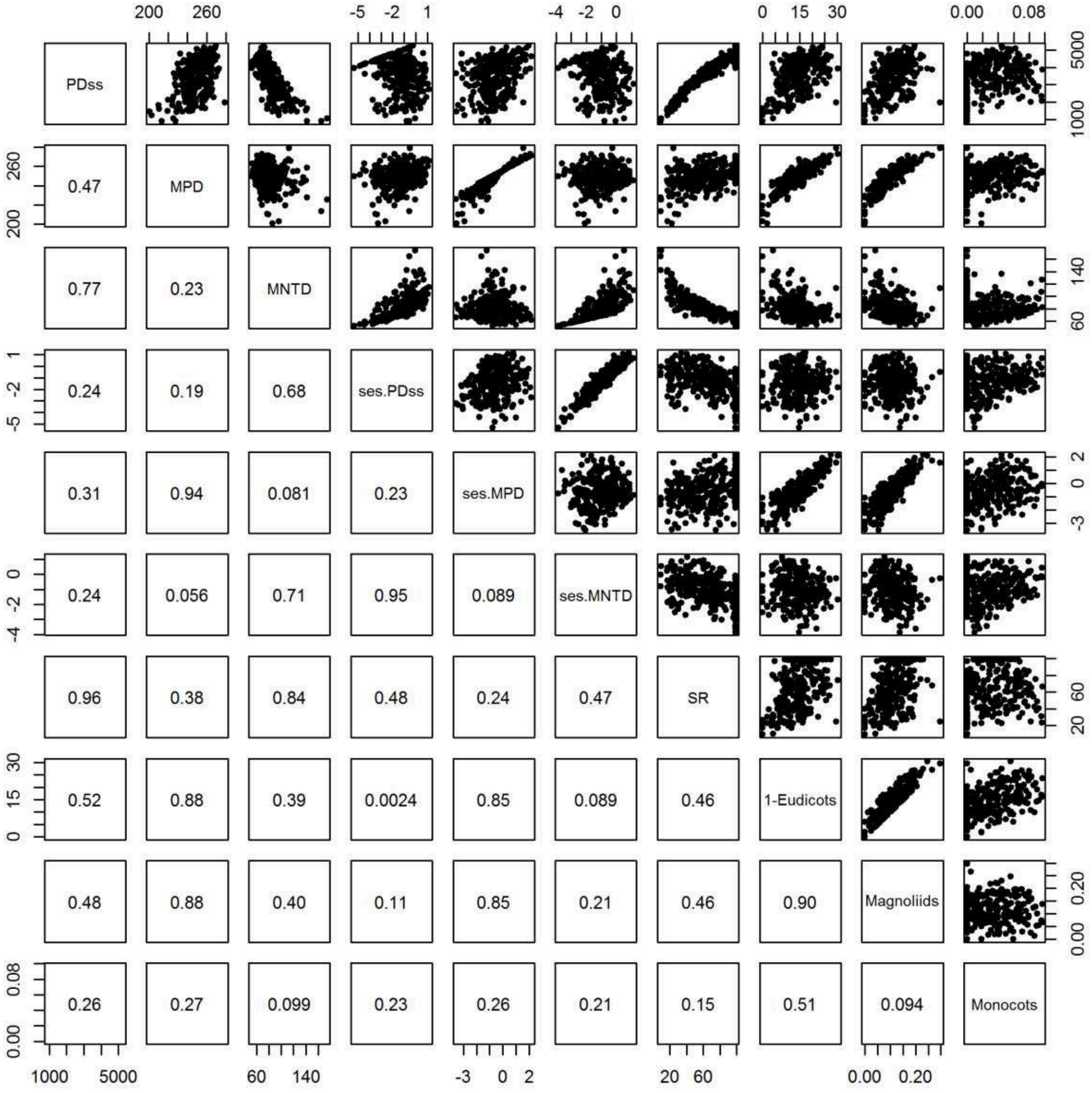

Figure S2. Relationships (upper triangle) and correlation values (lower triangle) among six phylogenetic diversity metrics (phylogenetic diversity *sensu stricto*: PDss, mean pairwise phylogenetic distance between species: MPD, mean nearest taxon distance: MNTD, and their equivalents, standardised for species richness: ses.PDss, ses.MPD, and ses.MNTD), species richness (SR), and the proportion of species of Magnoliids and Monocots (= 1 - Eudicots).

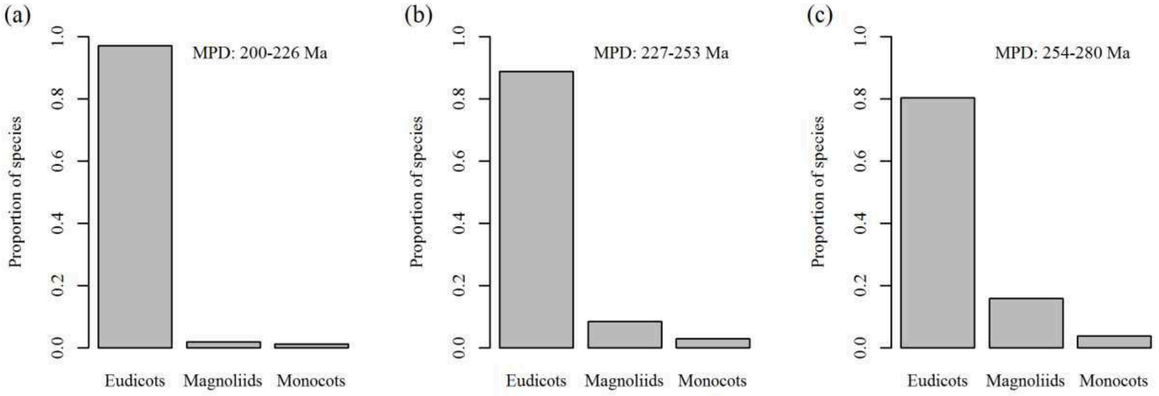

Figure S3. Distributions of species across the three major angiosperm clades for tree communities with increasing values of mean pairwise phylogenetic distance between species (MPD): (a) 200-226 Ma, (b) 227-253 Ma, and (c) 254-280 Ma. Note that MPD increases when clades are more evenly distributed in the community.

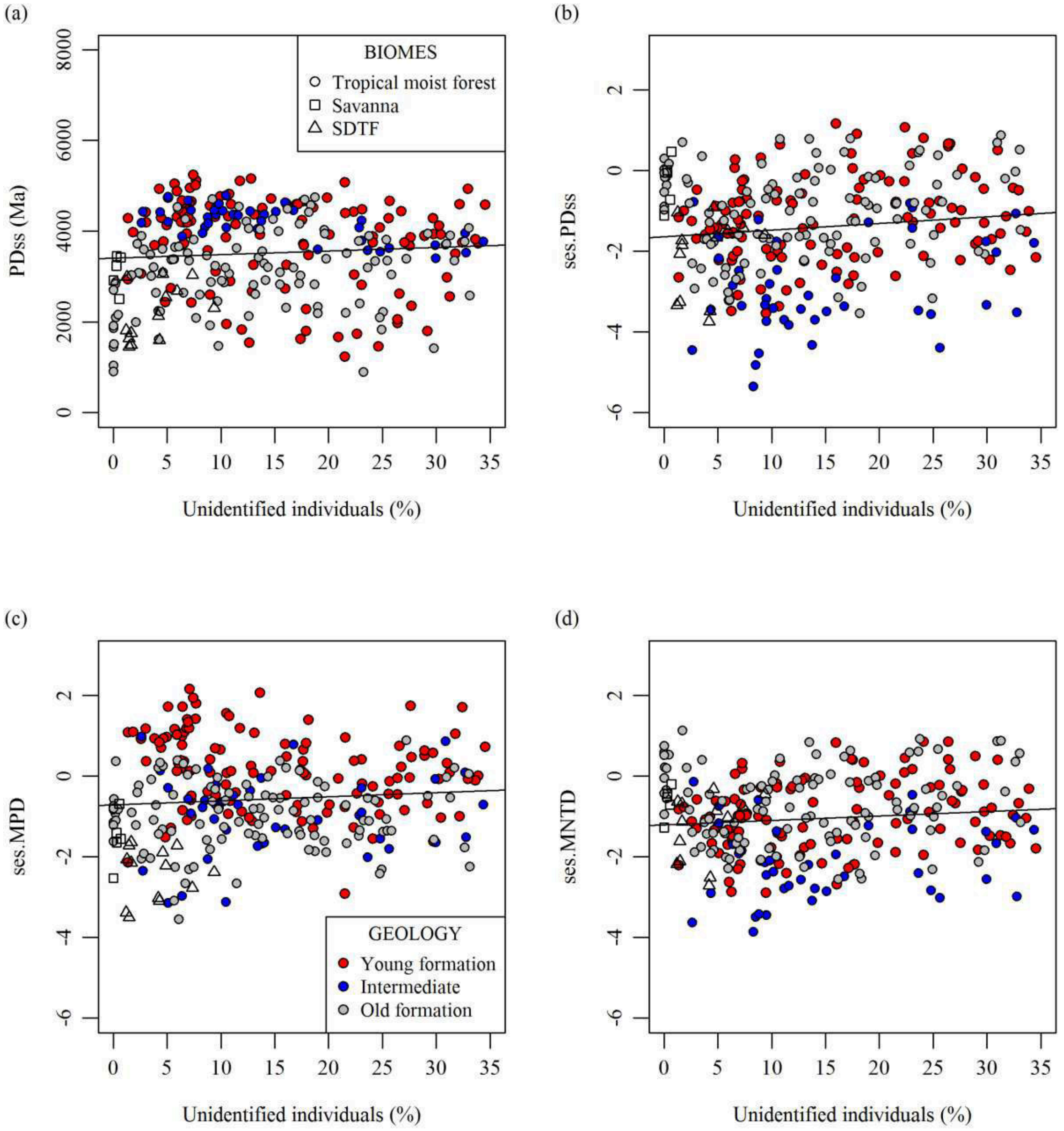

Figure S4. Relationships between phylogenetic diversity metrics and the percentage of unidentified individuals excluded for each plot. Linear regression fits are provided for (a) PDss (F = 1.63, $r^2 = 0.002$, $p = 0.20$), (b) ses.PDss (F = 4.61, $r^2 = 0.013$, $p < 0.05$), (c) ses.MPD (F = 2.09, $r^2 = 0.004$, $p = 0.15$), and (d) ses.MNTD (F = 3.05, $r^2 = 0.007$, $p = 0.08$).

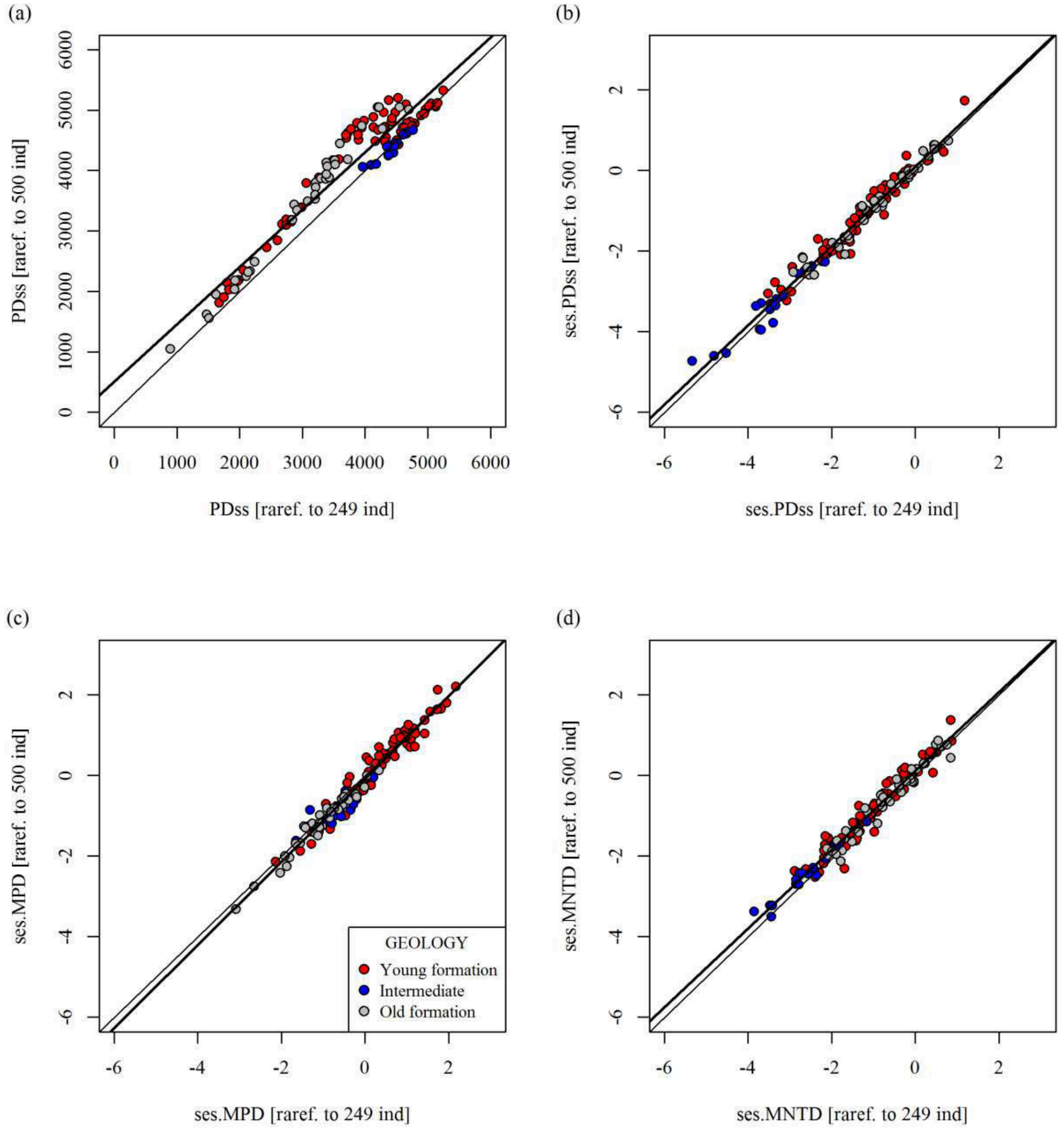

Figure S5. (a-d) Sensitivity analysis of phylogenetic diversity metrics for the tropical moist forest biome calculated using different number of individuals per plot. Values calculated using rarefaction procedure to 249 and 500 individuals per plot are compared. The regression fit (solid line) and the 1:1 (thin line) lines are similar, indicating that general patterns are conserved irrespective of the number of individuals used per plot in the analysis.

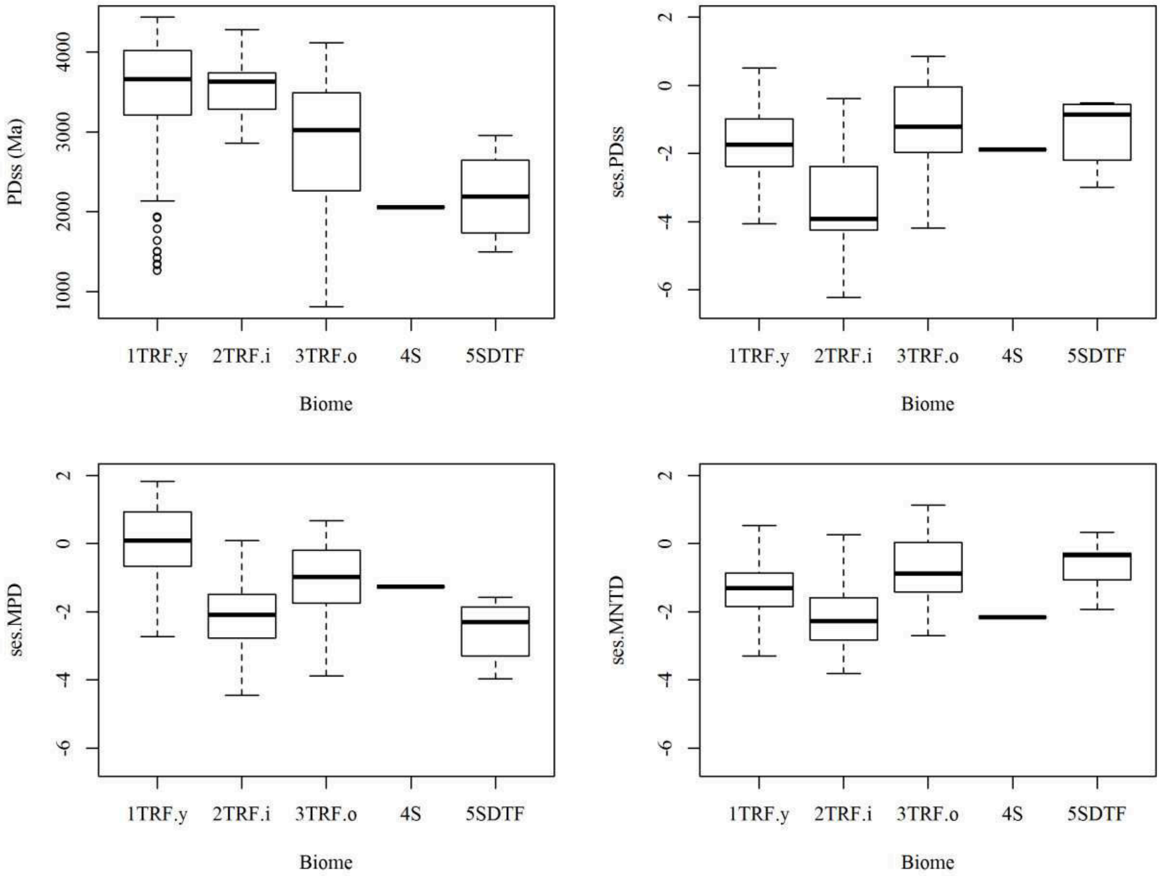

Figure S6. Variation in four phylogenetic diversity metrics across Amazonia calculated using the sequence-based genus-level phylogeny. Plots with more than 80% of species and individuals sampled in the genus-level phylogeny were used in the analysis: TRF.y = 111 plots, TRF.i = 41 plots, TRF.o = 95 plots, S = 1 plot, and SDTF = 9 plots.

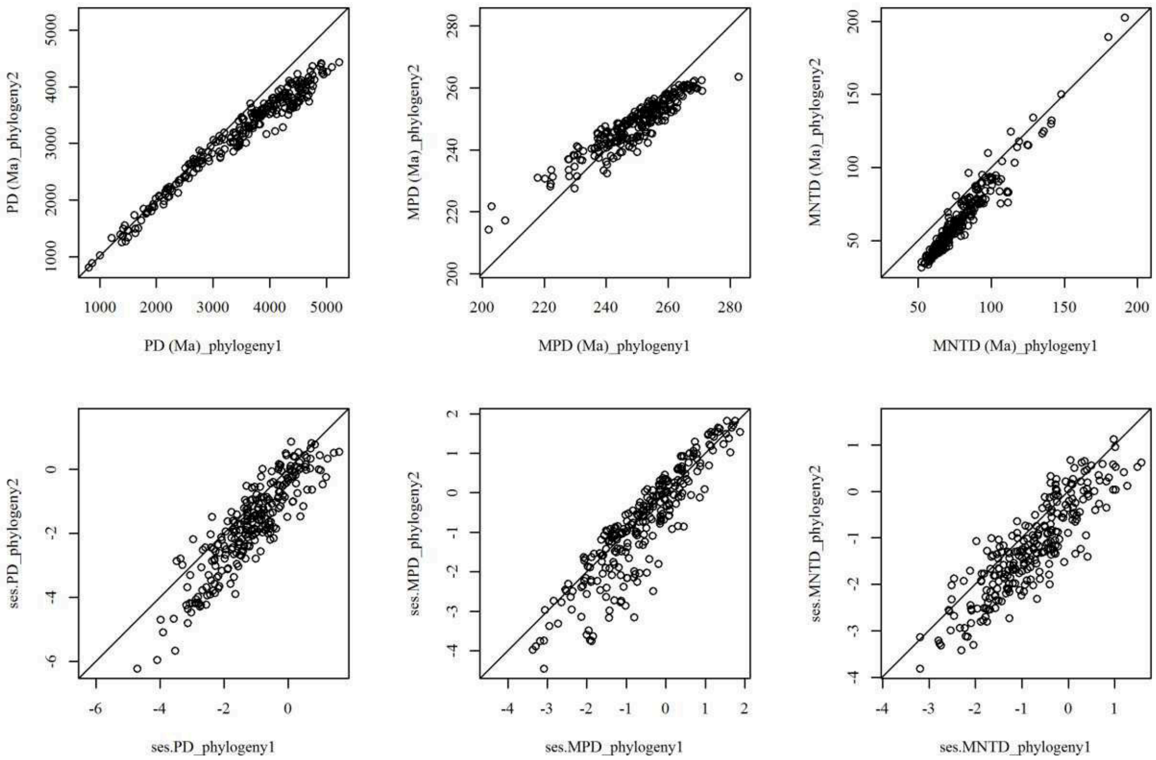

Figure S7. Sensitivity analysis of six phylogenetic diversity metrics calculated using the family-level phylogeny produced in PHYLOCOM (phylogeny 1) and the sequence-based genus-level phylogeny (phylogeny 2). The 1:1 lines are given in each graph (n = 257 plots).

Supplementary references

Bremer, B., Bremer, K., Chase, M.W., Fay, M.F., Reveal, J.L., Soltis, D.E., Soltis, P.S., Stevens, P.F., Anderberg, A.A., Moore, M.J., Olmstead, R.G., Rudall, P.J., Sytsma, K.J., Tank, D.C., Wurdack, K., Xiang, J.Q.Y., Zmarzty, S. & Angiosperm Phylogeny, G. (2009) An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. *Botanical Journal of the Linnean Society*, **161**, 105-121.

Drummond, A. & Rambaut, A. (2007) BEAST: Bayesian evolutionary analysis by sampling trees. *BMC Evolutionary Biology*, **7**, 214-222.

Gonzalez, M.A., Baraloto, C., Engel, J., Mori, S.A., Petronelli, P., Riera, B., Roger, A., Thebaud, C. & Chave, J. (2009) Identification of Amazonian trees with DNA barcodes. *PLoS ONE*, **4**, e7483.

Hollingsworth, P.M., Forrest, L.L., Spouge, J.L., Hajibabaei, M., Ratnasingham, S., van der Bank, M., Chase, M.W., Cowan, R.S., Erickson, D.L., Fazekas, A.J., Graham, S.W., James, K.E., Kim, K.J., Kress, W.J., Schneider, H., van AlphenStahl, J., Barrett, S.C.H., van den Berg, C., Bogarin, D., Burgess, K.S., Cameron, K.M., Carine, M., Chacon, J., Clark, A., Clarkson, J.J., Conrad, F., Devey, D.S., Ford, C.S., Hedderson, T.A.J., Hollingsworth, M.L., Husband, B.C., Kelly, L.J., Kesanakurti, P.R., Kim, J.S., Kim, Y.D., Lahaye, R., Lee, H.L., Long, D.G., Madrinan, S., Maurin, O., Meusnier, I., Newmaster, S.G., Park, C.W., Percy, D.M., Petersen, G., Richardson, J.E., Salazar, G.A., Savolainen, V., Seberg, O., Wilkinson, M.J., Yi, D.K., Little, D.P. & Grp, C.P.W. (2009) A DNA barcode for land plants. *Proceedings of the National Academy of Sciences of the United States of America*, **106**, 12794-12797.

Lopez-Gonzalez, G., Lewis, S., Burkitt, M. & Phillips, O. (2009) ForestPlots.net Database. Date of extraction [28/01/2013]. In, www.forestplots.net.

Lopez-Gonzalez, G., Lewis, S.L., Burkitt, M. & Phillips, O.L. (2011) ForestPlots.net: A web application and research tool to manage and analyse tropical forest plot data. *Journal of Vegetation Science*, **22**, 610-613.

Magallon, S. & Castillo, A. (2009) Angiosperm diversification through time. *American Journal of Botany*, **96**, 349-365.

Smith, S.A., Beaulieu, J.M. & Donoghue, M.J. (2010) An uncorrelated relaxed-clock analysis suggests an earlier origin for flowering plants. *Proceedings of the National Academy of Sciences*, **107**, 5897-5902.

Stamatakis, A. (2014) RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics*, **30**, 1312-1313.