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Phylogenetic diversity of Amazonian tree communities

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

Figure S1. Phylogenetic tree for the whole species pool for 283 floristic inventories.

Figure S2. Relationship between (a) phylogenetic diversity *sensu stricto* and the proportion of species of Magnoliids and Monocots, and between (b) mean pairwise phylogenetic distance and species richness.

Figure S3. Relationships between phylogenetic diversity metrics and the percentage of unidentified individuals excluded for each plot.

Figure S4. Sensitivity analysis of phylogenetic diversity metrics for the tropical moist forest biome calculated using different number of individuals per plot.

Understanding the distribution of phylogenetic diversity is critical to conservation prioritization and determining the origins of high species richness. We calculated the phylogenetic diversity (PD) present in 283 ~1 ha forest inventory plots from across Amazonia. We show that PD has a non-random spatial distribution. PD, measured as the sum of phylogenetic branch length in plots (PD *sensu stricto*, PDss), was highest in tree communities of central and western Amazonia. Because PDss is strongly correlated with species richness (SR), this is unsurprising. However, western Amazonian communities have higher PDss than predicted by SR alone, while central communities have lower than expected PDss. The Brazilian and Guiana Shields, while species poor and thus having low PDss, also have PDss greater than predicted by SR. We suggest that the excess PD in western Amazonia may be due to an easy-to-colonize environment (fertile, aseasonal), while the high values in the Shields may be due to their great age. Meanwhile, some particularly stressfull environments (white-sand and seasonally dry tropical forests) have lower than expected PDss, perhaps because the adaptations required in such environments present difficult to surmount evolutionary barriers. Conservation planning in Amazonia should consider PD and SR in future assessments.

Keywords: Amazon basin, phylogenetic diversity, savannas, seasonally dry tropical forests, species richness, white-sand forest

1. Introduction

A central task of biology is to quantify biodiversity and how it varies geographically [1]. Elucidating and understanding the dominant 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, Shannon-Wiener Index, 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, that quantify the lineage diversity of communities [2, 3].

Phylogenetic diversity (PD) is generally estimated as the total branch length of a phylogeny representing species in a community [2]. This metric tends to be 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 [4, 5]. However, some areas contain significantly greater or less PD than expected given their SR [6, 7], a pattern that could add complementary information about the evolutionary history and conservation significance of a site [8]. Some researchers have advocated other metrics that show less dependence on species richness, such as the mean phylogenetic distance between species in a community, as alternative metrics to represent the evolutionary diversity in communities [9-11]. The availability of different PD metrics, in conjunction with the recent developments of standardized floristic sampling across Amazonia [12, 13] and of a robust angiosperm phylogeny [14], now make it possible to examine how PD and its covariance with species richness vary at large spatial scales across the world's most species-rich tropical forest [see also 15]. By examining the PD of tree communities throughout Amazonia, we aim to provide insights into its biogeographical history and inform conservation prioritization.

Previous research [16] has shown tree species diversity in 1 ha plots across the Amazon to be highest in the western and central portions and lowest in the Guianan and Brazilian shields. Assuming that PD is correlated with SR, we would therefore expect that PD will be greatest in the western and central Amazon. However, 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 sediments of Pre-Cambrian origin [17], would have had the opportunity to accumulate lineage diversity over many millions years, and thus might have higher PD than expected given their low SR. In contrast, tree communities of western Amazonia overlying Pliocene and Pleistocene sediments from the Andes [17, 18] might be expected to show lower than expected PD because of the dominance of recent evolutionary radiations within certain clades [19, 20]. The branches leading to recently derived species should be short in comparison to the deep branches separating species from older diversification events [21]. Gentry [22] suggested that the Andean orogeny could have promoted high recent species diversification on the western Amazon fringe through repeated creation of new habitats and large-scale rearrangement of complex, dissected landscapes [see also 18]. Recent phylogenetic evidence has supported this notion, showing that radiations of some diverse Andean and pre-Andean genera apparently coincide with the uplift of the Andes [19, 20, 23].

Soil fertility and 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, while the poorest soils are found beneath white-sand forests that occur sporadically in small to large patches throughout the northern part of the basin [17]. In addition, the dry season varies from being essentially absent in the northwest to lasting 5-6 months in the southeast and some northern areas [24], where moist forests give way to savannas and seasonally dry tropical forest (SDTF). Some of these environmental conditions may represent stressful ecophysiological barriers that few lineages have been able to overcome [25, 26]. Thus an alternative hypothesis to the one above, based on substrate age, is that tree communities in areas of the Amazon with more potential ecophysiological barriers to entry (i.e. white-sand forests in north-western Amazonia and the Guiana Shield, savannas in south-western Amazonia, SDTF in the northern Andes and south-western Amazonia) will show the greatest negative deviation from expected PD given their SR [27].

We used a network of 283 forest inventory plots [RAINFOR; 28] to quantify the PD of tree communities and examine its spatial variation across Amazonia. We rarefied all plots to the same number of trees, and then calculated (i) the total phylogenetic branch length of all species occurring in each plot, PD *sensu stricto* [PDss; 2], (ii) the deviation from expected PD given SR [PDres; 6], and (iii) the mean pairwise phylogenetic distance among co-occurring species [MPDt; 11, 29]. We first tested the assumption that PDss largely depends on SR. We then tested the hypothesis, based on substrate age, that tree communities in the Guiana and Brazilian Shields will show the greatest PDres, while those in the western

Amazon will show the lowest PDres. While our sample sizes in savanna, SDTF, and white-sand forests are limited, we conducted a preliminary test of the hypothesis that tree communities in these stressful environments will show the lowest PDres. As MPDt is putatively independent of SR, we expected it to show the same patterns as PDres.

2. Methods

(a) Tree community plot data

In this study, we used a total of 283 inventory plots of the RAINFOR forest plot network [Date of extraction: 28/01/2013; 30; see supplementary material, Table S1]. Plots are generally one hectare in size (mean ± SD = 1.1 ± 0.6 ha) and sample all trees ≥ 10 cm diameter at breast height (DBH). We restricted analyses to old-growth forest plots. Each plot was treated as a community and classified into three main biomes (Figure 1): tropical moist forest, TMF (n = 267 plots), SDTF (n = 11), and savannas, 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.

The 267 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, while areas near to the Andes (western Amazonia and northern Andes) are dominated by younger sediments [TMF.y: < 20 Ma; 17] deposited mainly during the Pliocene and the Pleistocene [18] (Figure 1). All TMF plots were also classified by forest types: flooded forest (affected by the flooding of rivers or with a shallow water table), montane forest (at 1650 - 3000 m a.s.l.), terra firme forest (in the interfluvial plain on clayed or brown-sand soils), and white-sand forest (on white-sand soils). Note that, in our data set, not all of the forest types are represented for each of the geological formations (e.g. there were no communities of white-sand forests sampled overlaying the geological formations of intermediate age).

In total, the 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 [14], 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 (they were found in a total of 11 plots). Given this stochasticity and the strong effect of tree ferns and gymnosperms on phylogenetic diversity metrics (they are subtended by very long phylogenetic branches; [15, 31, 32]), we excluded them from phylogenetic diversity calculations. We also excluded all individuals not identified to species (13.6 %), while testing for the effect of doing so in the analyses (see below). The final dataset contained a total of 157,340 individuals, belonging to 3,868 species, 732 genera and 126 families of angiosperms.

(b) Phylogenetic tree and diversity metrics

A phylogenetic tree of the whole species pool (see supplementary material, Figure S1) was generated using Phylomatic in PHYLOCOM version 4.2 [33]. 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 [34]. 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.* [35]. 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 [36].

Three metrics were used to evaluate the evolutionary history present in communities, (i) phylogenetic diversity *sensu stricto* [PDss; 2], that is the total phylogenetic branch length of all species occurring in a given community, (ii) deviation from expected PDss given species richness (SR), that is a measure of the residuals from the relationship between PDss and SR [PDres; 6], and (iii) mean pairwise phylogenetic distance among co-occurring species [MPDt; 11, 29]. While other phylogenetic diversity metrics exist [e.g. 9, 10], these were chosen because of their simplicity and history of use in the literature [e.g. 6, 37, 38].

(c) Data assessment and analysis

To minimize the effects of sampling effort (i.e. plot size) and variation in tree density, we used a rarefaction procedure that standardized all plots to 249 individuals, which was the lowest observed number of individuals amongst all plots. Values for PDss, PDres, and MPDt for each rarefacted community were calculated using the package PICANTE [39] in the R Statistical Software version 2.15.1. SR was calculated as the total number of taxa in each rarefacted community. Each taxon was classified into one of the three major angiosperm clades (Magnoliids including Chloranthales, Monocots, and Eudicots) and the percentages of species and individuals in each clade were estimated. The mean of the phylogenetic diversity metrics, SR, and the proportion of major clades across 100 rarefactions were used for further analyses.

The relationship between the phylogenetic diversity metrics measured as PDss and MPDt were assessed against SR and the proportion of major clades. The level of significance of the deviations from the relationship of PDss on SR was tested for different biomes using a *t* test. The values of all three phylogenetic diversity metrics were compared among the different biomes using F-tests and Tukey tests. We also assessed the correlation of the phylogenetic diversity metrics with 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 PD metrics. Finally, we also re-analysed a subset of the data (n = 117 plots with large sample size) rarefying the plots to 500 individuals per sampling unit, to test the effect of sample size in the rarefaction procedure on estimating phylogenetic diversity.

3. Results

(a) 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 rarefacted 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, while 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. These values were similar when comparing percentages of individuals, except for Monocots, which tend to be more abundant in the western Amazon (Table 1). Early diverging clades such as Magnoliids and Monocots tend to have a higher percentage of species and individuals on young geological formations than on intermediate and old formations, while 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.

(b) Phylogenetic diversity metrics

Species richness strongly positively correlates with PDss ($r = 0.98$, $p < 0.001$; Figure 2a), following a power relationship ($\log(PD) \sim \log(SR) \approx PD = 230.6 \times SR^{0.7}$), which was a better fit than a linear relationship ($PD \sim SR \approx PD = 1160.0 + 37.1 \times SR$; $r = 0.92$, $p < 0.001$). We used the residuals of the power relationship as our measure of PDres ($= PD_{observed} - PD_{expected}$). A much weaker correlation was observed between species richness and MPDt ($r = 0.38$, $p < 0.001$; see supplementary material, Figure S2). In contrast, the percentage of species in Magnoliids + Monocots (i.e. = 1- Eudicots) correlates strongly with MPDt ($r = 0.88$, $p < 0.001$; Figure 2b), which is driven mostly by variation in the relative abundance of Magnoliids ($r = 0.88$, $p < 0.001$) rather than Monocots ($r = 0.27$, $p < 0.001$). The correlation of the percentage of species in major clades with PDss was mostly weaker ($r_{1\text{-Eudicots}} = 0.52$, $r_{Magnoliids} = 0.48$, $r_{Monocots} = 0.26$, all $p < 0.001$; see supplementary material, Figure S2).

(c) Spatial patterns

Our PD metrics show non-random spatial distributions across Amazonia (Figure 3). MPDt shows a strong longitudinal gradient, increasing from east to west ($r_{Longitude} = -0.45$, $p <$

0.001), while PDss ($r_{\mathrm{Latitude}} = 0.14$, $p < 0.05$; $r_{\mathrm{Longitude}} = -0.16$, $p < 0.05$) and PDres ($r_{\mathrm{Latitude}} = -0.15$, $p < 0.01$; $r_{\mathrm{Longitude}} = -0.14$, $p < 0.05$) show weaker, but still significant correlations with both latitude and longitude. PDss was greatest in communities on young and intermediate aged geological formations (Figure 3a), while PDres was greatest in communities on young and old geological formations (Figure 3b). MPDt was greatest in young geological formations (Figure 3c). These spatial patterns are conserved among forest types of the moist forest biome (Table 1). For all metrics, PD values of savannas were similar to moist forest communities, while SDTF consistently showed low phylogenetic diversity (Figure 3d-f).

PDss shows no relationship with the percentage of unidentified individuals excluded per plot ($r^2 = 0.002$, $p = 0.20$), while PDres ($r^2 = 0.02$, $p < 0.05$) and MPDt ($r^2 = 0.02$, $p < 0.05$) show weak relationships (see also supplementary material, Figure S3). In addition, for plots with sufficient sample size to assess, we found a strong 1:1 relationship between phylogenetic diversity metrics (PDres and MPDt) calculated with rarefactions of 500 versus 249 individuals (see supplementary material, Figure S4).

4. Discussion

Our results illustrate the non-random spatial distribution of phylogenetic diversity of tree communities across Amazonia. Consistent with previous studies (in savannas of North America [40] and in the Cape flora of South Africa [6]), phylogenetic diversity *sensu stricto* (PDss) in the Amazon shows a strong correlation with species richness (SR). Thus, communities of the most species-rich areas, central and western Amazonia [16], show the greatest PDss (Figure 3a). Interestingly, once the relationship between PDss and SR is taken into account, we found that western and central Amazonia show strikingly different patterns. Western Amazonian tree communities show significantly greater PDss than expected given their SR (i.e. strong positive PDres), while central Amazonian tree communities show significant negative PDres (Figure 3b). Among moist forests, communities of the Brazilian and Guianan Shields have the lowest values of PDss, but high PDres, on par with that found in western Amazonia. Among the drier biomes found on the edges of Amazonia, savannas have moderate PDss and high values of PDres, while seasonally dry tropical forests (SDTFs) have consistently low PDss and PDres (Figure 3d,e).

We found that the mean pairwise phylogenetic distance among co-occurring species (MPDt) does not correlate well with species richness, suggesting that it could be a better metric of phylogenetic diversity than PDss. However, we found that MPDt values depend primarily on how evenly taxa are distributed amongst the three major angiosperm clades (Magnoliids including Chloranthales, Monocots, and Eudicots), which is shown by the strong positive correlation between the MPDt values and the proportion of taxa in plots that are Magnoliids and Monocots (the two rarer clades; see Figure 2b). Thus, areas that have many Magnoliids and Monocots present (in our case western Amazonia), perhaps due simply to environmental conditions favourable to these early divergent taxa, show the greatest MPDt values. While it is important to have a measure of how evenly distributed taxa are across the major clades of a phylogeny, it is uncertain if MPDt is a useful metric upon which to make conservation decisions.

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

Communities on old geological substrates in the Brazilian and Guianan Shields and communities on young geological substrates showed equally high PDres (Figure 3e; TMF.o and TMF.y). Thus, the prediction that PDres would be positively correlated with substrate age was rejected. Nevertheless, we suggest that the high PDres found in the Guiana and

Brazilian Shields may be explained by their long-term geological history. Recent phylogenetic studies have shown that some of the most diverse and characteristic clades of the Shields are very old (e.g. *Licania*, ca. 46 Ma, [41]; *Pouteria*, ca. 60 Ma, Richardson, pers. comm.), and it seems diversity has been accumulating in these regions for many millions of years.

Rather, to understand the rejection of the hypothesis that geologically older substrates show the greatest PDres, we need to consider why tree communities of western Amazonia show such high PDres. That communities of western Amazonia show high PDss is unsurprising, as we have shown PDss to be strongly correlated with SR, and SR is substantially higher in the western Amazon [16]. However, much of this diversity is due to recently-radiated species-rich genera [22] such as *Inga* [19] and *Guatteria* [20], and short branches do not greatly increase phylogenetic diversity [21]. Another exceptional aspect of western Amazonian tree communities that must be considered is that they are occupied by lineages from the entirety of the angiosperm phylogeny. We propose that the fertile and aseasonal environments in the west may be easier for various lineages with diverse evolutionary backgrounds to invade. Moreover, the ability of diverse lineages to establish in the western Amazon may also be related to the high rates of disturbance and turnover in the region [42]. Finally, the complex geological configuration of western Amazonia [18, 43] may also contribute to high PDres by creating an environment suitable to maintaining high phylogenetic diversity.

(b) Do areas with more potential ecophysiological barriers show the lowest PD in their tree communities?

We expected that more extreme ecological conditions in seasonality and soil fertility may represent potential evolutionary barriers that few lineages have been able to overcome [25-27]. Both savannas and SDTF have a stressful dry season, but they show contrasting phylogenetic diversity patterns. While phylogenetic diversity metrics of savannas were similar to those of nearby communities in tropical moist forest, SDTF has consistently low phylogenetic diversity by all metrics (Figure 3d-f). Savannas and tropical moist forest communities may share similar lineages across the angiosperm phylogeny, a pattern that supports previous studies that suggested that savannas in south-western Amazonia are formed by the colonisations of lineages from nearby biomes that managed to adapt to fire around 4-10 Ma [44, 45]. Conversely, the low phylogenetic diversity values shown for SDTF communities suggest that fewer clades have succeeded in colonizing SDTF, and that consequently, SDTF is occupied principally by close relatives. However, our conclusions must be taken as preliminary given the low sample size and limited geographic extent of our savanna and SDTF plots.

Previous studies have indicated a strong habitat specialization in white-sand communities as indicated by the high number of individuals that belong to white-sand specialist species [46], and by the distinct herbivore and ecophysiological defences that these species have evolved to live in such poor-fertile soils [47]. Therefore, we also expected that white-sand forests would have a high frequency of closely related species and low phylogenetic diversity. Our results showed that only white-sand communities of the Guiana Shield have low PDres values (comparable to SDTF; Table 1). In contrast, higher values of PDres were found in the small patches of white-sand forests of north-western Amazonia, which may indicate a higher influence by the regional pool (i.e. species present in the surrounding terra firme forest) than in the larger, more contiguous white-sand patches of the Guiana Shield.

5. Conclusions

Our study has revealed a non-random spatial distribution of phylogenetic diversity across Amazonia, with some areas holding significantly more, or less, phylogenetic diversity than expected from their species richness alone. These results indicate that species richness may not give sufficient information to establish conservation priorities for evolutionary diversity in Amazonia. Other metrics, in particular PDres, should be considered [6, 8]. For example, the PDres differs between forests of central and western Amazonia, both of which have communities that are exceptionally species rich. Communities of central Amazonia are occupied by phylogenetically close relatives, while more distantly related taxa occur in western Amazonian forests. Moreover, the Brazilian and Guiana Shields, while species poor, also have great PDres. We suggest that the high PDres of the Shields is due to the accumulation of many lineages over their long history, while the high PDres of the western Amazon is due to the easy-to-colonize fertile and aseasonal environments present there. In addition, specific habitats elsewhere in the Amazon basin (e.g. white-sand and seasonally dry tropical forests) may require adaptations that are more difficult to evolve, and thus are dominated by close relatives from fewer lineages. 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 may need to incorporate phylogenetic information in order to explicitly account for the deviation of phylogenetic diversity from expectations based on species richness.

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Data accessibility: Dataset of the RAINFOR forest plot network is available at https://www.forestplots.net/

References

1. Myers N., Mittermeier R.A., Mittermeier C.G., da Fonseca G.A.B., Kent J. 2000 Biodiversity hotspots for conservation priorities. *Nature* **403**(6772), 853-858. (doi:10.1038/35002501).

2. Faith D.P. 1992 Conservation evaluation and phylogenetic diversity. *Biological Conservation* **61**(1), 1-10. (doi:10.1016/0006-3207(92)91201-3).

3. Vane-Wright R.I., Humphries C.J., Williams P.H. 1991 What to protect?—Systematics and the agony of choice. *Biological Conservation* **55**(3), 235-254. (doi:10.1016/0006-3207(91)90030-d).

4. 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**(1), 99-105. (doi:10.1016/s0006-3207(00)00103-8).

5. Rodrigues A.S.L., Gaston K.J. 2002 Maximising phylogenetic diversity in the selection of networks of conservation areas. *Biological Conservation* **105**(1), 103-111. (doi:10.1016/s0006-3207(01)00208-7).

6. 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., et al. 2007 Preserving the evolutionary potential of floras in biodiversity hotspots. *Nature* **445**(7129), 757-760. (doi:10.1038/nature05587).

7. 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. *Proc Natl Acad Sci U S A* **99**(4), 2067-2071. (doi:10.1073/pnas.251680798).

8. Winter M., Devictor V., Schweiger O. 2013 Phylogenetic diversity and nature conservation: Where are we? *Trends Ecol Evol* **28**(4), 199-204. (doi:10.1016/j.tree.2012.10.015).

9. Helmus M.R., Bland T.J., Williams C.K., Ives A.R. 2007 Phylogenetic measures of biodiversity. *Am Nat* **169**(3), E68-E83. (doi:10.1086/511334).

10. 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. *Ecol Lett* **13**(1), 96-105. (doi:10.1111/j.1461-0248.2009.01405.x).

11. Webb C.O., Ackerly D.D., McPeek M.A., Donoghue M.J. 2002 Phylogenies and community ecology. *Annu Rev Ecol Syst* **33**, 475-505. (doi:10.1146/annurev.ecolysis.33.010802.150448).

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

13. Malhi Y., Phillips O.L., Lloyd J., Baker T., Wright J., Almeida S., Arroyo L., Frederiksen T., Grace J., Higuchi N., et al. 2002 An international network to monitor the structure, composition and

dynamics of Amazonian forests (RAINFOR). *J Veg Sci* **13**(3), 439-450. (doi:10.1111/j.1654-1103.2002.tb02068.x).

14. 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., et al. 2009 An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. *Bot J Linnean Soc* **161**(2), 105-121. (doi:10.1111/j.1095-8339.2009.00996.x).

15. Chave J., Chust G., Thebaud C. 2007 The importance of phylogenetic structure in biodiversity studies. In *Scaling Biodioversity* (eds. Storch D., Marquet P.L., Brown J.H.), pp. 150-167. UK, Cambridge University Press.

16. ter Steege H., Pitman N., Sabatier D., Castellanos H., Van Der Hout P., Daly D.C., Silveira M., Phillips O., Vasquez R., Van Andel T., et al. 2003 A spatial model of tree α-diversity and tree density for the Amazon. *Biodivers Conserv* **12**(11), 2255-2277. (doi:10.1023/a:1024593414624).

17. 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**(6), 1415-1440. (doi:10.5194/bg-8-1415-2011).

18. 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., et al. 2010 Amazonia through time: Andean uplift, climate change, landscape evolution, and biodiversity. *Science* **330**(6006), 927-931. (doi:10.1126/science.1194585).

19. 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**(5538), 2242-2245. (doi:10.1126/science.1061421).

20. 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. *Mol Phylogenet Evol* **44**(1), 399-411. (doi:10.1016/j.ympev.2007.02.017).

21. Swenson N.G. 2009 Phylogenetic resolution and quantifying the phylogenetic diversity and dispersion of communities. *PLoS ONE* **4**(2), e4390. (doi:10.1371/journal.pone.0004390).

22. Gentry A.H. 1982 Neotropical floristic diversity: Phytogeographical connections between Central and South-America, Pleistocene climatic fluctuations, or an accident of the Andean orogeny. *Ann MO Bot Gard* **69**(3), 557-593. (doi:jstor.org/stable/2399084).

23. Särkinen T.E., Newman M.F., Maas P.J.M., Maas H., Poulsen A.D., Harris D.J., Richardson J.E., Clark A., Hollingsworth M., Pennington R.T. 2007 Recent oceanic long-distance dispersal and divergence in the amphi-Atlantic rain forest genus *Renealmia* L.f. (Zingiberaceae). *Mol Phylogenet Evol* **44**(3), 968-980. (doi:10.1016/j.ympev.2007.06.007).

24. 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**(7), 388-396. (doi:10.1579/0044-7447-30.7.388).

25. Miller E.T., Zanne A.E., Ricklefs R.E. 2013 Niche conservatism constrains Australian honeyeater assemblages in stressful environments. *Ecol Lett* **16**(9), 1186-1194. (doi:10.1111/ele.12156).

26. Anacker B.L., Harrison S.P. 2012 Historical and ecological controls on phylogenetic diversity in Californian plant communities. *Am Nat* **180**(2), 257-269. (doi:jstor.org/stable/10.1086/666650).

27. 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**(11), 1183-1191. (doi:10.1111/geb.12069).

28. Peacock J., Baker T.R., Lewis S.L., Lopez-Gonzalez G., Phillips O.L. 2007 The RAINFOR database: monitoring forest biomass and dynamics. *J Veg Sci* **18**(4), 535-542. (doi:10.1111/j.1654-1103.2007.tb02568.x).

29. Webb C.O. 2000 Exploring the phylogenetic structure of ecological communities: An example for rain forest trees. *Am Nat* **156**(2), 145-155. (doi:jstor.org/stable/10.1086/303378).

30. 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. *J Veg Sci* **22**(4), 610-613. (doi:10.1111/j.1654-1103.2011.01312.x).

31. Faith D.P., Reid C.A.M., Hunter J. 2004 Integrating phylogenetic diversity, complementarity, and endemism for conservation assessment. *Conservation Biology* **18**(1), 255-261. (doi:10.1111/j.1523-1739.2004.00330.x).

32. Kembel S.W., Hubbell S.P. 2006 The phylogenetic structure of a Neotropical forest tree community. *Ecology* **87**(7), S86-S99. (doi:10.1890/0012-9658(2006)87[86:TPSOAN]2.0.CO;2).

33. Webb C.O., Ackerly D.D., Kembel S.W. 2008 Phylocom: Software for the analysis of phylogenetic community structure and trait evolution. *Bioinformatics* **24**(18), 2098-2100. (doi:10.1093/bioinformatics/btn358).

34. Webb C.O., Donoghue M.J. 2005 Phylomatic: Tree assembly for applied phylogenetics. *Mol Ecol Notes* **5**(1), 181-183. (doi:10.1111/j.1471-8286.2004.00829.x).

35. Wikström N., Savolainen V., Chase M.W. 2001 Evolution of the angiosperms: Calibrating the family tree. *Proc R Soc Lond B* **268**(1482), 2211-2220. (doi:10.1098/rspb.2001.1782).

36. Gastauer M., Meira-Neto J.A.A. 2013 Avoiding inaccuracies in tree calibration and phylogenetic community analysis using Phylocom 4.2. *Ecological Informatics* **15**(0), 85-90. (doi:10.1016/j.ecoinf.2013.03.005).

37. 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**(4), 552-565. (doi:10.1111/j.1600-0587.2010.06548.x).

38. 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. *J Ecol* **98**(1), 137-146. (doi:10.1111/j.1365-2745.2009.01607.x).

39. 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**(11), 1463-1464. (doi:10.1093/bioinformatics/btq166).

40. Cadotte M.W., Dinnage R., Tilman D. 2012 Phylogenetic diversity promotes ecosystem stability. *Ecology* **93**(8s), S223-S233. (doi:10.1890/11-0426.1).

41. Bardon L., Chamagne J., Dexter K.G., Sothers C.A., Prance G.T., Chave J. 2013 Origin and evolution of Chrysobalanaceae: insights into the evolution of plants in the Neotropics. *Bot J Linnean Soc* **171**(1), 19-37. (doi:10.1111/j.1095-8339.2012.01289.x).

42. Quesada C.A., Phillips O.L., Schwarz M., Czimczik C.I., Baker T.R., Patiño S., Fyllas N.M., Hodnett M.G., Herrera R., Almeida S., et al. 2012 Basin-wide variations in Amazon forest structure and function are mediated by both soils and climate. *Biogeosciences* **9**(6), 2203-2246. (doi:10.5194/bg-9-2203-2012).

43. Higgins M.A., Ruokolainen K., Tuomisto H., Llerena N., Cardenas G., Phillips O.L., Vásquez R., Räsänen M. 2011 Geological control of floristic composition in Amazonian forests. *J Biogeogr* **38**(11), 2136-2149. (doi:10.1111/j.1365-2699.2011.02585.x).

44. 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. *Proc Natl Acad Sci U S A* **106**(48), 20359-20364. (doi:10.1073/pnas.0903410106).

45. Simon M.F., Pennington R.T. 2012 Evidence for adaptation to fire regimes in the tropical savannas of the Brazilian cerrado. *Int J Plant Sci* **173**(6), 711-723. (doi:10.1086/665973).

46. 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. *Ann MO Bot Gard* **97**(3), 283-305. (doi:10.3417/2008068).

47. Fine P.V.A., Mesones I., Coley P.D. 2004 Herbivores promote habitat specialization by trees in Amazonian forests. *Science* **305**(5684), 663-665. (doi:10.1126/science.1098982).

Table and figure captions

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), deviations from expected PDss accounting for species richness (PDres), and mean pairwise phylogenetic distance among co-occurring species (MPDt) are given in millions of years (Ma)).

Figure 1. Location of 283 permanent RAINFOR plots indicating geological formations and biomes in South America. Geographical regions used in the text are indicated in bold.

Figure 2. Relationship between (a) phylogenetic diversity *sensu stricto* and species richness, and between (b) mean pairwise phylogenetic distance among co-occurring species and the proportion of species of Magnoliids and Monocots (= 1 - Eudicots). Tropical moist forest biome is classified based on maximum age of geological formations [young: < 20 Ma; intermediate: 20-100 Ma, old: > 500 Ma; 17].

Figure 3. (a-c) Variation in the spatial distribution and (d-f) among biomes of phylogenetic diversity in South America. Phylogenetic diversity *sensu stricto* (PDss), deviations from expected PDss accounting for species richness (PDres), and mean pairwise phylogenetic distance among co-occurring species (MPDt) are provided in different columns. Maps show mean values of PD for tree inventories in one-degree grid. 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; 17]. 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; $p < 0.05$). Asterisks indicate the level of significance of PDres (*t* test; * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$), i.e. communities with higher or lower PDss values than expected by their species richness.

Table 1

Biome (max. geological age)	Forest type	Nº of plots	Sample area (ha)	Indiv. ID to spp (%)*	Species & individuals (mean, %)						Mean diversity values			
					Magnoliids		Monocots		Eudicots		SR	PDss (Ma)	PDres (Ma)	MPDt (Ma)
					spp	ind	spp	ind	spp	ind				
Tropical moist forest (< 20 Ma)	Flooded	12	17	86	16	15	6	18	78	67	72	3,963	83	260
	Montane	16	16	80	12	10	1	1	87	89	29	2,180	78	255
	Terra firme	88	97	85	14	14	5	14	81	72	77	4,101	55	256
	White sand	4	4	83	10	5	5	5	85	91	42	2,839	192	254
Tropical moist forest (20 - 100 Ma)	Flooded	2	2	73	9	5	0	0	90	95	72	3,478	-409	242
	Terra firme	39	54	85	12	9	1	2	87	89	88	4,200	-255	248
Tropical moist forest (> 500 Ma)	Flooded	17	16	89	5	4	2	4	93	92	34	2,368	61	238
	Terra firme	85	94	87	10	10	3	6	87	85	56	3,310	54	247
	White sand	4	4	87	7	1	0	0	93	99	22	1,608	-178	233
Savanna	Savanna	5	4	100	5	4	2	2	93	94	47	3,105	189	239
SDTF	Dry forest	11	12	96	2	1	3	3	95	96	35	2,214	-183	223
TOTAL		283	320	86	11	10	3	8	86	82	63	3,510	3	249

* The mean proportion of individuals identified to species.

Figure 1

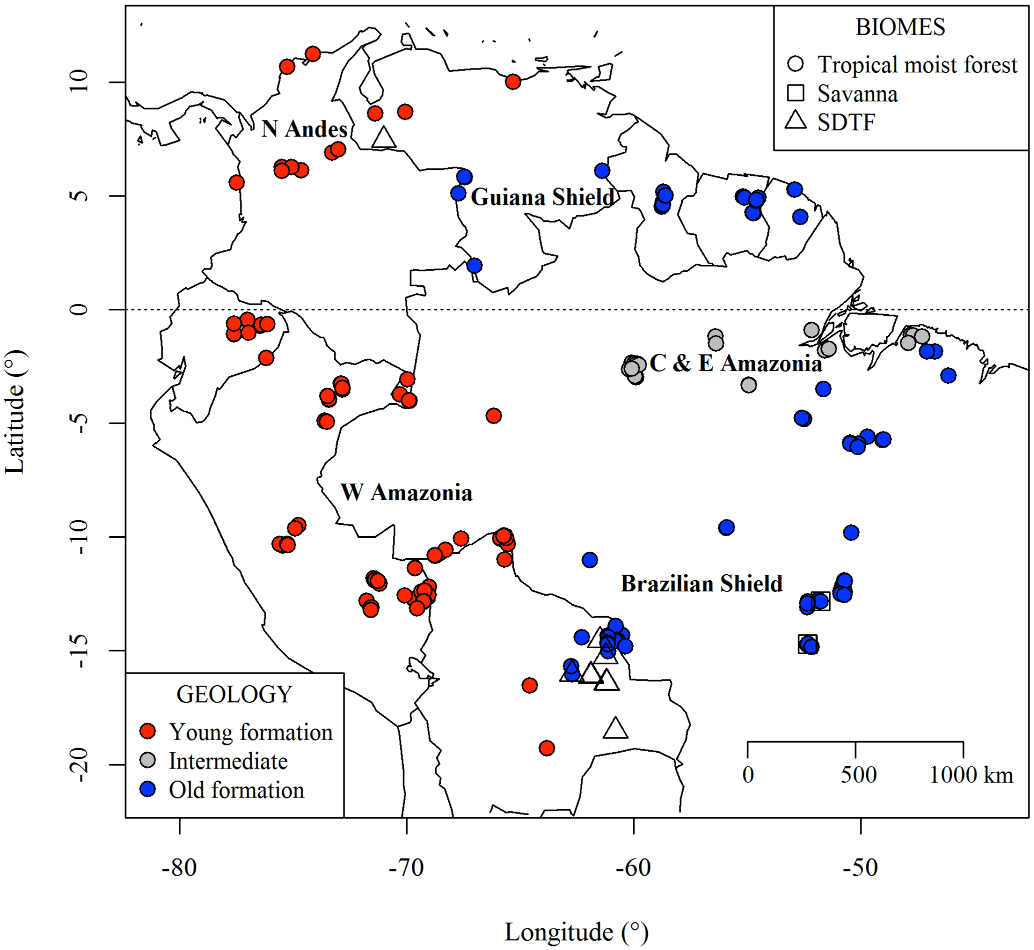

BIOMES
○ Tropical moist forest
☐ Savanna
△ SDTF
N Andes
Guiana Shield
C & E Amazonia
W Amazonia
Brazilian Shield
GEOLOGY
● Young formation
● Intermediate
● Old formation
0
500
1000 km
10
5
0
-5
-10
-15
-20
Latitude (°)
-80
-70
-60
-50
Longitude (°)

Figure 2

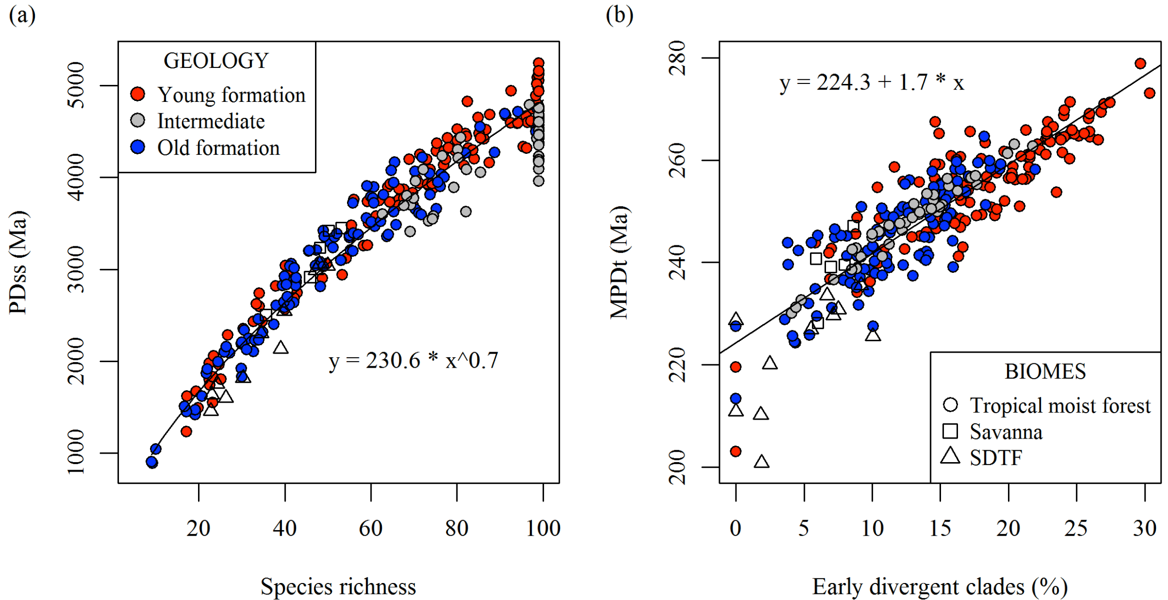
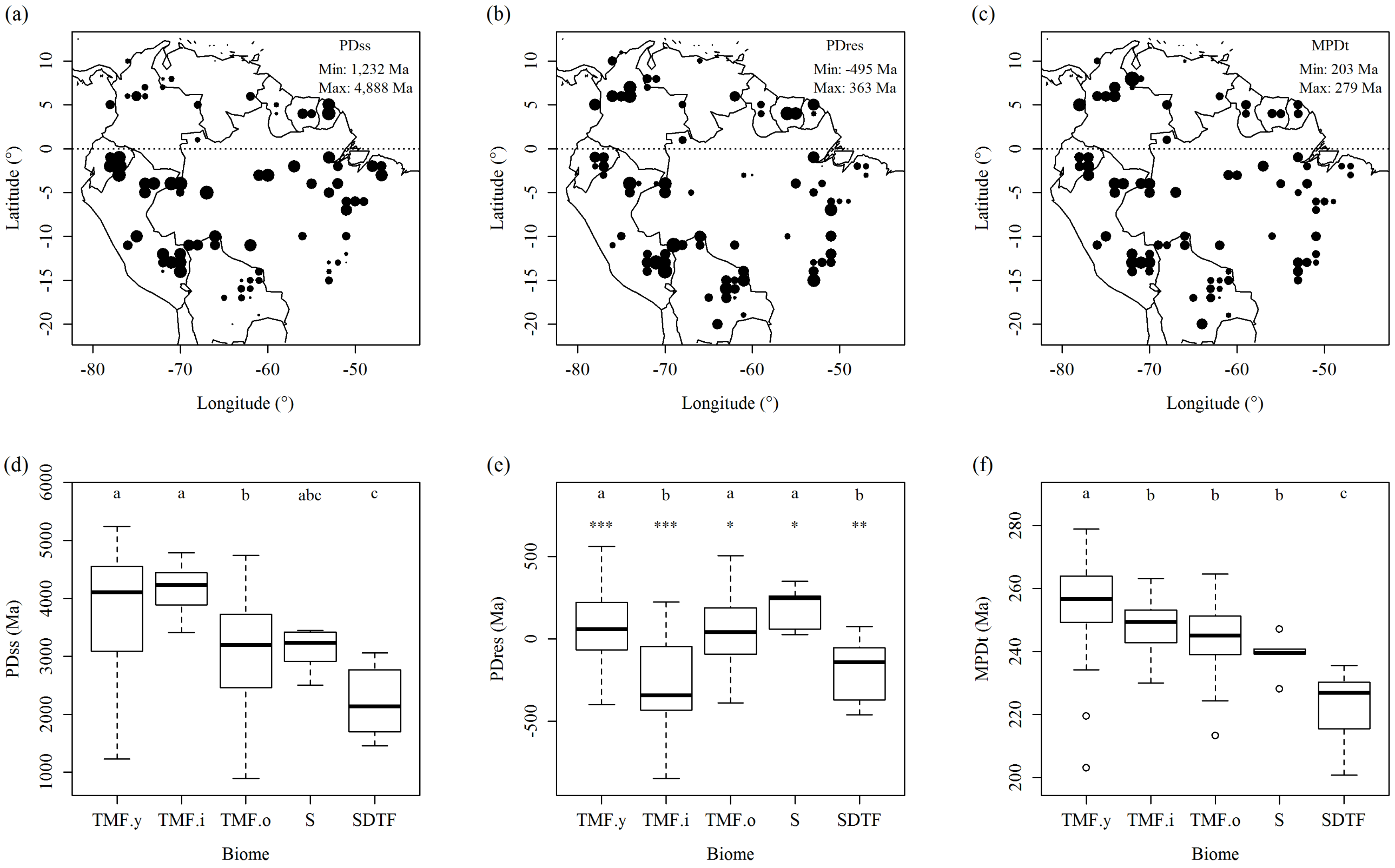

(a)
GEOLOGY
Young formation
Intermediate
Old formation
PDss (Ma)
1000
2000
3000
4000
5000
y = 230.6 * x^0.7
20
40
60
80
100
Species richness
(b)
y = 224.3 + 1.7 * x
BIOMES
Tropical moist forest
Savanna
SDTF
MPDt (Ma)
200
220
240
260
280
0
5
10
15
20
25
30
Early divergent clades (%)

Figure 3


(a)
PDss
Min: 1,232 Ma
Max: 4,888 Ma
(b)
PDres
Min: -495 Ma
Max: 363 Ma
(c)
MPDt
Min: 203 Ma
Max: 279 Ma
Latitude (°)
10
5
0
-5
-10
-15
-20
Longitude (°)
-80
-70
-60
-50
(d)
PDss (Ma)
1000
2000
3000
4000
5000
6000
a a b abc c
(e)
PDres (Ma)
-500
0
500
a b a a b
*** *** * * **
(f)
MPDt (Ma)
200
220
240
260
280
a b b b c
TMF.y
TMF.i
TMF.o
S
SDTF
Biome