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ABSTRACT

Amazonian tree species vary enormously in their total abundance and range size, while Amazonian tree genera vary greatly in species richness. Here, we construct a phylogenetic hypothesis that represents half of Amazonian tree genera in order to analyse evolutionary patterns of range size, abundance, and species richness. We find several clear, broad-scale patterns. Firstly, there is significant phylogenetic signal for all three characteristics, i.e. closely related genera tend to have similar numbers of species and similar mean range size and abundance. Additionally, the species richness of genera shows a significant, negative relationship with the mean range size and abundance of their constituent species, while mean range size and abundance are significantly, positively correlated. These correlations are stronger in the raw data, but still significant when using phylogenetically independent contrasts. We suggest that tree stature and/or other phylogenetically related biological traits underlie these results. Lineages comprised of small-statured trees show greater species richness and smaller range sizes and abundances. Lastly, the phylogenetic signal that we evidence for range size suggests that should many small ranged species go extinct, greater phylogenetic diversity may be lost than expected if range size were distributed randomly across the phylogeny.

Key Words: Amazon, diversification, trees, range size, hyperdominance, phylogenetic signal

Introduction

Some Amazonian tree species attain incredibly high abundance (tens to hundreds of millions of mature individuals), while most have small populations sizes, numbering in the thousands to tens of thousands (ter Steege *et al.* 2013). Similarly, the range of some Amazonian tree species extends across the entire Amazon basin, while most are restricted to much smaller areas (Kristiansen *et al.* 2009). A similar imbalance is observed in species to genus ratios. Over half of all Amazonian tree species belong to genera with 100 or more species, while the majority of genera (52%) have ten or fewer species (Gentry 1993). Recent studies have begun to document variation in the range size (Feeley & Silman 2009) and abundance (ter Steege *et al.* 2013) of Amazonian tree species and in the species richness of Amazonian tree genera (Baker *et al.* 2014), but these studies have largely failed to find causal factors to explain the variation (although see Baker *et al.* 2014). Here, we explore broad-scale evolutionary patterns for these characteristics for the first time using a newly derived, genus-level phylogeny that covers half of all Amazonian tree genera.

Methods

We intersected a list of all Neotropical tree genera (from ctfs.arnarb.harvard.edu/webatlas/neotropicaltree) with a list of Amazonian plant species (Feeley & Silman 2009) in order to generate a list of Amazonian tree species. The Feeley and Silman (2009) dataset additionally includes estimates of range size for all species. We obtained estimates for the total abundance of Amazonian tree species from ter Steege *et al.* (2013).

We obtained sequences of the *rbc*L plastid gene for 631 Amazonian angiosperm tree genera (Table S1), with 568 sequences coming from Genbank (www.ncbi.nlm.nih.gov/genbank/) and an additional 64 genera being newly sequenced following protocols outlined in Baraloto *et al.* (2012). We obtained sequences of the *mat*K plastid gene from Genbank for 452 of the 631 genera with *rbcL* data (Table S1). Sequences were aligned using the MAFFT software (Katoh & Standley 2013) and then manually checked and edited. Preliminary phylogenetic analyses allowed us to exclude sequences from GenBank that likely represent taxonomic misidentifications.

We estimated an initial phylogeny using maximum likelihood analysis in RAxML v8.0.0 (Stamatakis, Hoover & Rougemont 2008), on the CIPRES web server (www.phylo.org). We included sequences of *Amborella trichopoda* (Amborellaceae) and *Nymphaea alba* (Nymphaeaceae) as outgroups. This initial tree was used as a starting point for simultaneous topology and divergence time estimation in the software BEAST v1.82 (Drummond & Rambaut 2007). We implemented fossil-based age constraints for 25 nodes distributed across the phylogeny (see Table S2).

For each genus in the phylogeny, we calculated the mean range size and abundance for all constituent species in the Feeley and Silman (2009) and ter Steege *et al.* (2013) datasets. Of the 631 genera in the phylogeny, 493 had an abundance estimate for at least one species in ter Steege *et al.* (2013). We considered the number of species for each genus in the Feeley and Silman (2009) dataset as an estimate of the species richness of that genus in the Amazon. As an alternative estimate, we used the Neotropical species richness estimates for genera in Gentry

(1993). We assessed correlations amongst these genus-level characteristics, both in the raw data and using phylogenetically independent contrasts.

We tested for phylogenetic signal for each of these genus-level characteristics using Pagel's λ (Freckleton, Harvey & Pagel 2002). Under Brownian motion evolution, where trait values drift randomly over evolutionary time and where the phylogenetic relationships of taxa perfectly predict the covariance among taxa for trait values, the expected value of λ is one. When the phylogenetic relationships of taxa do not predict the covariance at all, the expected value of λ is zero. We compared the fit of different values for λ (one, zero and the maximum likelihood estimate) using the Akaike information criterion (AIC).

In order to determine which lineages may be responsible for significant phylogenetic signal for a given characteristic (e.g. mean range size of genera), we used the following approach. We first estimated the ancestral value at each node in the phylogeny using maximum likelihood ancestral state reconstruction (Schluter *et al.* 1997). We then randomised the tips of the phylogeny 1000 times, reconstructed ancestral values at nodes each time, and compared the observed reconstructed value to that across the randomisations. If the observed value for a node was greater than that in 97.5% of the randomisations, we considered the lineage descending from that node to show significantly high values for the trait, while if the observed value was lower than 2.5% of the randomisations, we considered the lineage to show significantly low values.

Results

The phylogeny derived from these sequences spans from the Magnoliids to the Asterids, thus encompassing all major lineages of angiosperms (Fig. 1). Most orders and families were monophyletic in the phylogeny with the notable (previously known) exceptions of Olacaceae and Icacinaceae, while the large-scale phylogenetic relationships are largely in agreement with those from recent, angiosperm-wide phylogenetic analyses (*e.g.* Magallón *et al.* 2015).

The species richness of genera is negatively correlated with mean range size ($r = -0.40$, $p < 0.001$) and mean abundance ($r = -0.38$, $p < 0.001$). These relationships are weaker, but still significant, when using phylogenetically independent contrasts (PICs), indicating that phylogenetically related traits partially underlie the correlations (mean range size PICs: $r = -0.28$, $p < 0.001$; mean abundance PICs: $r = -0.24$, $p < 0.001$; Fig. 2). Meanwhile, mean range size and abundance of genera are strongly positively correlated, using both the raw data and PICs ($r = 0.44$, $p < 0.001$; PICs: $r = 0.43$, $p < 0.001$). All of the genus-level characteristics show significant phylogenetic signal, but less than what would be expected under a Brownian motion model of evolution (Table 1).

Significant phylogenetic signal for these characteristics is driven by significantly high or low values in many lineages (Fig. 1, Table S3). Diverse lineages in the Magnoliids and the Asterids show high species richness and low mean range size and abundance, including the Lamiales and multiple lineages in the Rubiaceae and Solanales. One marked exception to the general pattern in the Asterids is Lecythidaceae, which shows low species richness and high abundance. Meanwhile, diverse lineages in the Rosids show low species richness and high mean range size and abundance, including Euphorbiaceae, Salicaceae and Moraceae. Within the Rosids, the

137 exception to this pattern is found in multiple lineages in the Myrtales, including the
138 Melastomataceae, which show a pattern similar to most lineages in the Asterids. The
139 Leguminosae (Fabaceae), the most genus-rich family in our dataset, does not show any
140 significant departures from null expectations, although individual lineages therein show low
141 species richness and high mean range size. Within the monocots, the Arecaceae show
142 significantly low mean range size, while one lineage (*Iriartea* with *Socratea*) shows significantly
143 high abundance.
144
145 All results concerning species richness were highly similar when analyses alternatively used
146 species richness estimates from Gentry (1993).
147
148 **Discussion**
149 Our analyses have revealed that fundamental characteristics of Amazonian tree genera, such as
150 their species richness and mean range size, show strong relationships with phylogeny (Fig. 1)
151 and with each other (Fig. 2). Closely related genera have similar numbers of species and are
152 comprised of species with similar range sizes and abundances, while the species richness of
153 genera shows a significant negative correlation with mean range size and abundance. This
154 negative relationship is pervasive across multiple phylogenetic scales. At a broad scale, we found
155 that various lineages in the Rosids are comprised of genera that show low species richness and
156 high mean range size and abundance, while lineages in the Magnoliids and Asterids show the
157 opposite pattern.
158

159 Many of the lineages in our study that show high species richness and small geographic ranges
160 (e.g. Myrtaceae, Melastomataceae, Rubiaceae, Asterales, Solanales, and Lamiales) tend to be
161 small in stature. Previous studies have shown a positive relationship between the height of
162 Amazonian trees and their range size (Kristiansen *et al.* 2009, Ruokolainen *et al.* 2002). Such a
163 relationship may be due to larger-statured trees being able to disperse their seeds greater
164 distances, likely through greater fecundity, which would increase the chances that at least some
165 seeds make it a long distance and would, for animal-dispersed species, potentially attract more
166 dispersers. Increased dispersal ability would also increase gene flow among distant populations,
167 which, in turn, could reduce opportunities for allopatric isolation and contribute to reduced
168 diversification. Smaller statured trees may also have shorter generation times, which could
169 contribute to increased diversification (Baker *et al.* 2014). Thus, small-stature may be a
170 biological trait that spurs diversification and may also underlie the negative correlation between
171 mean range size and species richness of genera.
172
173 Small-statured lineages also show lower abundances, although this is partly, if not entirely,
174 explained by the abundance estimates being derived from tree plots that survey individuals >10
175 cm diameter at breast height (ter Steege *et al.* 2013). In any case, we are keen to emphasise that
176 the genus-level characteristics that we studied here do not represent biological traits *per se*, but
177 rather reflect underlying biological traits that are driving the observed phylogenetic signal and
178 correlations. Traits other than tree stature (*e.g.* dispersal syndrome) may also show phylogenetic
179 signal and be responsible for the observed correlations; large-scale compilations of trait data for
180 Amazonian trees are clearly needed to advance our understanding of these patterns.
181

182 The mean range size of genera shows higher phylogenetic signal than mean abundance or species
183 richness, and it is the characteristic most relevant for conservation. Should many small-ranged
184 species go extinct, more phylogenetic diversity may be lost than if range size were distributed
185 randomly across the phylogeny as deeper phylogenetic branches would be more likely to be lost
186 (Purvis *et al.* 2000).
187
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196
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Data accessibility

DNA sequences: Genbank accession, see Table S1. New sequences are in the process of being uploaded to Genbank.

Phylogeny: TreeBASE, http://purl.org/phylo/treebase/phylows/study/TB2:S19277?x-access-code=38f1545d97977839af2bf6a9498817a7&format=html

Authors' contributions

KD and JC contributed to the design of the study, acquisition and analysis of data, and to writing the manuscript. Both authors approve of the final version.

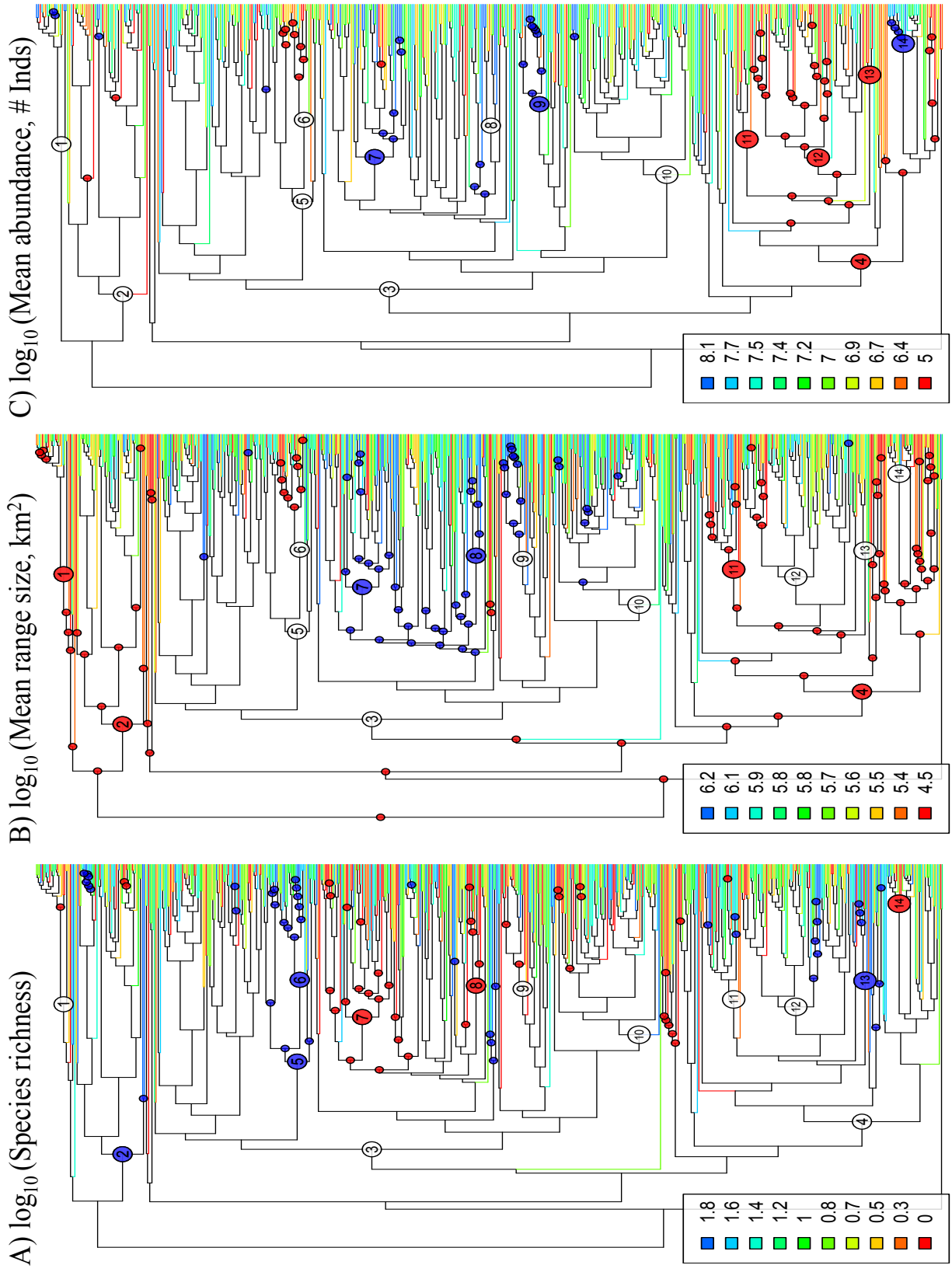
Table 1: ΔAIC values for different evolutionary models of trait evolution for genus-level characteristics and for different values of Pagel's λ.

Genus attribute	Evolutionary Model	λ	ΔAIC
log (Species richness)	estimated λ	0.32	0
	no phylogenetic dependence	0	-10.7
	Brownian motion	1	-215.4
log (Mean range size)	estimated λ	0.41	0
	no phylogenetic dependence	0	-65.0
	Brownian motion	1	-246.5
log (Mean abundance)	estimated λ	0.32	0
	no phylogenetic dependence	0	-33.4
	Brownian motion	1	-283.4

Figure 1: Phylogeny of 631 Amazonian tree genera with terminal branches coloured according to the **(A)** species richness, **(B)** mean range size, and **(C)** mean abundance of genera. The following numbered nodes are mentioned in the main text: 1=Arecaceae, 2=Magnoliids, 3=Rosids, 4=Asterids, 5=Myrtales, 6=Melastomataceae, 7=Euphorbiaceae, 8=Salicaceae, 9=Moraceae, 10=Leguminosae, 11=Lamiales, 12=Rubiaceae, 13=Solanales, and 14=Lecythidaceae. Nodes that are coloured blue indicate lineages whose constituent genera show significantly higher values for the given genus-level characteristic than expected by chance, while nodes coloured red show significantly lower values than expected by chance.

Figure 2: Relationships between species richness and mean range size and abundance for Amazonian tree genera. Histograms of each genus-level characteristic are given on the diagonal. Below the diagonal the raw relationships are given with the best-fit linear relationship and the Pearson correlation coefficient. Above the diagonal, the relationship of phylogenetically independent contrasts are given (PICs) with the best-fit linear relationship that is forced through the origin given, along with the Pearson correlation coefficient.

284 **Figure 1**



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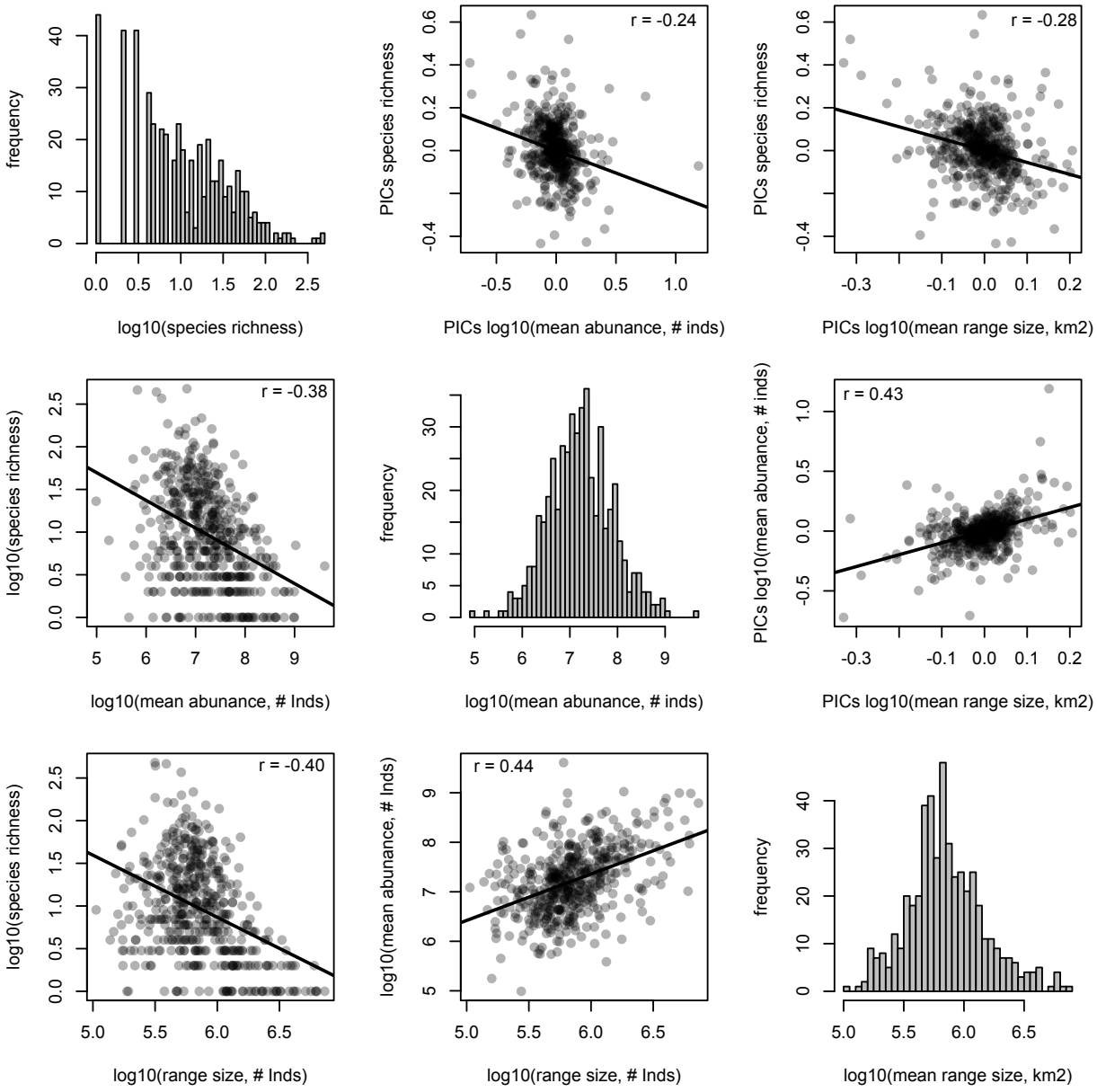
286 **Figure 2**



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