

Rapid turnover promotes high diversification of Amazonian trees

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Abstract

The Amazon rain forest sustains the world's highest tree diversity but it is unclear why some clades of trees are hyperdiverse whereas others are not. Using dated phylogenies, estimates of current species richness and trait and demographic data from a large network of forest plots, we show that short turnover times - short generation times - have promoted diversification in 48 clades of canopy-tree, across multiple tree families and orders. This result is robust to assuming that diversification rates are either constant or decline over time. We also find that turnover times are related to total species richness across all 150 genera of canopy trees where this demographic trait can be estimated, suggesting that this relationship is found across a broad range of Neotropical tree lineages. These findings highlight the crucial role of ecological variation among clades for understanding the origin of the remarkable diversity of Amazonian trees and forests.

INTRODUCTION

Amazonian forests are among the most biologically diverse ecosystems on Earth, sustaining at least 12,500 species of canopy trees or $\approx 28\%$ of global tree diversity and some communities contain over 300 species of at least 10 cm diameter at breast height (dbh) within a single hectare (Gentry 1988). As for any ecosystem, this diversity is result of an interaction between extrinsic factors - historical events that have caused extinction or provided opportunities for speciation - and the intrinsic characteristics of different lineages that affect how they respond to these events (Vamosi & Vamosi 2011). For Amazonia, there has been a strong focus on identifying the role that extrinsic factors have played in promoting high speciation rates, related to vicariance processes associated with the uplift of the Andes (Gentry 1982; Hoorn *et al.* 2010), climatic

variation during the Pleistocene (Haffer 1969), or the development of a wide range of edaphic conditions since the Miocene (Hoorn *et al.* 2010; Higgins *et al.* 2011). Indeed, a wide range of these processes is likely to have been important across different groups: recent phylogenetic studies have shown that independent speciation events throughout the Cenozoic have generated the high tree diversity observed today related to a range of historical events (Hoorn *et al.* 2010). However, a framework based solely on extrinsic factors cannot explain some of the most noteworthy aspects of Amazonian tree biodiversity: the wide variation in rates of diversification amongst clades (e.g. Couvreur *et al.* 2010) and the existence of a number of highly diverse groups in unrelated lineages with high diversification rates (e.g. *Inga* \approx 300 species, Richardson *et al.* (2001); *Guatteria* \approx 265 species; Erkens *et al.* (2007)). These patterns suggest that the intrinsic characteristics of certain clades have also determined why they have become so species-rich (Dial & Marzluff 1989; Marzluff & Dial 1991).

The search for intrinsic, ecological traits to explain variation in species richness among clades has a long history and a range of morphological and life-history traits have been shown to correlate with patterns of species richness and diversification rates (Dial & Marzluff 1989; Givnish 2010). For example, amongst Neotropical taxa, song structure correlates with patterns of diversity in antbirds (Seddon *et al.* 2008b) and diet and body size amongst bats (Rojas *et al.* 2012). Amongst plants, clades with poorly dispersed seeds, shorter generation times, larger geographic range sizes and monoecious breeding systems have all been shown to be related to higher diversification, presumably because these factors increase the probability of reproductive isolation (Davies *et al.* 2005; Givnish 2010; Vamosi & Vamosi 2011). However, there are only a few studies of the ecological correlates of diversification in trees (Marzluff & Dial 1991; Verdu 2002) and

none that have focussed on species-rich tropical forests. The lack of studies for tropical trees reflects the paucity of data that has existed on the life-history strategies and evolutionary relationships within these groups until the recent emergence of large demographic and trait databases (e.g. Kattge *et al.* 2011; Lopez-Gonzalez *et al.* 2011; Lopez-Gonzalez *et al.* 2012) and dated phylogenies for a range of clades (e.g. Erkens *et al.* 2007; Simon *et al.* 2009; Couvreur *et al.* 2010).

Testing the relationships between ecological factors and the diversification rate (r), the difference between the rate of speciation (λ) and extinction (μ), requires an underlying model of how these processes vary over time. In many studies, diversification has been calculated based on a constant rate, birth/death process that assumes that the number of species within a clade increases exponentially over time (Magallon & Sanderson 2001). However, based on observations that the rate of appearance of new taxa in the fossil record often declines over time and that clade age and species richness are not correlated in many extant lineages (Rabosky 2009b; Rabosky *et al.* 2012), it has been suggested that 'density-dependent' diversification, where the rate of diversification slows down as species accumulate, may be a more appropriate model for many clades. Here, we therefore explicitly test whether ecological factors improve estimates of current species richness using models that are based on both a constant and declining rate of diversification. This approach allows us to determine the model of diversification that is most appropriate for these clades and explore whether our results are robust to these assumptions. We show that a model where diversification rates decline over time best fits our data, and that short generation times, estimated using data on the survivorship of trees within each clade, are associated with higher diversification.

MATERIALS AND METHODS

We searched the literature for dated phylogenies of plant families that contain predominately Neotropical, free-standing, woody genera of canopy trees (with average species-level maximum height ≥ 15 m; Baker *et al.* (2009)) to obtain stem or crown-node ages for as many clades as possible. Data were available for 48 clades in eight families that are broadly representative of angiosperm canopy tree diversity in Neotropical forests (See Table S1 in Supporting Information, Doyle *et al.* 2004; Davis *et al.* 2005; Weeks *et al.* 2005; Zerega *et al.* 2005; Erkens *et al.* 2007; Simon *et al.* 2009; Couvreur *et al.* 2010). Genera known to be polyphyletic were either excluded (*Oxandra*, Annonaceae; *Trophis*, Moraceae; *Stryphnodendron*, *Acacia*, Fabaceae), or, in cases where two or more polyphyletic genera form clades, the more inclusive, higher-level monophyletic groups were used (neotropical *Protium*, *Crepidospermum* and *Tetragastris*; *Brosimum*, *Helicostylis* and *Trymatococcus*; *Clarisia* and *Batocarpus*). In addition, genera that include lianas, stranglers or other non-tree growth forms (e.g. *Bauhinia*, *Croton*, *Ficus*) were excluded. We also compiled estimates of extant species richness for each clade (Pennington *et al.* 2004; The Plant List 2010).

To test whether diversification is related to variation amongst clades in generation time, range size, maximum size, dispersal mode or breeding system, we obtained trait data for each clade. We estimated a proxy for generation time using data on the turnover time of trees ≥ 10 cm diameter within each clade from 207 long-term, lowland (< 500 m a.m.s.l.), old-growth forest plots (Table S2, Fig. S1). These plots form part of the RAINFOR (Amazon Forest Inventory) network and have been re-censused every 4-5 years, since their establishment from the 1970s onwards. The data were extracted from the ForestPlots database (Lopez-Gonzalez *et al.* 2011; Lopez-Gonzalez *et al.* 2012). Each

census comprises diameter measurements of all living trees ≥ 10 cm dbh, and records of tree mortality, and measurements and identifications of all new recruits. We used data only from plots with annual precipitation > 1300 mm a^{-1} based on the WorldClim dataset (Hijmans *et al.* 2005) and basal area > 13 m^2 ha^{-1} , to exclude plots in dry forest and savanna biomes. The plots encompass 212.9 hectares, monitored on average for 14.6 years, and sample the major climatic and edaphic gradients across Amazonia (Table S2, Fig. S1). By sampling across these gradients, our aim was to estimate the typical turnover times for different groups under the conditions where they occur (Quesada *et al.* 2012); we excluded trees monitored for less than two years to avoid including the effect of short-term climatic extremes on tree mortality rates (e.g. Phillips *et al.* 2009). The annual probability of mortality, P , of an individual tree, i , within each genus was estimated as a function of tree diameter, following Lines *et al.* (2010), as

$$P(\text{mortality}, i) = \frac{1}{1 + e^{-\beta_1(\text{dbh})} \exp(\beta_2 \text{dbh})}$$

where β_1 and β_2 are constants. This function allows flexibility in the form of the relationship between tree size and mortality, although over the size range of trees in this study, tree mortality rates are relatively constant (e.g. Fig. S2).

Using this model, M , over the monitoring period, t , for each individual of each genus, the log likelihood of the patterns of survivorship and mortality in the data, X , was estimated, following Lines *et al.* (2010), as:

$$l(X|M) = \sum \ln \left\{ \begin{array}{l} [1 - P(\text{mortality}, i)]^t \text{ if tree survives} \\ [P(\text{mortality}, i) \times (1 - P(\text{mortality}, i))^{t-1}] \text{ if tree dies} \end{array} \right\}$$

The value of this function was maximised using simulated annealing and the annual probability of mortality was estimated for trees of median diameter for each genus (m). Median, rather than mean, values of diameter were used to standardise estimates of mortality rates to account for the typically strongly skewed distributions of tree diameter within genera. Turnover times, T , for a median-sized tree for each clade were calculated as $\frac{1}{m}$.

Resampling varying numbers of individuals of common genera demonstrated that confidence limits of m widen sharply at small sample sizes (e.g. for *Inga*, Fig. S3). We therefore only estimated m for genera with >100 individuals. However, given the large size of the forest dynamics dataset (128,938 trees ≥ 10 cm diameter), our dataset retained clades that encompass the full range of diversity levels, from very low to very high values of species richness (Table S1).

The range size of each clade was classified as pantropical, neotropical, Amazonian, or Guiana Shield, based on Pennington *et al.* (2004). The predominant dispersal type that leads to successful reproduction within each clade was classified as explosive/unassisted, arboreal or ground dwelling mammal, bat or bird, water, or wind, based on Seed Information Database (SID) Version 7.1 (2008). The average maximum height per clade, H , was calculated from species-level estimates compiled from a range of floras (Baker *et al.* 2009). Breeding system for each clade was classified as dioecious or monoecious, based on Pennington *et al.* (2004).

A range of approaches exists for relating traits to variation in diversification, extinction and speciation rates. For large (>500 species), well-resolved phylogenies, likelihood-based approaches can be used to explore correlations among traits and the probability

of speciation and extinction within an explicit phylogenetic framework (Fitzjohn 2010). However, more typically, studies correlate estimates of the diversification rate under a constant-rate model (Magallon & Sanderson 2001) with the traits of interest (e.g. Seddon *et al.* 2008a). In contrast, if the diversification is thought to have varied over time, correlating $\log(N)$ with a set of traits, where N is the number of extant lineages, has been proposed as a reliable method to explore the controls on diversification within a lineage (Rabosky 2009a).

Although suitable for smaller datasets where detailed, dated phylogenetic information does not exist, neither of these last two methods allow a direct test of how well different underlying models of the diversification process fit the observed data, or whether the significance of any relationships between traits and diversification are sensitive to these assumptions. Incorporating tests of the appropriate model to use within these kinds of analyses would help to resolve debates concerning the role of ecological factors in limiting diversification (Rabosky 2009a; Wiens 2011). We therefore compared the role of ecological factors in explaining variation in species richness based on models of both constant and declining rates of diversification by developing methods presented in Rabosky (2009b).

In general, the mean number of lineages, N , from a non-homogeneous diversification process is given as (Bailey 1964, equation 9.40):

$$\log N = \log(a) + \int_0^t r(t) dt \quad (1)$$

where a is the number of ancestral lineages (one for a clade with a stem node age and two for a clade with a crown node age), t is the age of the clade, and r is the net diversification rate:

$$r(t) = \lambda(t) - \mu(t) \quad (2)$$

where λ is the speciation rate and μ is the extinction rate.

We then developed different estimators of $r(t)$, based on constant or declining rates of diversification and including and excluding ecological covariates (Fig. 1). These different estimates of $r(t)$ were used to predict species richness using equation (1) for comparison with observed values.

We used two forms for the diversification rate (Rabosky 2009b). Firstly, we fit a constant rate model:

$$r = \lambda(1 - \varepsilon) \quad (3)$$

where ε is the relative extinction rate, μ/λ .

We then adapted this model to relate the diversification rate to an ecological covariate, A :

$$r = cA(1 - \varepsilon) \quad (4)$$

We fit a series of models with A represented by either continuous variables, turnover time and maximum height, or factors (range size, dispersal mode and breeding system) that we hypothesised would be related to diversification. We incorporated turnover time and maximum height as $\frac{1}{\log(T)}$ and $\frac{1}{H}$ respectively, as we hypothesised that these terms would be negatively correlated with diversification. We used log-transformed values of T to ensure that this variable was normally distributed.

Secondly, we estimated r as:

$$r = \lambda_0 e^{-zt}(1 - \varepsilon) \quad (5)$$

which simulates the diversification rate if speciation and extinction rates decline exponentially over time, consistent with a 'density-dependent' model (Fig. 1, Rabosky

2009b). We modified this model to allow ecological covariates to influence the initial diversification rate:

$$r = cAe^{-zt}(1 - \varepsilon) \quad (6)$$

where A represents the same ecological covariates as above.

For the two continuous ecological variables (mortality rate and maximum height), we also explored models where the effect of these variables was allowed to vary among the major plant groups (Fabaceae, Moraceae, Annonaceae and other families) represented in our data. We did not fit more complex models involving interactions among terms as the size of the dataset ($n = 48$) precludes effective fitting of more parameters (number of parameters $\approx n/10$, Burnham and Anderson (2002)). All models were run with both high ($\varepsilon = 0.9$) and low ($\varepsilon = 0$) relative extinction rates. Models were fit using simulated annealing and evaluated by comparison of AICc values (Burnham & Anderson 2002).

For the ecological variable found to be the most important predictor of current species richness, we explored whether there was a significant correlation between this trait and $\log(N)$ for all canopy-tree genera that lack ages but where suitable trait and species richness data could be obtained (Table S3).

RESULTS

Overall, the model that incorporates a decline in diversification rates over time provided a superior fit to the data compared to models with a constant rate of diversification: for all models containing equivalent terms, the model with declining rates of diversification resulted in lower values of AICc (Table 1).

Based on the exponentially declining model of diversification, turnover time was the only ecological trait that significantly improved predictions of species richness (for $\varepsilon = 0$, AICc = 22.7 for the model including turnover time, $\Delta\text{AICc} = 8.3$ compared to a model excluding ecological covariates; for $\varepsilon = 0.9$, AICc = 23.5 for the model including turnover time, $\Delta\text{AICc} = 7.5$ compared to a model excluding ecological covariates; Table 1). This result suggests that higher initial diversification rates and subsequently higher total diversification is found in clades with shorter turnover times. Of the other ecological factors, only range size provided some improvement to model predictions ($\varepsilon = 0$, AICc = 29.2 for the model including range size, $\Delta\text{AICc} = 1.8$ compared to a model excluding ecological covariates; $\varepsilon = 0.9$, AICc = 30.0 for the model including range size, $\Delta\text{AICc} = 1$ compared to a model excluding ecological covariates; Table 1), with a small tendency for clades with larger range sizes to have achieved greater species richness.

The trend for higher species richness in genera with fast turnover times is evident in several different families (e.g. *Inga*, *Tachigali*, Fabaceae; *Guatteria*, Annonaceae; *Cecropia*, Urticaceae; Fig. 2) and the best predictions of current species richness were achieved by a model that incorporated an exponential decline in diversification rates over time and a family-specific relationship between turnover rate and the initial rate of diversification (for $\varepsilon = 0$, AICc = 17.1; for $\varepsilon = 0.9$, AICc = 18.6; Table 1, Fig. 2). Allowing the effect of turnover rate on diversification to vary among families allowed better predictions of the differing levels of species richness among families (e.g. low in the Moraceae and high in the Fabaceae; Fig. 2). This model of diversification explained 32 % of the total variation in current species richness among clades (Fig. 2). Similarly, the best predictions among models based on a constant rate of diversification included a family-specific relationship between turnover time and diversification rate (Table 1).

This result shows that irrespective of the underlying model of diversification, including data on the turnover time of the clade improves predictions of current species richness.

We tested whether the relationship between diversification and turnover rate is found across a broader range of clades where ages are not available, by comparing total diversification to turnover times (Fig. 3). The relationship was significant even when all 150 genera where turnover times can be estimated are included in the analysis ($F_{1,149} = 17.23$, $P < 0.001$; Fig. 3, Table S3). This analysis also demonstrates that groups with published, dated phylogenies are broadly representative of the levels of species richness and turnover times found across a wide range of Amazonian canopy-tree genera (Fig. 3).

DISCUSSION

Our results demonstrate that shorter turnover times are related to higher diversification amongst these clades of tropical rain forest canopy tree. The finding is robust to different underlying models of the diversification process, variation in extinction rates and is consistent across a wide range of lineages.

Short turnover times amongst tropical trees are related to a suite of traits associated with rapid resource acquisition, effective dispersal and fast growth in size (Turner 2001). However, in the context of diversification, the link between fast turnover and short generation times is probably the most important relationship. More commonly estimated for animals than long-lived plants, mean generation time is the sum of the number of non-reproductive years and the turnover time of reproductive individuals (Galliard *et al.* 2005). This simple way of estimating generation time is based on

assumptions of constant rates of survival and fecundity after the age of first reproduction. For tropical forest canopy trees, these assumptions appear to be reasonable: mortality rates remain relatively constant with increasing size above 10 cm dbh (e.g. Fig. S2) and the few data available on reproductive output are consistent with a minimum reproductive size of 10 cm diameter and constant reproductive output above this threshold: for 12 species of trees with maximum height ≥ 15 m in Panama, the average minimum diameter for reproduction was 14.8 cm and reproduction did not decline at large sizes (Wright *et al.* 2005). Variation in turnover times of trees ≥ 10 cm diameter will therefore be related to variation in generation times among species if there are no substantial switches in the life-history strategies of tropical trees during ontogeny (e.g. if species do not change from having high to low turnover rates, and vice versa, when they start to reproduce). Although there are some species of tropical tree where these transitions may occur (e.g. Dalling *et al.* 2001), substantial switches between different life history strategies (e.g. switching from occurring in high to low light conditions) during ontogeny is not common amongst tropical trees (e.g. Poorter *et al.* 2005).

Short turnover times are likely to promote both of the mechanisms, high speciation and low extinction rates, which lead to rapid diversification (Marzluff & Dial 1991). The capacity of populations to increase rapidly in size allows clades to undergo more rapid selection as new habitats and different resources become available, and to have faster rates of molecular evolution (Smith & Donoghue 2008). Both of these processes may promote more rapid speciation, whether driven ultimately by vicariance, isolation due to long-distance dispersal or habitat specialization. Furthermore, shorter turnover times may also provide greater resilience to disturbances that cause extinction, such as

climatic variation over interglacial cycles, by allowing successful migration to habitats with suitable environmental conditions and a greater ability to recolonize areas following such events.

The results of this study are broadly consistent with the few previous studies that have examined the relationship between diversification and proxies of generation time amongst woody plants. For example, Marzluff and Dial (1991) found negative, but non-significant, correlations between the age of first reproduction and total species richness for 10 gymnosperm and 19 angiosperm groups of North American trees, and Verdu (2002) found a significant negative correlation between genus species richness and age at maturity in a broader analysis across 174 genera focussed on North American trees and shrubs. However, this is the first study of the correlates of diversification to focus on species-rich tropical forest trees, the first to develop comparative tests of different diversification models using a range of traits, and the first to use directly measured, demographic data from permanent plots to quantify a proxy of generation time: previous studies have used estimates and compilations of the age of first reproduction from the forestry literature (Marzluff & Dial 1991; Verdu 2002). Such compilations are inevitably limited to species of commercial interest. In contrast, the expansion of both permanent plot networks (e.g. Lopez-Gonzalez *et al.* 2011) and studies of the phylogenetic relationships of tree taxa in the tropics (e.g. Baraloto *et al.* 2012) provides a new opportunity to explore the role of life-history traits in determining evolutionary patterns across a wide range of clades in this biome.

Our study provides strong support for a model of diversification where rates decline, rather than remain constant, over time (Table 1). This kind of model, and the limits to diversity that it implies within specific clades and regions (Fig. 1, Rabosky 2009a), has

been proposed to explain the lack of correlation between clade age and species richness observed in many taxonomic groups (Rabosky *et al.* 2012) as well as the similar levels of diversity in different families of tropical plants on different continents (Ricklefs & Renner 2012). The precise mechanisms that determine this kind of pattern remain uncertain and debated (Wiens 2011; Rabosky *et al.* 2012), but processes that might contribute include explosive radiations resulting from the emergence of novel ecological opportunities or morphological innovation (Rabosky *et al.* 2012), and/or 'carrying capacities' in the number of species that different regions can support (Rabosky 2009a). Where diversification rates vary over time, interpreting how ecological covariates might influence the diversification process is more challenging than in constant rate models. In the broadest sense, significant relationships between ecological factors and the total species richness of different clades suggests that, integrated over the age of the clade, those factors must have promoted speciation and/or reduced extinction rates (Rabosky 2009a). More specifically, our analyses suggest that intrinsic factors which affect the *initial* rate of diversification and expansion of a clade is one way ecological covariates might influence the total levels of diversification that clades achieve. Similarly, Rabosky (2009b) found that relating range size to the initial rate of diversification improved predictions of species richness across 88 tribes of birds compared to a model without ecological covariates. In the context of Amazonia, this framework could be interpreted as indicating that clades with shorter generation times are able to exploit specific opportunities for diversification more rapidly, following geological events such as the deposition or exposure of particular edaphic conditions (Hoorn *et al.* 2010; Higgins *et al.* 2011). More broadly, the wide range of clade ages in our study (Table 1) suggests that there may have been an interaction between clades with short turnover times and a diverse suite of historical events to generate current patterns of species richness.

Overall, this interpretation emphasises the close links between historical processes and the intrinsic traits of different lineages in generating observed patterns of diversity.

Some ecological factors that are often associated with patterns of diversification in plants, such as range size and maximum height (Givnish 2010), were not significant in this study. However, the focus of this study on Neotropical canopy trees of at least 10 cm dbh meant that many of the clades had similar values for these traits. For example, we excluded some species-rich genera of woody understory plants (e.g. *Psychotria*, Rubiaceae) that are typical of certain Neotropical forests (LaFrankie *et al.* 2006); maximum height might also be an important ecological determinant of diversification when all species of free-standing, Neotropical, woody plants are considered. Range size marginally improved predictions of diversification, with clades with large range sizes containing more species (Table 1). Range size may therefore be a more important factor explaining diversification in larger-scale, pantropical analyses.

Although our focus here is on understanding variation in species richness among clades of tropical trees, our results also have implications for understanding community-level patterns of diversity within Amazonia. This is because genera with fast turnover times make an especially large contribution to the diversity of canopy trees in western Amazonian forests which comprise some of the most diverse tropical forests in the world (Fig. 4, Gentry 1988). The abundance of species-rich clades with fast turnover rates in this region suggests that the ecological characteristics of these taxa, in conjunction with the diverse range of historical events, such as altitudinal vegetation shifts, and the biophysical characteristics of the region, have contributed to the high diversity of these forests.

The ecological trait of short turnover times is shared by some of the most species-rich groups of Amazonian trees, such as *Inga* and *Guatteria*, which have ≈ 300 and ≈ 265 species respectively. Overall, our results indicate that ecological differences among clades of tropical trees have strongly influenced their diversification, and the high level of diversification in lineages with short turnover times has played a key role in the generation of the spectacular diversity of Amazonian forests.

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Table 1. AICc values for the fit of 28 different models of diversification for 48 clades of tropical canopy tree. Models based on both constant rate and exponentially declining rates of diversification, high and low extinction rates, and including and excluding ecological factors. Δ AICc values calculated in relation to the best model (highlighted in bold) with either constant rate or exponentially declining models of diversification.

Model number	Framework	Traits	Family-specific	No. parameters	$\varepsilon = 0.9$		$\varepsilon = 0$	
					AICc	Δ AICc	AICc	Δ AICc
1	Constant rate	None	No	1	76.92	7.51	76.92	7.47
2	Constant rate	Turnover time	No	1	74.99	5.58	74.99	5.54
3	Constant rate	Dispersal mode	No	4	74.85	5.44	75.25	5.80
4	Constant rate	Range size	No	4	81.19	11.78	81.58	12.13
5	Constant rate	Max ht	No	1	77.26	7.85	77.26	7.81
6	Constant rate	Breeding system	No	4	78.39	8.98	78.40	8.95
7	Constant rate	Turnover time	Yes	4	69.41	0.00	69.45	0.00
8	Exponential decline	None	No	2	31.02	12.43	31.00	13.86
9	Exponential decline	Turnover time	No	2	23.54	4.95	22.70	5.56
10	Exponential decline	Dispersal mode	No	5	37.29	18.70	37.06	19.92
11	Exponential decline	Range size	No	5	29.98	11.39	29.20	12.06
12	Exponential decline	Max ht	No	2	54.82	36.23	54.83	37.69
13	Exponential decline	Breeding system	No	5	32.50	13.91	32.13	14.99
14	Exponential decline	Turnover time	Yes	5	18.59	0.00	17.14	0.00

Fig. 1. Alternative predictions of the trajectory of diversification under a constant rate (black) or exponentially declining (blue) model of diversification. For each model, dashed lines show possible effect of ecological covariates on model predictions.

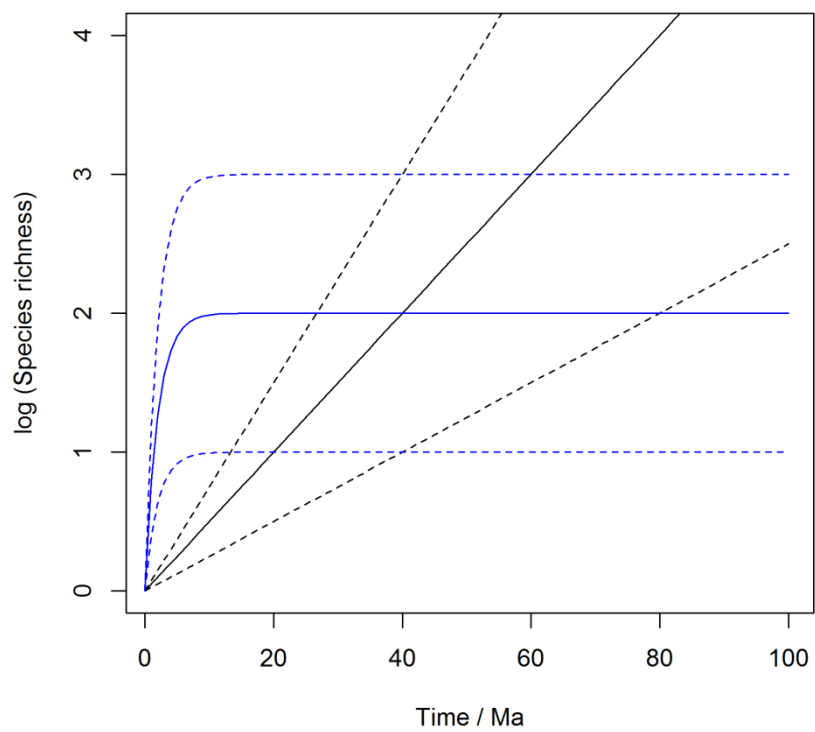


Fig. 2. Relationship between predicted and observed species richness for 48 clades of neotropical canopy trees. Predicted values based on an exponentially declining model of diversification and high relative extinction rate ($\epsilon = 0.9$; model 14 in Table 1). Symbol size is inversely proportional to the turnover time of the clade. Key genera with high observed and predicted species richness and short turnover times are highlighted.

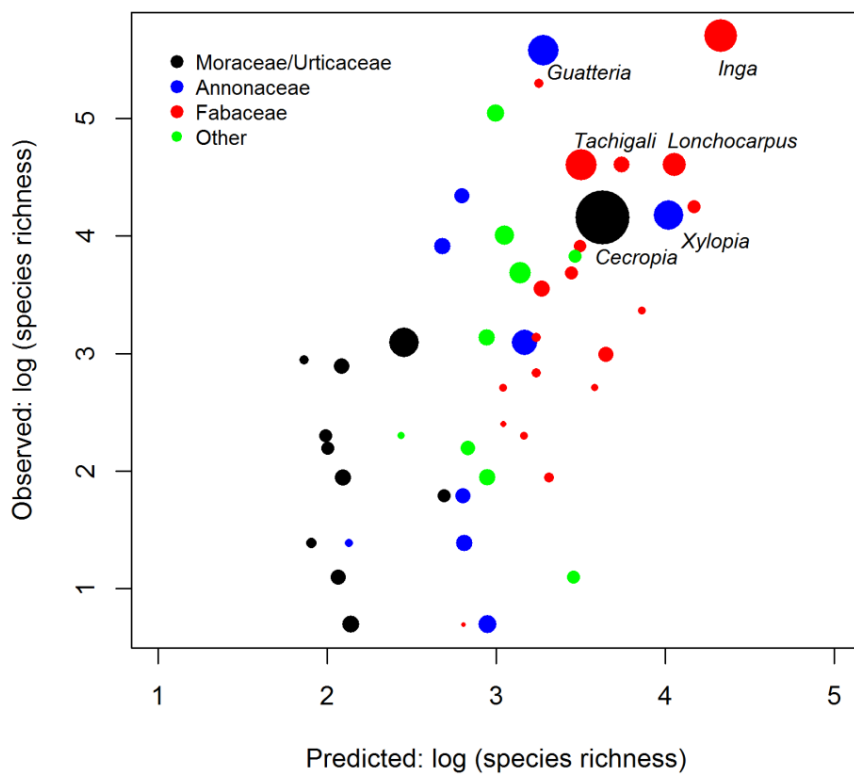


Fig. 3. Relationship between species richness and turnover time for groups included in dated phylogenetic studies (solid circles), and all additional genera where turnover time can be estimated using the forest plot data (open circles). Regression line show relationship for all 150 groups.

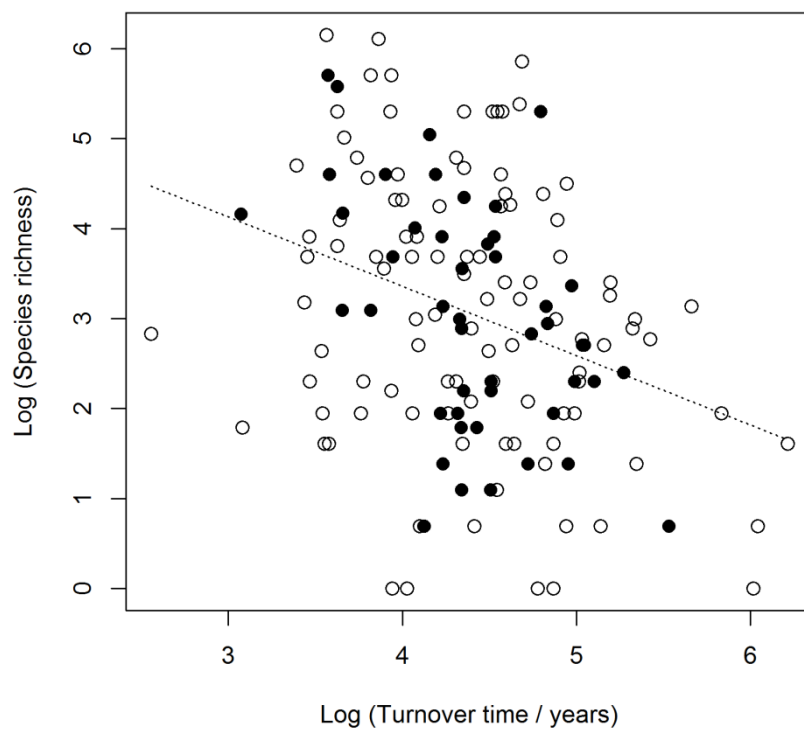
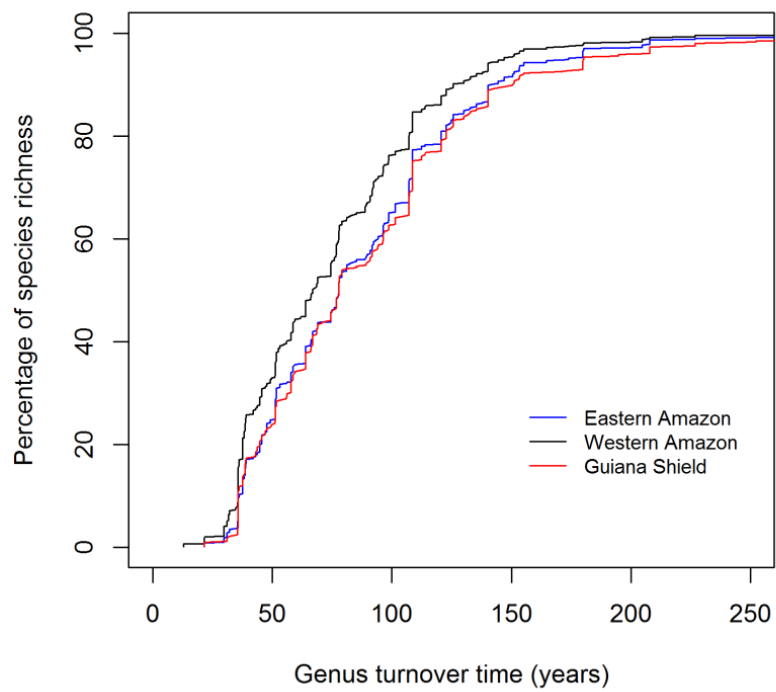


Fig. 4. Contribution of genera with different turnover times to the overall species richness of western and eastern Amazonian forests and forests on the Guiana Shield.



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