

Linking high diversification rates of rapidly growing Amazonian plants to geophysical landscape transformations promoted by Andean uplift

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Amazonia is extremely biodiverse, but the mechanisms for the origin of this diversity are still under debate. We propose a diversification model for Amazonia based on the interplay of intrinsic clade functional traits, habitat associations and past geological events, using as a model group the species-rich Neotropical family Marantaceae. Our results show that the species richness of the lineage is predicted by functional strategy, rather than clade age, and thus the fast vs. slow growth functional trade-off is a major determinant of clade diversification in Marantaceae. Rapidly growing clades were mostly associated with highly productive habitats, and their origin and diversification dynamics matched the expansion of fertile soils mediated by Andean uplift c. 23 Mya. Fast-growth strategies probably led to fast molecular evolution, speeding up speciation rates and species accumulation, resulting in higher numbers of extant species. Our results indicate that pure allopatric-dispersal models disconnected from past geological and ecological forces may be inadequate for explaining the evolutionary and diversity patterns in Amazonian lowlands. We suggest that a coupling of the functional trait-niche framework with diversification dynamics provides insights into the evolutionary history of tropical forests and helps elucidate the mechanisms underlying the origin and evolution of its spectacular biodiversity.

ADDITIONAL KEYWORDS: functional traits – geology – leaf mass per area – Marantaceae – speciation.

INTRODUCTION

Amazonia harbours one of the greatest diversity of plants and animals in the world, but such enormous

diversity is not evenly distributed between clades (Baker *et al.*, 2014; Smith *et al.*, 2014), and mechanistic explanations linking past events to diversification dynamics and diversity patterns remain elusive. The variation in species richness between clades can be viewed ultimately as the result of differences

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in speciation and extinction rates (Ricklefs, 2006). Historical events such as past climate oscillations and physical and geochemical landscape transformations have been historically considered as the main drivers of diversification of Amazonian lineages, creating new opportunities for speciation or causing extinctions (Haffer, 1969; Hammen & Hooghiemstra, 2000; Hoorn *et al.*, 2010a; Ribas *et al.*, 2012). Alternatively, some clades can be richer than others simply because they originated earlier and have had more time to accumulate species. In the latter case, there is no need to invoke historical events, such as the emergence of physical barriers or even the differences in diversification rates, to explain variation of species richness among clades (Smith *et al.*, 2014). Besides these extrinsic factors, some intrinsic traits of different lineages can also affect diversification and diversity, but this driver has been less well explored. For instance, the duration of organism life cycles directly affects molecular evolution, with fast cycles increasing the rate of mutations and consequently speeding speciation rates (Nabholz, Gle & Galtier, 2009; Nikolaev *et al.*, 2007; Galtier, Jobson & Blier, 2007; Smith & Donoghue, 2012). A study combining phylogenetic trees across 51 tree genera and plot-based demographics in Amazonia showed that clades of species with a fast growth strategy and short generation times had markedly higher rates of diversification and tended to be richer than clades with a slow-growth strategy (Baker *et al.*, 2014).

Direct measurements of the life cycles of organisms are not straightforward, especially in highly diverse ecosystems and in broad-scale applications, so ecologists have been using a set of functional plant traits as proxies for plant growth strategy, e.g. height, leaf mass per area (LMA) and seed size (Westoby, 1998; Reich, 2014; Díaz *et al.*, 2016). Growth rates (and consequently life cycles) of organisms are directly linked to functional traits and strategies (Poorter & Remkes, 1990; Cornelissen, Diez & Hunt, 1996; Poorter & Bongers, 2006), suggesting that functional spectra, such as the leaf economic spectrum (Wright *et al.*, 2004), are essential for understanding the process of diversification. LMA strongly summarizes the global spectrum of leaf economics, running from fast to slow return of investment in leaf tissues (Wright *et al.*, 2004). Ecological theory predicts that when resources (nutrients, light, water) are scarce, species grow slowly and invest in highly durable tissues in leaves, stems and/or roots (Reich, 2014). In agreement with this, slow growth (conservative strategy) is associated with high LMA, whereas fast growth (acquisitive strategy) is associated with low LMA (e.g. for herbs: Poorter & Remkes, 1990; Lambers & Poorter, 1992; Veneklaas, Santos Silva & Den Ouden, 2002; Pandey *et al.*, 2008;

Sun & Frelich, 2011; Durand & Goldstein, 2016). Fast growth leads to higher mortality (the growth–survival trade-off) and thus fast life cycles (e.g. Kobe *et al.*, 1995; Poorter & Bongers, 2006; Kursar *et al.*, 2009; Russo *et al.*, 2010; Wright *et al.*, 2010; Esquivel-Muelbert *et al.*, 2020). There is also evidence of a direct link between low LMA and lower herb longevity (Mulkey, Smith & Wright, 1991; Dubey, Raghubanshi & Singh, 2011). Short life cycles associated with low LMA leads to fast demographic rates that can be expected to speed molecular evolution.

The availability of resources across topographic and soil gradients of tropical forests was shown to be associated with these functional strategies at the community/ecosystem level (ter Steege *et al.*, 2006; Kraft *et al.*, 2008; Fyllas *et al.*, 2009; Quesada *et al.*, 2012). Trees with a fast-growth acquisitive functional strategy predominate in nutrient-rich habitats and in locally moist conditions, such as in valleys, whereas conservative functional strategies are more common in nutrient-poor habitats and locally drier conditions, such as in upland hills and plateaus (Fyllas *et al.*, 2009; Cosme *et al.*, 2017; Schmitt *et al.*, 2020). However, the spatial distribution of resources, such as soil nutrients and water, has changed throughout the evolution of the Amazon landscape.

Palaeo-environment reconstruction indicates that after uplift of the Andes in the Miocene, the Amazonian landscape was gradually transformed from stable, low-productivity terrains to dynamic and highly productive terrains (Bicudo *et al.*, 2019). The intense geological activity promoted input of nutrients, resurgence of rich soils and physical transformation of the drainage system, most strongly in the western Amazonia, but also extending along the central corridor towards the east (Hoorn *et al.*, 2010a; Wanderley-Filho *et al.*, 2010). These geophysical changes and the formation of wetlands are closely related to several patterns of spatial diversity and evolution in Amazonian plants. Soils derived from the Miocene wetlands are markedly richer in nutrients, and the corresponding forests harbour a distinct floristic composition and have higher species richness than forests growing on poorer soils of fluvial origin (Higgins *et al.*, 2011; Tuomisto, Zuquim & Cárdenas, 2014; Tuomisto *et al.*, 2016). Species–habitat associations mapped onto a plant phylogenetic tree revealed that closely related species have different soil affinities, multiple events of speciation probably occurred under parapatric speciation across a heterogeneous edaphic landscape, and the origin of species associated with clay soils coincided with sedimentation history in the Miocene (Fine *et al.*, 2005; Lehtonen *et al.*, 2015). All these findings suggest that the Andean uplift may have left a deep imprint in diversification patterns through the

geochemical and physical transformation of edaphic landscapes, favouring the emergence of new habitats and species divergence mediated by the association of functional traits to resource gradients.

Past climate changes have also been invoked as drivers of Amazonian diversification patterns (Hoorn *et al.*, 2010a). Global climate has substantially changed in the last 65 My, but how it has affected plant diversification dynamics in Amazonia is still under debate. The theory of climate refuges proposed in the 1970s postulated that the drop in temperature and humidity in the Plio-Pleistocene (3 Mya) isolated populations through forest fragmentation, favouring allopatric speciation (Haffer, 1969, 2008). However, this theory was not supported by palynological or phylogenetic data. Conversely, palynological reconstructions have shown a rise of diversity in warmer periods due to the expansion of tropical forests, but a general decline in plant diversification due to increased extinction rates (Hammen & Hooghiemstra, 2000; Jaramillo, Rueda & Mora, 2006). Species with a fast-growth acquisitive strategy may depend on relatively high temperature and humidity to sustain their higher metabolic rates, and thus it can be expected that these fast-growth species are more susceptible to climate changes than slow-growth conservative species. Again, the connection between the functional perspective and the historical evolution of climates to understand diversification and diversity patterns is missing.

To understand the interplay of geological and climate changes on trait selection and its consequences for diversification, we used phylogenetic data and a functional trait proxy for the acquisitive–conservative functional strategy trade-off (LMA) for 170 species from seven clades of a species-rich understorey herbaceous family (Marantaceae, *c.* 230 recognized species in Amazonia), and 400 plot-based environmental data (soil and topography). This enabled us to propose an ecological model of diversification based on the history of geochemical and physical transformations of the Amazonian substrate and palaeoclimate oscillations since 45 Mya. First, we asked if clades containing predominantly species with a fast-growth acquisitive strategy have higher diversification rates than clades of predominantly conservative species and tested the relative importance of diversification rates and clade age to explain among-clade species richness. Second, we determined if the fast-growth acquisitive clades are associated more with productive habitats (high fertility and bottomlands), to support the scenario in which emergence of these new habitats has promoted the origin and diversification of this group. Finally, we determined the temporal congruence between changes in diversification rates (and of speciation and extinction rates) and past geological and climatic events, under

the expectation that diversification of acquisitive clades increased after nutrient-rich environments became widespread (i.e. uplift of the Andes) and that the diversification dynamics of acquisitive clades was more sensitive to palaeo-environmental changes than that of conservative clades.

MATERIAL AND METHODS

TAXON PRESENTATION

Marantaceae are a species-rich pantropical monocot family in the order Zingiberales (gingers). Marantaceae are predominantly rhizomatous herbs, varying in habit from small rosulate (10 cm height) to tall palm-like or scandent plants (4 m tall). They represent a good model group given the availability of phylogenetic, trait and habitat data and, additionally, most species occupy forested environments in Amazonia, so their evolutionary history can be compared to other forest taxa in the reconstruction of the evolutionary history of Amazonian environments. Nearly 550 species of Marantaceae are recognized worldwide, but most of the diversity (*c.* 450) is found in the Neotropics (Prince & Kress, 2006). Here, we focused on the Neotropical *Calathea* clade, a rich lineage represented by four genera (*Calathea* G.Mey., *Goeppertia* Nees, *Ischnosiphon* Körn. and *Monotagma* K.Schum.) with 360 species occurring in Amazonia, the Atlantic Forest and Central America. *Goeppertia* is the richest genus in Marantaceae (*c.* 250 species) and has been split into six well-supported clades defined in previous phylogenetics studies (Borchsenius *et al.*, 2012; Saka, 2016): *Breviscapus*, *Comosae*, *Microcephalum*, *Ornata*, *Scapifolia* and *Straminea*. Clades with higher diversity outside the lowland rain forest Amazon basin (*Calathea*, the *Scapifolia* and a sub-clade of the *Breviscapus* clade) were removed from the main analyses. However, these clades and all the other genera of the family (including extra-Neotropical groups) were used to build a wide species time-calibrated phylogenetic tree at the family level (see details in next section). In summary, all analyses were based on the seven Amazonian clades (Supporting Information, Tables S1 and S2): five clades in *Goeppertia* (Amazonian *Breviscapus*, *Comosae*, *Microcephalum*, *Ornata* and *Straminea*) and *Ischnosiphon* and *Monotagma*. Images and taxonomic details of species included here can be found in Costa, Espinelli & Figueiredo (2011).

MOLECULAR DATA

Our molecular data included sequences of 170 Marantaceae taxa overall, considering both plastid and nuclear markers (Supporting Information, Table S1). For 70 taxa, DNA samples were collected by our

team during field expeditions conducted in Amazonia and the Atlantic Forest. Remaining sequences were obtained from GenBank, accessed via <https://www.ncbi.nlm.nih.gov/genbank/>. The GenBank data included not only species analysed here, but all available sequences of Marantaceae used to calibrate the tree of Amazonian clades. DNA was extracted from leaf tissue using the CTAB extraction protocol or the DNeasy Plant minikit (Qiagen, Valencia, CA, USA). Molecular analyses were based on sequences of nuclear ribosomal internal transcribed spacer regions (ITS 1 and 2; 850 bp) and the plastid *matK* gene and flanking 3' *trnK* intron, as described by Borchsenius *et al.* (2012). The outgroups were specimens of *Donax* Lour., *Maranta* Plum. ex L., *Stachyphrynium* K.Schum. and *Sarcophrynium* K.Schum. (Table S1). Sequencing of both forward and reverse primers for each locus was conducted at Laboratório de Temático de Biologia Molecular at INPA, Brazil, and at Macrogen Inc., Seoul, South Korea. We aligned sequences using default parameters of the MAFFT algorithm (Katoh *et al.*, 2002) as implemented in the Geneious software, v.9.1.4, and then fine-tuned the alignments manually.

PHYLOGENETIC AND TEMPORAL RECONSTRUCTION

To estimate our time-calibrated topology, we performed a Bayesian analysis using BEAST v.1.8.3 (Drummond *et al.*, 2016). The analysis followed two stages. (1) We first estimated a family-wide time-calibrated topology using the 151 *matK* sequences (Supporting Information, Table S1). The root age of our plastid tree was based on diversification times estimated from an order-level topology calibrated with three well-identified fossils in gingers (Janssens *et al.*, 2016). We set the root age of the *matK* tree using a normal distribution prior with mean 60 Mya and 2 standard deviations (SD). The analysis was performed using a GTR substitution model (gamma site heterogeneity model with four categories), uncorrelated relaxed clock with lognormal relaxed distribution (ucl) and a birth–death model of speciation. Exponential priors with mean 0.001 and 0.5 were set for ucl.mean and ucl.sd, respectively. (2) Based on node ages estimated in the first step, we estimated the ITS tree containing 150 sequences of taxa from the *Calathea* clade only (Table S1), setting the root age as 45 Mya (normal distribution with 5 SD). We applied the same settings used for the *matK* tree, but with different values for ucl.mean and ucl.sd, 0.003 and 0.6, respectively. As we obtained some low effective sample size (ESS) values for some parameters, we repeated the analysis using a simpler model, choosing the HKY substitution model and the Yule process model of speciation. For each topology, the plastid and nuclear tree, the tree

parameters were obtained after running 2×10^7 generations of Markov chain Monte Carlo (MCMC), sampling each 20 000 generations. For both analyses, the ESS values exceeded 200, which indicated good convergences in parameter estimations. We utilized a burn-in of 10% of the 1000 Bayesian trees and obtained the maximum clade credibility (MCC) tree using the TreeAnnotator software (available as part of the BEAST software). The MCC trees from plastid and nuclear markers are presented in Figures S1 and S2, respectively, and the tree file is available at https://github.com/gamamo/marantacea_amazon.

TRAIT DATA

LMA (g/m^2) was used to summarize the functional strategy of clades. The link of LMA to plant relative growth rates (RGR) can be described by the equation $\text{RGR} = \text{NAR} \times \text{LMR} \times \text{SLA}$, where NAR is the net assimilation rate (dry mass production per area and time), LMR is the leaf mass ratio (the ratio of leaf mass to all plant mass) and SLA is the specific leaf area; LMA is $1/\text{SLA}$. A literature review (Lambers & Poorter, 1992; Reich, Walters & Ellsworth, 1992) and studies specifically on herbs (e.g. Poorter & Remkes, 1990; Veneklaas *et al.*, 2002; Pandey *et al.*, 2008) indicate that SLA often has the largest contribution to growth rates among the components of the relative growth equation. As an important component of the growth strategies, LMA is associated with the growth–survival trade-off. This trade-off implies that fast growth leads to low survival, given the differences in allocation of resources; that is, high allocation to strong tissues and defence compounds protect plants from biotic and abiotic hazards but divert resources from growth, whereas higher allocation to growth diverts resources from protection, increasing the hazards and thus lowering survival (e.g. Sterck *et al.*, 2006; Esquivel-Muelbert *et al.*, 2020). Thus, LMA describes not only the spectrum of leaf economics, running from fast to slow return on investments of resources and dry mass in leaves, but also a whole-plant spectrum related to fitness of an organism and population demographic rates (Reich, 2014). Species with low LMA have an acquisitive strategy, implying fast growth, high mortality rates and short generation times, and the opposite is true for species with a high LMA conservative strategy.

LMA was obtained from 190 individuals of 118 species (Supporting Information, Table S2) sampled in our field plot inventories (see plot-based data description below). LMA is the ratio between the dry leaf mass and fresh (completely expanded) leaf area (Perez-Harguindeguy *et al.*, 2013). Here, we adapted the original method to estimate LMA, using small

pieces of the lamina of dried material from herbarium collections. For each individual, a maximum of four pieces (3 cm² on average) were cut from different parts of the lamina (at the middle and close to the base and apex), excluding the main vein. We carefully chose leaf pieces where the tissue had no or little shrinkage and avoided young leaves. LMA for each species was calculated as the average of values obtained in a maximum of six individuals and a minimum of one individual, when the species was rare and collected only once.

PLOT-BASED DATA

Presence–absence data for species in Amazonian Marantaceae were obtained in 448 plots of 500 m² established in non-inundated forests across the Amazon (Supporting Information, Fig. S3; data available at https://github.com/gamamo/marantacea_amazon). Data came from two plot designs: (1) 409 plots of 250 m × 2 m set up on the topographical isoclines following the RAPELD protocol (Magnusson *et al.*, 2005); and (2) 39 plots of 100 m × 5 m subsampled from 500-m × 5-m transects orientated to include representative local topographic variation (Tuomisto *et al.*, 2016). Elevational values for each 5-m point along the 500-m transect were extracted from a digital elevation model to guide the selection of the continuous 5-m subunits with as low internal topographical variation as possible to make the two sampling designs comparable. Sample units of RAPELD design are aggregated in spatial modules with minimum geographical distance between plots of 1 km. Details of the field sampling can be found in Figueiredo *et al.* (2014) and Tuomisto *et al.* (2016).

ENVIRONMENTAL DATA

To represent soil fertility, topographic and climatic gradients we used the concentration of exchangeable base cations (Ca, Mg and K) defined as the sum of bases, the vertical distance from drainage (VDD) and the dry season length, respectively. The sum of bases is a good proxy of soil fertility in Amazonia since it is well correlated with phosphorus concentration (Quesada *et al.*, 2010) and is strongly related to diversity patterns across the basin (Higgins *et al.*, 2011; Tuomisto *et al.*, 2016). Soils from central and eastern Amazonia were collected following the protocol described by Moulatlet & Emilio (2011). In each plot, six surface soil samples (the top 5 cm of the mineral soil) were taken every 50 m and bulked to obtain a single composite sample. The soil samples were analysed for exchangeable Ca, K and Mg using the Mehlich I protocol (KCl 1 M method). In plots at the western Amazonia composite surface soil samples (top 5 cm of the mineral soil) were

taken at *c.* 200-m intervals such that they represented the topographical extremes along the transect. Each soil sample consisted of five subsamples collected in an area of *c.* 5 m × 5 m and bulked (Tuomisto *et al.*, 2016). Base cations were extracted using 1 M ammonium acetate.

The topographical descriptor was based on the VDD, extracted from SRTM digital elevation models (SRTM-DEM). VDD has been successfully used to map local hydrological conditions and to explain floristic patterns in Amazonia (Rennó *et al.*, 2008; Moulatlet *et al.*, 2014; Schietti *et al.*, 2014). Plots with low VDD values are closer to bottomlands and consequently closer to the water table and with better access to water than plots with high VDD values, often located in hilltops and plateaus, distant from the water table. VDD was obtained from three similar algorithms. For 198 plots, located in the Purus–Madeira interfluvium and in Pará state, VDD was derived from the height above nearest drainage (HAND) algorithm using the 90-m SRTM-DEM (Rennó *et al.*, 2008; Moulatlet *et al.*, 2014; Pinheiro, Rennó & Escada, 2015). For 193 plots located north of the Amazonas river in central Amazonia, VDD was obtained from the elevation over channel network algorithm using the hydrological tools of the SEXTANTE spatial data analysis library, coupled with the open-source gvSIG v.1.10 software (<http://www.gvsig.org/web/>) (see details in Figueiredo *et al.*, 2014). For the remaining plots, VDD was obtained from the 30-m SRTM-DEM using the vertical distance to channel network (Bock & Köthe, 2008) algorithm, implemented in the QGIS software through the SAGA-toolbox.

The climatic variable (dry season length) was estimated with data from the TRMM satellite (Kummerow *et al.*, 1998) available at <http://disc.sci.gsfc.nasa.gov>. We converted monthly precipitation data from 1998 to 2004 of the TRMM product 3B43 V6 at 0.25° resolution (*c.* 28 km at the Equator) into the dry season length variable, defined here as the maximum number of consecutive months with < 100 mm of precipitation in that period. For each plot, the dry season length value was extracted after rescaling the data to a 0.05° (*c.* 5 km) spatial resolution. We used the *raster* package in R to manipulate and process the TRMM data (Hijmans *et al.*, 2020).

INTRINSIC CLADE DIVERSIFICATION RATE AND RELATIONSHIPS WITH CLADE LMA, AGE AND SPECIES RICHNESS

The diversification rates for each of the seven Amazonian clades of Marantaceae were estimated using maximum likelihood inference, implemented in the R RPANDA package (Morlon *et al.*, 2016). For each phylogenetic tree, we fitted six different

models: three pure birth models (no extinction) with different parameterization for speciation rates (time-constancy, time-linear variation and time-exponential variation), and three birth–death models allowing constant extinction, combined with the same parameterization of speciation rates used before. Diversification rates were defined here as the maximum rate for each clade observed through time. For instance, in the case of models with ascending diversification rates, rates would be defined at present while for descending-rate models rates would be defined at clade origin (initial diversification rates). For models with constant rates, no time adjustment is needed. Essentially, model parameters are estimated according to a time-calibrated phylogenetic tree, the total time over which the process happened (crown age or stem age) and the number of extant species. A fourth optional parameter is the fraction of the extant species represented in the phylogenetic tree. This is essential in this study because we do not have a complete phylogeny and the sampling effort is unbalanced across clades. We extracted accepted taxon names by genus in the World Checklist of Selected Plant Families, accessed at <http://apps.kew.org/wcsp/home.do>. Based on ancillary literature and our taxonomic knowledge about the group, we removed invalid taxa and added others not included in the list. Taxa were also classified based on their occurrence in the four major regions in the Neotropics: Amazonia, Atlantic Forest, Cerrado and Central America. We assumed that taxa not identified at the species level included in our phylogenetic tree are not new species but rather one of those in the World Checklist of Selected Plant Families, and thus the sampling fraction of each clade was defined as the ratio of tips in the phylogenetic tree and the total accepted taxa belonging to that Amazonian clade. Diversification rates were estimated using both crown and stem ages. The best model was assessed by comparing Akaike's information criterion with corrected sample size (AICc).

To test if clade diversification rates were related to clade life-history strategy, we applied a simple linear model using the mean LMA of clades as independent variables. Since the time-constant rate model was selected for all clades as the best model, no temporal adjustment was needed to estimate the speciation rate for each clade. We estimated the mean LMA values for each clade fitting a t family distribution with three parameters (mean, variance and skewness) over the distribution of species' LMA values, using the *gamlss* R-package (Rigby & Stasinopoulos, 2005), to reduce the effect of outliers in the mean estimates. To evaluate whether the functional strategy, diversification rates and clade age predict clade species richness, we performed a multiple linear model. Two models were fitted separately, one using LMA

and clade age as independent variables, and the other using diversification rates and clade age. This was done since we presume that diversification rates and LMA were correlated, and because we do not have enough statistical degrees of freedom to fit more complex models. The relative importance of each variable was obtained by estimating the reduction in the adjusted R^2 after removing each variable from the model. Linear models were run using the *stat* R package.

CLADE HABITAT ASSOCIATION

We estimated clade habitat affinities by fitting a generalized linear model with a binomial family distribution and log-link function (logistic regression). The presence–absence data for each clade obtained in the 448 plots were regressed against the log sum of bases, log vertical distance from drainage and dry season length. Linear and second-order polynomial response curves were allowed, and best-fitting models were chosen based on AIC values. All species recorded in the plot inventories were included, even when they were not represented in the phylogenetic tree.

DIVERSIFICATION DYNAMICS AND RELATION TO PAST EVENTS

To evaluate changes in the trajectory of diversification dynamics between clades with different functional strategies and their association with past geological and climatic events, we used a compound Poisson process on mass-extinction times (CoMET) algorithm implemented in the *TESS* R package (Höhna May & Moore, 2016). The advantage of CoMET is that it does not assume a priori a unique and independent branching process generating the branching pattern of our tree, e.g. a pure birth model or birth–death process with exponential varying rates. Instead, it estimates rates (speciation, extinction and mass extinction) at any point of time using a compound Poisson process (CPP) model and reversible-jump MCMC to average over a vast set of possible birth–death processes (Höhna *et al.*, 2016). We merged our seven clades into two groups, consisting of the three clades with low LMA values (the acquisitive clades *Breviscapus*, *Comosae* and *Microcephalum*) and the conservative clades with the four remaining lineages, and performed the CoMET analysis separately for each of them. We did not consider the mass extinction events in our model and thus we disabled this option before running the algorithm. The priors for speciation and extinction rates were defined using the automatic empirical hyperprior procedure already implemented in CoMET. To ensure sufficient convergence in reversible-jump MCMC, we used the auto-stopping rules setting a high number of maximum iteration (10^8) and the minimum ESS equal

to 500. Thus, the MCMC stops after this threshold has been reached. The main geological events related to Andean uplift (Hoorn *et al.*, 2010a) and palaeoclimate reconstruction (Zachos *et al.*, 2001) were plotted in conjunction with diversification dynamics profiles to identify potential associations between past events and shifts in diversification rates.

RESULTS

ANCESTRAL LIFE-HISTORY STRATEGY RECONSTRUCTION

The patterns of LMA distribution among clades indicate that the oldest clades had higher LMA and thus suggest that the ancestral life-history strategy was conservative with the most recent common

ancestor of the acquisitive clades dated at 23.7 Mya (19.7–29.8, 95% confidence interval; Fig. 1).

LIFE-HISTORY STRATEGY, NOT CLADE AGE, EXPLAINS DIVERSIFICATION RATES

For the diversification rates, six models were tested, running from simple (pure birth process with constant speciation rates) to more complex models (birth–death process with speciation rates varying exponentially through time). Species richness, diversification rates (r), clade ages and mean LMA values varied markedly across the seven Amazonian lowland rain forest lineages in Marantaceae (Fig. 1). For all seven clades, diversification rates were better estimated by a pure birth model process (no extinction, and constant speciation rates,

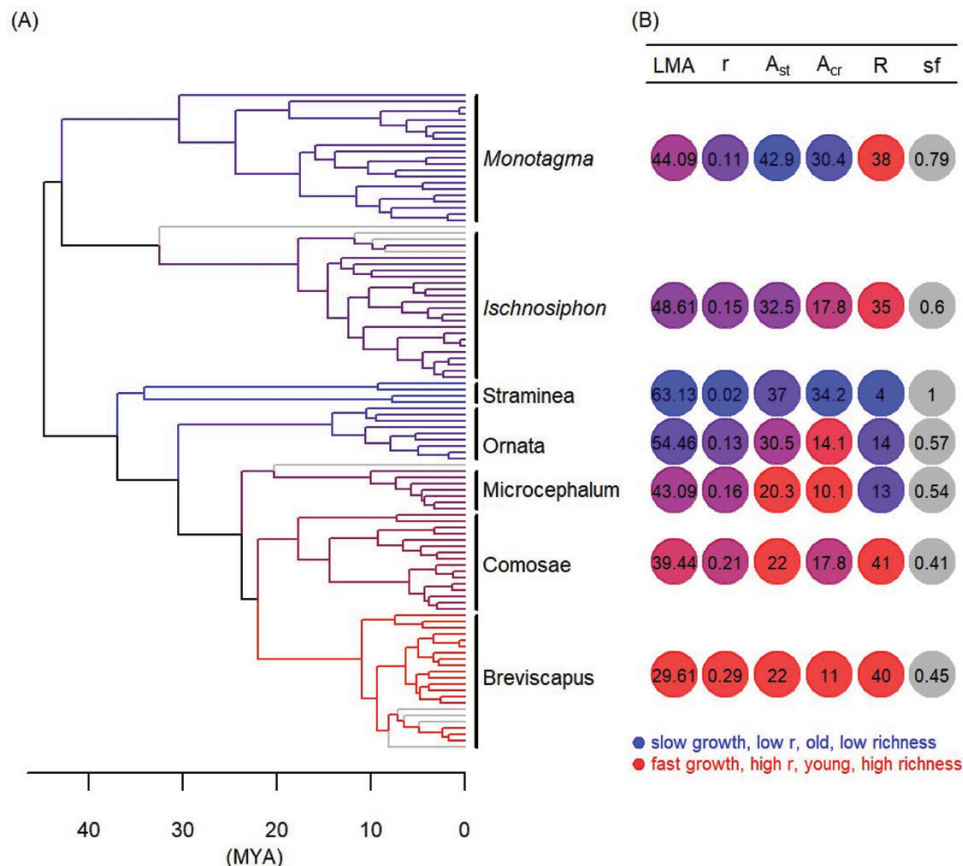


Figure 1. Bayesian maximum clade credibility time-calibrated phylogenetic tree based on the nuclear ITS marker (A) and intrinsic clade factors across the seven Amazonian lineages of Marantaceae (B). Clades in A are coloured according to their diversification rates (r) exhibited in B, and grey represents non-Az Amazonian lineages, which were collapsed in a unique node (see the complete phylogenetic tree in Supporting Information, Fig. S2). In B are the mean clade LMA (in g/m^2), diversification rates (r , in events per My), stem ages (A_{st} , in My), crown ages (A_{cr} , in My), clade species richness (R) and sampling fraction (sf , the proportion of extant taxa represented in the phylogenetic tree). The diversification rates were estimated fitting a pure birth process, which was the best model compared with models assuming birth–death processes (see details in Methods).

Supporting Information, Table S3). The three clades with the highest diversification rates (*Breviscapus*, *Comosae* and *Microcephalum*) were also those with the lowest LMA, i.e. clades with an acquisitive life-history strategy were, on average, younger than the conservative clades (Fig. 1). In fact, the intrinsic diversification rates were strongly related to the clade LMA (Fig. 2E), and both diversification rate and LMA predicted species richness across the seven lineages (Fig. 2B–D). Clades with high LMA (acquisitive life-history strategy) had higher diversification rates and more species than those with low LMA (Fig. 2B–D). Contrary to predictions of the age-dispersal model, species richness was not associated with clade age (Fig. 2C–E).

CLADE HABITAT ASSOCIATION RELATED TO FUNCTIONAL TRAITS AND TIME OF ORIGIN

The habitat affiliations of the seven clades were also clearly related to the diversification rates, life-history strategies and time of origin (Fig. 3). Clades with a conservative strategy and lower diversification rates (*Straminea*, *Monotagma*, *Ischnosiphon* and *Ornata*) that originated > 30 Mya tended to be associated with soils with low to medium concentrations of nutrients. Clades *Straminea* and *Ornata* were associated with uplands, whereas *Monotagma* and *Ischnosiphon* did not have clear topographic preferences. On the other hand, the three lineages that originated 25–20 Mya (*Breviscapus*, *Comosae* and *Microcephalum*) had the highest diversification rates and an acquisitive functional strategy; these were

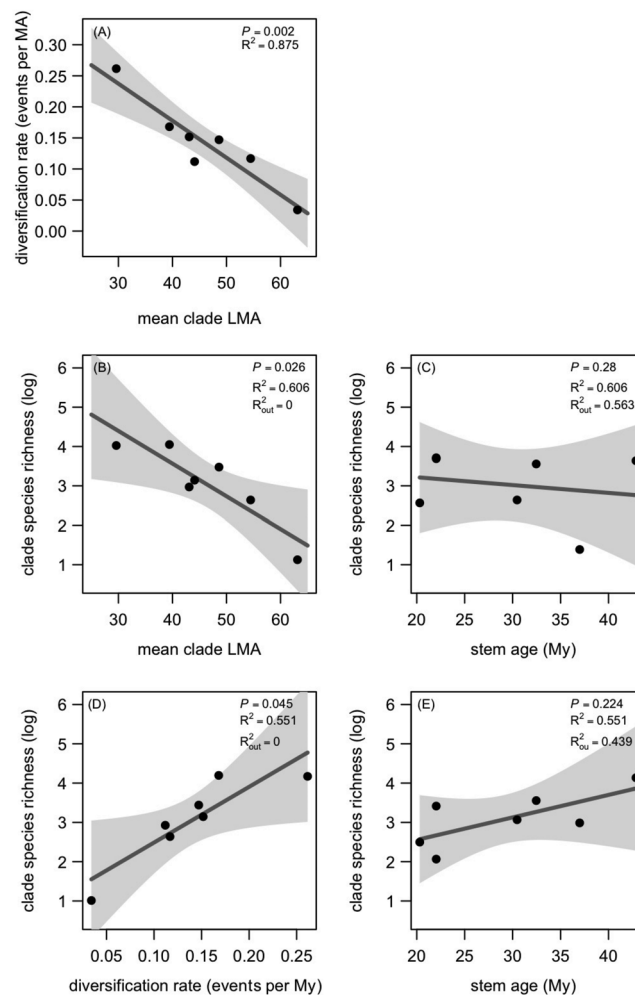


Figure 2. Relationships between diversification rates, leaf mass per area (LMA), clade species richness and clade age. A, the simple relationship between diversification rates and LMA. B and C, partial regressions of the model including LMA and stem age as predictor variables; D and E, the partial regressions of the model including diversification rates and LMA as predictors. The fitted line in B–E was obtained using conditional plots implemented in the *visreg* R package. R^2 gives the goodness-of-fitness of models including all variables and R^2_{out} the goodness-of-fitness of models without that variable.

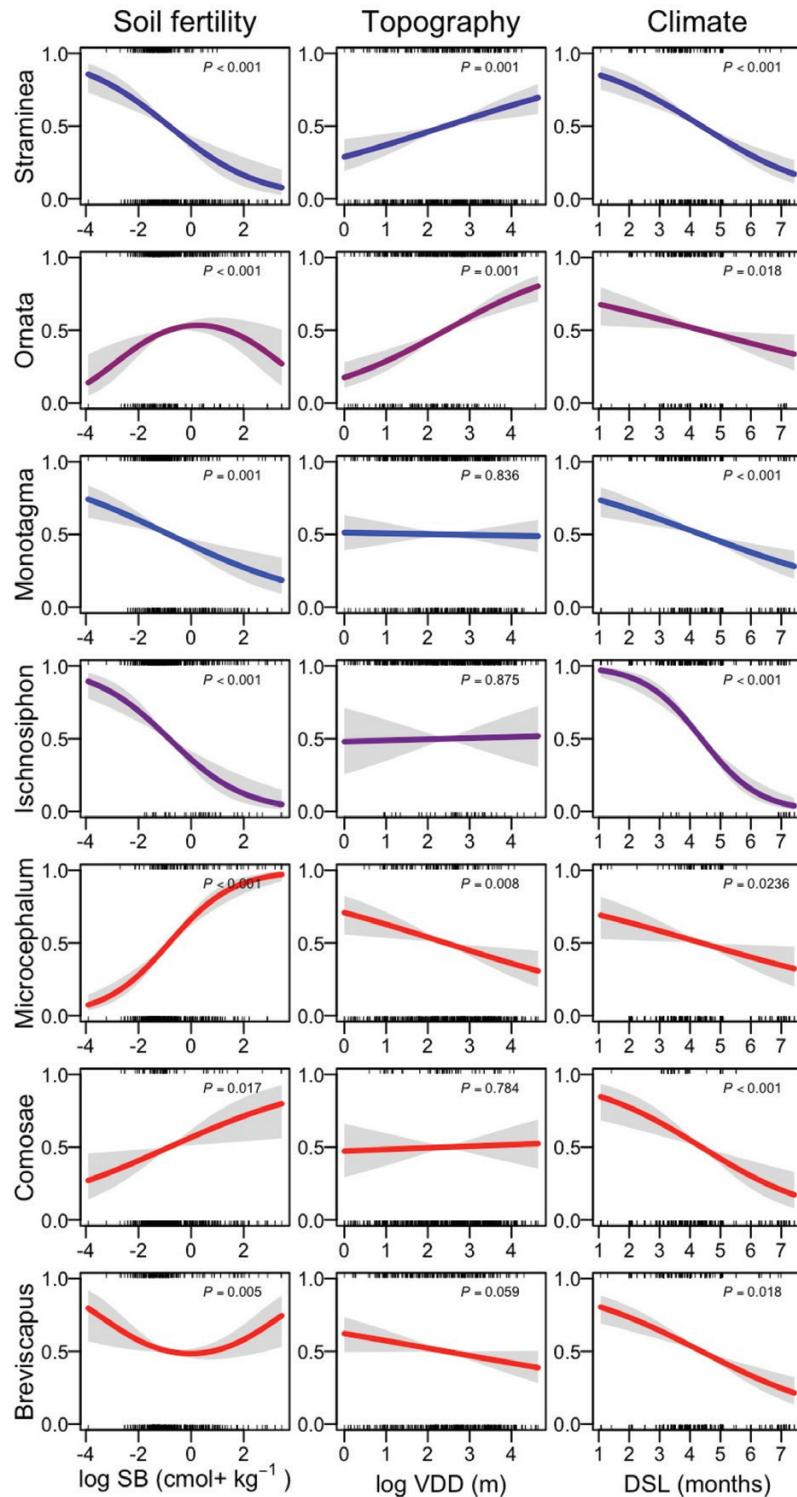


Figure 3. Habitat associations of the seven Marantaceae clades. Vertical axes denote the occurrence probabilities scaled to 0–1 using a contrasting plot implemented in the *visreg* R package. Horizontal axes denote the logarithm of the sum of bases Ca, Mg and K (SB), logarithm of vertical distance from drainage (VDD) and the dry season length (DSL). From top to bottom panels, clades are arranged in order of their leaf mass per area (LMA) values and colours are based on their stem age, red representing the youngest and blue the oldest clades. The statistical significance of clade–habitat associations is given by the *P* values extracted from a generalized linear model using all the three variables.

more associated with richer soils and locally humid environments such as valleys and bottomlands. In the *Breviscapus* clade, species soil nutrient preferences were variable, with some species associated with richer soils and others with poorer soils, and a few species associated with intermediate levels of nutrients. All clades preferred wetter climates and tended to avoid drier climates.

DIVERSIFICATION DYNAMICS RELATED TO PALAEO-EVENTS

Allowing diversification rates to vary over time revealed remarkable links between life-history diversification patterns and palaeo-geological and climatic events, and markedly distinct behaviour dynamics between clades with different functional strategies (Fig. 4). The diversification of conservative life-history clades started c. 45 Mya, during the Mid-Eocene (Fig. 4B). Speciation (Fig. 4C) and extinction rates (Fig. 4D) remained low and constant until the Late Oligocene to Early Miocene (c. 20 Mya). This period marks a phase of intensification of Andean uplift and the beginning of the fluvial-wetland system (c. 23 Mya) and coincides with a slight increase in speciation and diversification rates. After that, a constant regime of speciation and extinction rates of these clades predominates until the present. By contrast, the diversification dynamics of acquisitive life-history clades started later and was more dynamic than the diversification history of conservative clades (Fig. 4B). The early stages of the western fluvial-wetlands system in Amazonia (Fig. 4A) coincided with the emergence of clades with an acquisitive life-history 23.7 Mya in Marantaceae (cf. Fig. 1). The speciation rates remained constant for the following 10 My. The extinction rates of these clades gradually increased until the Mid-Miocene (c. 15 Mya), making differences indistinguishable between net diversification rates of acquisitive and conservative clades. The speciation rates of acquisitive clades only started to speed up slightly before the end of the Pebas phase and the beginning of the Acre system (c. 10 Mya), the same period during which extinction rates started to decline, resulting in a rapid increase in diversification rates. Speciation and diversification rates reached a peak around the end of the Pliocene, followed by an abrupt decline at the beginning of the Pleistocene (c. 3 Mya) and stabilized only in the last 1000 000 years.

DISCUSSION

EMERGENCE OF THE ACQUISITIVE FAST-GROWTH LIFE-HISTORY STRATEGY ACCELERATED DIVERSIFICATION RATES AND INCREASED DIVERSITY

Many studies have suggested the link between Andean uplift and Amazonian species evolutionary dynamics

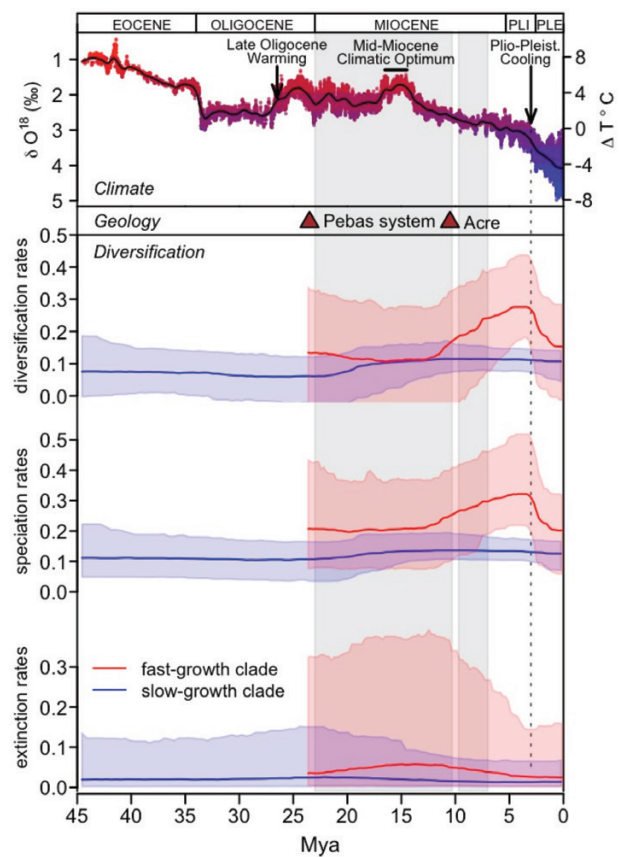


Figure 4. Diversification dynamics of the fast-growth and slow-growth clades along the palaeoclimate temporal trends from 45 Mya to the present (first line). Palaeoclimate trends are based on data from Zachos *et al.* (2001), assessed via <https://www.ncei.noaa.gov/products/paleoclimatology>. ΔT is the approximate difference from present-day temperature scaled according to the concentration of isotopes of oxygen ($\delta^{18}\text{O}$) based on the benthic foraminifera record (see details in figure 2 of Zachos *et al.*, 2001). Palaeoclimate points are coloured representing the gradient running from warm conditions (red) to cooler conditions (blue). Geological events (start marked with red triangles in the second row, and extensions marked with grey polygons across the panel) were obtained from Hoorn *et al.* (2010a). The third row exhibits the posterior mean (lines) and the 95% credible interval (polygons) for diversification, speciation and extinction rates. Fast-growth clades include *Breviscapus*, *Comosae* and *Microcephalum* and slow-growth clades include *Ischnosiphon*, *Monotagma*, *Ornata* and *Straminea*.

(e.g. Antonelli *et al.*, 2009; Elias *et al.*, 2009; Hazzi *et al.*, 2018; Esquerré *et al.*, 2019). To our knowledge, this is the first attempt to link those events to the functional trade-offs involved in Amazonian plant species diversification dynamics. Here we show a strong eco-evolutionary pattern linking the emergence and diversification of clades with a fast-growth acquisitive

life-history strategy to palaeo-geomorphological transformations. Our findings for Amazonian clades of Marantaceae do not support the age-diversity model. By contrast, recent clades of Marantaceae often show diversification rates high enough to compensate for their recent origin. Here we suggest that this rapid diversification observed in younger clades was a result of the evolution of the fast-growth acquisitive strategy allowed by the novel geochemical Amazonian landscape. Other studies have related diversification rates to life-history strategies in Amazonia by showing that tree genera with higher turnover rates tend to also have higher diversification rates (Baker *et al.*, 2014) or showing the impressive recent radiation of a fast-growing Amazonian tree genus, *Inga* Mill. (Richardson *et al.*, 2001). Here we show that LMA is correlated with higher diversification in a phylogenetically and morphologically distinct plant group, but also expand these findings by demonstrating the temporal overlap between the emergence of fast-growth acquisitive clades and the resurfacing of highly productive environments in Amazonia.

LANDSCAPE EVOLUTION SHAPING DIVERSIFICATION OF LIFE-HISTORY STRATEGIES IN AMAZONIAN CLADES

The diversification signature of two groups with distinct life-history strategies was quite distinct in terms of their responses to past geological and climatic events. The diversification rates of conservative clades were in an almost pure steady state throughout their 44 My of existence, with a gradual reduction in extinction rates and a short increase in the speciation rates in the Early Miocene (c. 20 Mya). The intense transformation of the landscape driven by intensification of Andean uplift seems to have only slightly impacted the speciation rates of conservative clades. Some clades in this group have intermediate values of LMA that must have been favoured by the increasing high-productivity environments.

Although the diversification dynamics of conservative clades can be described as a constant and stable process, the same does not apply to fast-growth acquisitive clades. Palaeo-environmental reconstruction suggests that fluvial environments evolved to a huge and complex mega-wetland, formed by lacustrine, swamp and riverine systems in the Mid- to Early Miocene (c. 16–11 Mya, Pebas phase). The expansion of terrestrial habitats over the wetlands, supported by a predominance of continental vertebrates in fossil records (Latrubesse *et al.*, 2007), resulted in an area represented today by the western lowlands (Hoorn *et al.*, 2010a, b). Although fast-growth acquisitive clades would have been already present during the Pebas phase, the steady state of speciation rates during this period and the slight increase in

extinction rates led to a reduction in net diversification to levels indistinguishable from diversification rates of conservative clades. This scenario suggests that diversification of western lineages associated with non-inundated forest was not favoured by the expansion of the mega-wetlands, probably due to the reduction of suitable terrestrial areas. Evidence of the inhibitory effect of the Pebas system on the speciation process has also been found in the evolutionary history of Neotropical palms (Roncal *et al.*, 2013). The boosted diversification of fast-growth acquisitive clades was only observed at the end of Pebas phase when a new stage of intensification of Andean uplift drove the gradual replacement of mega-wetlands by fluvio-tidal wetlands and the onset of an early Amazon river system (c. 11–7 Mya; Acre phase) (Hoorn *et al.*, 2010b).

The functional fast–slow trade-off observed across lineages considered here correlates with their preferences along the resource–substrate gradients (Fig. 3). This relationship is in accordance with previous studies demonstrating the soil-fertility gradient as the main driver of the fast–slow growth trade-off in tropical forests (Russo *et al.*, 2008; Quesada *et al.*, 2012). However, the role of the soil–resource gradient as a driver of ecological patterns transcends ecological time scales and goes deep into the evolutionary scale, as we have shown here. In Marantaceae, clades with fast-growth acquisitive life history also tend to be associated with fertile soils, whereas clades with conservative life-history strategy tend to be associated with soils of low to intermediate fertility (Fig. 3). The slow-growth clades evolved early in the Eocene, whereas the emergence of fast-growth clades dated from the Late Oligocene. Since the acquisitive fast-growth strategy is strongly conditioned by resource availability (Reich, 2014), this suggests that the emergence of these clades was only made possible by the expansion of highly productive environments in Amazonia. Palaeo-geological and ecological evidence strongly support the area reduction of a low-productivity craton-derived landscape and the expansion of a highly productive fluvial system and an incipient wetlands landscape in Western Amazonia in the Late Oligocene to Early Miocene (c. 23 Mya) driven by an intense phase of Andean uplift (Hoorn *et al.*, 2010a, b). Occasional marine incursions observed in this period (Flynn & Wyss, 1998; Wesselingh & Salo, 2006) may have also contributed significant levels of nutrients, especially calcium, to Amazonian ecosystems. Even today, it is possible to detect the soil–resource gradients related to sediments from the early Miocene (Pebas formation) structuring ecological and biogeographical patterns in western Amazonian forests, including for the herbaceous groups analysed here (Salovaara, Cárdenas & Tuomisto, 2004; Tuomisto *et al.*, 2016). The gap–disturbance regime also tends to be faster on

richer soils, due to shorter generation times and higher mortality rates of trees (Quesada *et al.*, 2012), allowing higher penetration of light to the understorey, which is another important resource structuring the fast–slow growth trade-off (Reich, 2014). Therefore, our results suggest that the emergence of highly productive and dynamic habitats was essential to the evolution of a fast growth strategy and, consequently, to the increase of diversification rates.

The imprint of the long-term topographic transformation through Amazonian history on functional and evolutionary patterns across clades of Marantaceae is less evident than that by geochemical transformation because most clades showed no preference along topographic gradients. However, associations exclusively with uplands were found in clades with high LMA and associations exclusively with bottomlands were observed for the *Breviscapus* clade, which had the highest diversification rates and LMA. The establishment of the modern Amazonian drainage system started only in the Late Miocene (c. 9 Mya) and is relatively more recent than the geochemical transformation that took place in Amazonia in the Early to Mid-Miocene (Hoorn *et al.*, 2010b, 2017), which may favour recent speciation events driven by adaptive radiation along topographic gradients. In central Amazonia, for instance, it is common to find a valley-occurring species with a sister species associated with plateaus (Cosme *et al.*, 2017), suggesting that speciation across topographical gradients may be relatively recent and may have occurred several times within clades. This evolutionary pattern would lead to the absence of a general topographical association at any higher level than the species level itself.

PALAEOCLIMATE IMPACT ON CLADE AND LIFE-HISTORY DIVERSIFICATION THROUGH TIME

The negative effect of cooling-dry conditions observed only in the fast-growth acquisitive clades suggests that fast-growth tropical plants may depend on relatively high temperatures and humidity, possibly to sustain their higher metabolic rates. Net diversification rates accelerated towards the Late Pliocene and abruptly declined in the Early Pleistocene (c. 3 Mya). The Plio-Pleistocene period marked a transition from warm to cold and dry climatic conditions (Haffer, 1969; Zachos *et al.*, 2001), suggesting a possible role of climate on the reduction of diversification rates. Evidence from fossil pollen records also indicates a general decline in plant diversification during the Pleistocene due to an increase of extinction rates (Hammen & Hooghiemstra, 2000). Due to biophysical constraints, a strict fast-growth strategy is only possible if all vital resources (e.g. nutrients, carbon, water and radiation) are provided in

enough quantities to keep metabolic rates high (Reich, 2014). In contrast, current evidence has shown that slow-growth species are less sensitive to drought (Ouedraogo *et al.*, 2013), supporting the distinct response between fast-growth acquisitive and slow-growth conservative clades to palaeoclimatic changes.

The dependence of acquisitive clades on warm-wet conditions also suggests that the rapidly rising temperatures during the Late Oligocene could also have favoured their emergence. The increase of palynological diversity in the Neotropics associated with warming periods from the Palaeocene to the Early Miocene (65–20 Mya) (Jaramillo *et al.*, 2006) has been attributed to a speed up in biochemical kinetics, rates of molecular evolution and speciation rates driven by the increase of temperatures (Jaramillo & Cárdenas, 2013). However, diversification rates in Amazonian Marantaceae did not increase during the Miocene Climatic Optimum warming period (17–15 Mya), and a strong increase in diversification rates happened in the Mid- to Late Miocene (c. 10 Mya) when the temperature conditions resembled those before the Late Oligocene warming period. Therefore, the palaeoclimate cycles alone were unlikely to have favoured the emergence of fast-growth acquisitive clades and accelerated the diversification rates in Amazonian Marantaceae.

CONCLUSIONS

By combining analyses of plant growth trade-offs and long-term diversification dynamics, we have provided clear evidence that landscape transformation boosted by Andean uplift was the paramount driver of the diversification history of clades of Marantaceae in Amazonian lowland rain forest. This process may have involved two main mechanisms, each prevailing at a different stage. The intense Andean uplift (c. 23 Mya) drove the emergence of highly dynamic and productive environments and promoted the evolution of lineages with fast demographic strategies to live in such abundant resource conditions via trait-niche divergence. Fast-growth strategies associated with short generation times led to rapid molecular evolution, speeding up speciation rates (Smith & Donoghue, 2012). This process, however, stayed latent for the next 10 My due to low availability of vast continental areas. As the mega-wetlands system provided space for terrestrial environments due to the second phase of intense mountain uplift (c. 10 Mya), new extensive areas of terrestrial habitats became available. Then, over this vast and heterogeneous topographic landscape, diversification has increased by the combination of allopatric dispersal and adaptive divergence (Fine *et al.*, 2005; Kawecki, 2008; Smith *et al.*, 2014). Diversification slowed down in the cooling

phase during the Pleistocene, but until then, most of the species known today had already originated. With no evident effect of extinction, the higher the speciation rates, the higher was species accumulation, resulting in a high number of extant species. Since > 50% of species in the Amazonian Marantaceae belong to three fast-growth clades, it is reasonable to conclude that such tumultuous past events caused by Andean uplift in Amazonia significantly contributed to the current diversity of its lowland rain forest.

Our results support the idea that it is not necessary to invoke a strict allopatric vicariance–geological model to explain evolutionary history and diversity patterns in Amazonia. Nevertheless, a pure dispersal model, disconnected from past geological events, ecological forces and focused on recent speciation events does not seem to be the best alternative (Smith *et al.*, 2014; Dexter *et al.*, 2017). We propose that a coupling of the functional trait–niche framework to the long-term diversification dynamics provides good insight into the complex evolutionary history of tropical forests and potential mechanisms underlying the origin and evolution of its spectacular biological diversity. We conclude that geological and ecological forces contributed greatly to shape the evolutionary history and diversity patterns of Amazonian forests.

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DATA AVAILABILITY

All data used in this paper is either provided in the supplementary materials or through links to the sources along the text.

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