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DISENTANGLING REGIONAL AND LOCAL TREE DIVERSITY IN AMAZONIA

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ABSTRACT

Amazonian forests are one of the most diverse and extensive forests in the world. So far, their regional and local tree diversity have been explained by current environmental factors such as rainfall seasonality and soil fertility. However, environmental factors have been far from stable over the history of Amazonia. Identifying the main drivers shaping the current pattern of tree diversity in Amazonia requires hence a proper historical perspective. Here, we partition tree diversity into its regional and local components. We hypothesize that regional diversity is influenced by large-scale, long-term processes, whereas local diversity is mainly regulated by small-scale, short-term processes. We analyze the most extensive dataset of tree inventory plots covering the Amazon Basin and the Guiana shield. We find that palaeo-climatic stability and long-term large-scale ecosystem dynamics explain 31% and 14%, respectively of the regional tree diversity. Actual rainfall seasonality is correlated with regional tree diversity (19%), but we argue that this is of little consequence for the evolutionary drivers of regional diversity. Local ecosystem dynamics explain 17% of the variation in local tree diversity. Our results suggest that reliable predictions of future changes of species diversity require an approach which considers evolutionary and ecological processes at the scale at which they are most relevant.

INTRODUCTION

Large-scale patterns of biodiversity are often explained by current climate. A well known example is the latitudinal gradient in species richness that is most often explained in terms of available energy, rainfall, or combinations thereof (Currie, 1991, Currie et al., 2004, O'Brien, 2006, Kreft and Jetz, 2007). The large-scale pattern of tree diversity in Amazonia (ter Steege et al., 2006) has also mostly been explained in terms of annual rainfall (Clinebell et al., 1995), seasonality (ter Steege et al., 2003), and soil fertility (Clinebell et al., 1995). Climate, however, has been far from stable over the history of the existence of Amazonian forests – viz the last c. 55 million years (Morley, 2000, Burnham and Johnson, 2004, Jaramillo et al., 2006). In fact, the current climate may be representative of only a small fraction of the history of Amazonia (ibid.). As species richness, the number of existing species, is ultimately the sum of three long-term processes – speciation, extinction, and immigration (Ricklefs and Schluter, 1993, Rosenzweig, 1995), the current pattern of diversity have to be interpreted in a proper historical perspective. Local diversity (here measured on 1-ha plots, see ter Steege et al., 2003) is also influenced by small-scale, short-term ecological processes such as competition, predation, and random local extinction. To understand which part of the variation of species diversity is regulated by long-term, large-scale versus short-term, small-scale processes a conceptual model linking them is needed (Ricklefs and Schluter, 1993, Rosenzweig, 1995, Willis and Whittaker, 2002). We propose a conceptual model with two species pools: a regional species pool, which is mainly influenced by the large-scale, long-term processes, and a local species pool, which is regulated by small-scale, short-term processes and receives species from the regional species pool. The link between regional and local species pool determines *which* and *how many* species from the regional species pool are present in the local species pool (Fig. 2.1). We, therefore, propose that an analysis of the tree diversity in Amazonian forests should take evolutionary and ecological processes into account at the scale at which they are relevant.

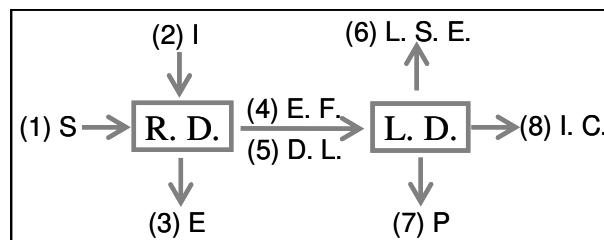


Figure 2.1: Diversity is influenced by regional and local processes (Hubbell, 2001, ter Steege and Zagt, 2002, Ricklefs and Schluter, 1993). Regional diversity is controlled by processes such as speciation (S, 1), immigration (I, 2), and extinction (E, 3), whereas the local diversity is controlled by local stochastic extinction (L. S. E., 6), interspecific competition (I. C., 8), and predation (P, 7). Regional and local diversity are linked via environmental filters (E. F., 4) and dispersal limitation (D. L., 5).

Regional tree diversity and regional processes

At low latitudes, the extent and location of the tropical rain forests are related to changes in global climate over time which, in turn, are influenced by the well-known 'Milankovitch cycles' (Gates, 1993). The global temperature and rainfall regime has a major cycle related to the 'eccentricity cycle' (ibid) with a periodicity of c. 100,000 years. During warm and wet interglacial periods, tropical rainforests covered a much larger latitudinal range than during cold and dry glacial periods (Morley, 2000, Mayle and Beerling, 2004, Maslin et al., 2005). The 'precession cycle', with a periodicity of 20,000 years causes shift changes southwards and northwards of the location of the Intertropical Convergence Zone (ITCZ) (Martin et al., 1993, Martin et al., 1997, Haug et al., 2001). As a consequence, Amazonia experienced a more stable climate in its centre than at its edges (Hooghiemstra and van der Hammen, 1998). As the ITCZ on the South American continent shifts slightly southward (see Martin et al., 1997), this stable area should have a centre just south of the equator. In the east-west direction, a more stable climate, in terms of rainfall, is found in western Amazonia due to the orographic rain caused by the Andes (Hooghiemstra and van der Hammen, 1998). Long-term climatic variability is considered to be one of the important explanations for low diversity in certain regions (Araujo et al., 2008). In general, species with small ranges size are thought to be more susceptible to extinction partially caused by long-term climate change than large-range size species (Dynesius and Jansson, 2000, Jetz et al., 2004, Araujo et al., 2008).

Additionally, there is a sharp contrast in landscape evolution in eastern and western Amazonia (Sombroek, 2000). In western Amazonia, soils developed on sediments originating from Andean orogeny during the Cenozoic (~66 Ma and more recent), while in the south-east and north-east, on the Brazilian and the Guiana shield, respectively, soils developed on crystalline bedrock from the Proterozoic (~2,500 Ma) and its sediments. The soils of these two major geological series differ markedly in fertility (Sombroek, 2000), productivity (Malhi et al., 2004), forest tree composition (ter Steege et al., 2006), wood density (Baker et al., 2004, ter Steege et al., 2006), and seed mass (ter Steege et al., 2006). Higher productivity leads to higher turn-over in the forest (ter Steege and Hammond, 2001, Phillips et al., 1994, Malhi et al., 2004). Species with fast growth rates have low wood density and high mortality and recruitment rates (Nascimento et al., 2005), and we assume, short generation times. These species would experience faster rates of evolution than species with long generation times (Marzluff and Dial, 1991, Verdú, 2002), consequently leading to higher diversification (Allen and Gillooly, 2006).

Local tree diversity and local processes

Local variation in tree species diversity has been documented for Amazonia (see e.g. Pitman et al., 2002, Oliveira and Nelson, 2001). Tree species diversity of 1-ha plots located close to each other and thus, under similar climatic conditions, can exhibit huge differences in tree species diversity (Valencia et al., 2004, ter Steege et al., 2003). Local differences are partially influenced by competitive exclusion, which is driven by local disturbance, such as gap formation by fallen trees or branches, as explained by the Intermediate Disturbance

Hypothesis (Connell, 1978, Huston, 1979, Huston, 1994), which predicts highest diversity at intermediate disturbance regimes or in the mid-term of a primary or secondary succession (but see Wright, 2002, Sheil and Burslem, 2003 for critical reviews). As shown in Fig. 2.1 predation is thought to decrease local tree diversity. Predation, however, can also increase tree local diversity through frequency dependent mortality (Janzen, 1970, Connell, 1972). Frequency-dependent mortality reduces the potential of species to become dominant in ecosystems (for Amazonia, see Givnish, 1999). Density-dependent mortality of plants may be caused more frequently by insects and infestation by microbes and fungi than by mammal herbivores (Hammond and Brown, 1998, Wright, 2002).

In this Chapter, we apply a hierarchical approach to identify regional and local patterns and potential drivers of variation in tree species diversity in Amazonia. We focus on the relative contribution of regional and local processes determining tree species diversity at the relevant scale. We analyze the Amazon Tree Diversity Network (ATDN) dataset, which contains 781 tree inventory plots and spans the entire area of the Amazon basin and the Guiana shield (here collectively called 'Amazonia'). In this dataset, many localities have multiple plots, sometimes up to 80. This offers a unique opportunity to analyze both regional and local variation of tree species diversity in one of the largest and most ecologically diverse tropical forests in the world.

METHODS

Data

We updated the ATDN dataset (ter Steege et al., 2003) by adding 1) the number of tree species and 2) the number of individual trees with diameter at breast height ≥ 10 cm, compiled from both newly published and unpublished floristic inventory plots and plots included in the RAINFOR dataset (version FT29.06.06; Peacock et al., 2007). In total, we compiled data from 781 tree inventory plots spread across Amazonia and placed in different forest (and soil) types: terra-firme (latosol, oxisol, and ultisol), white-sand (podzol), swamp (histosols), and floodplain (alluvial). Out of this total, we selected 752 plots ranging from 0.23 ha to 1 ha to our analysis. Plots larger than 2 ha (29 plots out of 781) were excluded from the analyses to avoid inclusion of beta-diversity. The 752 plots were classified into two groups according to the age of the geological formation on which they occurred: Proterozoic/Palaeozoic versus Cenozoic. Plots located on and around the Brazilian and the Guiana shield were classified as Proterozoic, and plots located on the Andean sediments were classified as Cenozoic (Sombroek, 2000). For all 752 plots, we extracted rainfall seasonality (coefficient of variation; Bioclim 15 in the WORLDCLIM dataset) in the period of 1950-2000 with 30 arc-seconds resolution (~ 1 km) from WORLDCLIM (Hijmans et al., 2005).

We extracted the species list of 113 terra-firme plots (41 RAINFOR plots and 72 plots located in 'Reserva Florestal Adolpho Ducke', central Amazonia) for which the botanical identification is consistent among the plots. For the RAINFOR plots we calculated the percentage of individuals from softwood genera, i.e., with oven-dried wood density < 0.6 g cm⁻³. For the plots at 'Reserva Florestal Adolpho Ducke' we first

classified the genus on categories of pioneer and non-pioneer, afterwards we calculated the percentage of individuals belonging to pioneer genera. The wood density values and the classification of pioneer genera were extracted from Chave et al. (2006) and the RAINFOR dataset. The percentages are considered to be proxies for disturbance in the plots (ter Steege and Hammond, 2001).

Data analyses

Tree diversity was calculated with Fisher's alpha, hereafter referred to as tree alpha-diversity, which is relatively insensitive to sample size (Fisher et al., 1943). To calculate tree alpha-diversity, we used the number of species and individuals given for each plot, which sometimes contain a considerable number of morpho-species. As a consequence of this approach, if the morpho-species are split artificially we over-estimate tree alpha-diversity. By contrast, if the morpho-species are grouped artificially we underestimate tree alpha-diversity. We think, however, that it is of minor importance to the results as for those plots where the morpho-species were finally resolved, Fisher's alpha changed little (Nigel Pitman, pers. obs.).

We applied a stepwise approach to analyze the total variation of tree alpha-diversity (TAD) as a function of regional tree diversity (RTD), which is a reflection of the regional species pool (RSP), and local tree diversity (LTD) plus error (ϵ):

$$\text{TAD} = \text{RTD} + \text{LTD} + \epsilon \quad (2.1)$$

We separated the signal of the RTD from that of the LTD + ϵ by means of spatial interpolation. First, we attempted to interpolate TAD using universal kriging (ter Steege et al., 2003); this, however, proved to be impossible because of high local variation of TAD in locations with several plots (see Fig. 2.2). The high local variation causes our data to show no significant spatial auto-correlation. We, therefore, applied local (loess) regression (Venables and Ripley, 1997, Kalunzy et al., 1998) to interpolate TAD for Amazonia. Loess regression is a non-parametric regression technique that allows for greater flexibility than traditional regression techniques because, unlike traditional regression techniques, it does not fit a single regression model to the entire dataset (Osborne et al., 2007). Instead, loess regression gives a predicted value at each point of the dataset by fitting a weighted linear regression to it. A smooth regression curve is used to connect the predicted values. The smoothness of the regression curve is affected by a span value, which controls the degree at which the weight of points decreases with distance from the point of interest. Therefore, small span values (close to zero) produce an over fitted model, in contrast high span values (close to one) cause an excessively smooth model. We fitted a 2nd degree polynomial equation to our data (i.e., degrees of latitude and longitude of each plot as independent variable and observed TAD as dependent one) using a span value of 0.5. With the fit of this loess model, we mapped TAD for the entire Amazonia at a spatial resolution of one degree grid cells. We assume that the fit of our loess regression model represents the signal of the RTD. We estimated the ordinary residuals of the loess model by subtracting the observed

TAD values from the estimated ones. These residuals represent the variation of TAD that is not explained by regional effects, i.e., LTD plus the error variance of our loess regression model.

We then assessed to what extent regional and local variables related to the variation in RTD (loess fit), LTD (loess residuals), the link between RTD and LTD (also in loess residuals), and original Fisher's alpha values of each plot in a stepwise fashion. The regional variables used were: 1) latitude and longitude as proxies for palaeo-climatic stability, 2) actual rainfall seasonality, and 3) bedrock age (Proterozoic vs. Cenozoic). We considered these variables as regional variables, because they, as we argued in the introduction, mainly affect the processes of speciation and extinction and hence the RTD. We used latitude and longitude as model variables for the loess regression and also as explanatory variables because we consider them to be important proxies for palaeo-climatic stability (see Introduction). The influence of current rainfall seasonality on RTD was also analyzed with loess regression. The influence of bedrock age on RTD was determined with single factor ANOVA.

The next set of analyses focused on local tree alpha-diversity and its interaction with regional tree alpha-diversity. We started by quantifying the contribution of soil type (as a proxy for environmental filters) to the local tree alpha-diversity. We performed a single factor ANOVA to determine whether LTD is explained by plot forest type. Finally, we determined the effect of actual forest dynamics on LTD, as hypothesized by the Intermediate Disturbance Hypothesis. One hundred and thirteen plots located in terra firme forest were included in this analysis. Out of this total, 41 plots are located at different regions of Amazonia and 72 plots are located at 'Reserva Florestal Adolpho Ducke' (central Amazonia). We used a quadratic regression model (consistent with the expectation of the Intermediate Disturbance Hypothesis), to model LTD as a function of the percentage of individuals with wood density $< 0.6 \text{ g cm}^{-3}$ for the 41 RAINFOR plots (our proxy for frequency of disturbance, see above). We analyzed the 72 terra-firme plots located at 'Reserva Florestal Adolpho Ducke', separately, as due to their geographical proximity there is no variation in RTD. For these plots, we analyzed the relationship between the percentage of individuals of pioneer species and TAD with a quadratic regression model. All statistical analyzes were performed in S-PLUS 2000 (Mathsoft Inc.).

RESULTS

Regional tree diversity and regional processes

The loess regression explained 46% of the total variation in TAD (see Table 2.11 and Fig. 2.22), i.e., 46% of the total variation of tree alpha-diversity occurred at the regional scale, whereas the remaining 54% residual variation occurred at the local scale or represented the residual error (Table 2.1). The spatial interpolation reveals two rather simple gradients, related to latitude and longitude. On the latitudinal gradient, species diversity peaks at 4°–3° south and decreases towards a latitude of 15° south and 8° north. On the longitudinal gradient, diversity is low in the eastern areas of Amazonia and increases close to the western border of the study area (Fig. 2.3). Latitude accounted for 73% of the

variation in this model and longitude 20% (Table 2.1) (Fig. 2.4). Current rainfall seasonality explained 37% of the variation in RTD and 19% in variation of total TAD. Fitted values for TAD explain observed values of TAD well, but at locations with many plots variation in TAD encompassed nearly all variation present in the model (Fig. 2.2). Average TAD differed among plots on the two different geological substrates (mean (Cenozoic) = 85.2; mean (Proterozoic) = 59.7) (Table 2.2). This two-class division explained 14% of the variation in RTD (ANOVA $F_{[1,750]} = 129.35$, $p < 0.001$) and 6% of the total variation of TAD. It is important to note that all regional variables, which we considered to be related to long-term evolutionary processes, had much higher explanatory power for RTD than for LTD (Table 2.1), consistent with our expectation.

Table 2.1: Contribution of regional and local drivers to the variation of total, regional, and local tree alpha-diversity in the Amazon basin and the Guiana shield. TAD: Tree Alpha-Diversity, observed value of Fisher’s alpha for 752 tree inventory plots (ATDN 2008); RV: Regional Variation (fitted values of Fisher’s alpha as a function of latitude and longitude estimated with Local regression model); LV: Local Variation (residuals of the Local regression model); Final effect: proportion of the total variation estimated by the Local regression model (0.46) that is explained by regional and local factors; LRM: loess regression model ; ANOVA: Analysis of Variance; QRM: Quadratic Regression Model. TF: terra firme forest, WS: white sand forest; SW: swamp forest; FL: floodplain forest. Regional variables (Latitude, Longitude, Age of Bedrock and actual rainfall seasonality) have mainly an effect (values in bold) on the RV, while local factors (forest type, frequency of disturbance) have mainly an effect on the LV. Bold values signify, the parameters we consider important at the scale at which they act

Factor	Variable	Scale	TAD	RV	LV	Final effect	Analysis
Regional diversity	latitude and longitude	R	0.46	0.99	0.08		LR
Palaeo-climatic stability	latitude	R	0.31	0.73	0.02	0.34	LR
Palaeo-climatic stability	longitude	R	0.14	0.2	0.03		LR
Actual rainfall seasonality	CV of rainfall	R	0.19	0.37	0.07		LR
Bedrock age	Categories: Cenozoic / Proterozoic	R	0.05	0.14	0	0.06	ANOVA
Forest/soil type	Categories: TF, WS, SW, FL	Link R-L	0.13	0.04	0.28	0.15	ANOVA
Actual ecosystem dynamics	% individuals with wood density < 0.6	L	n/a	n/a	0.17	0.09	QRM
Total						0.64	

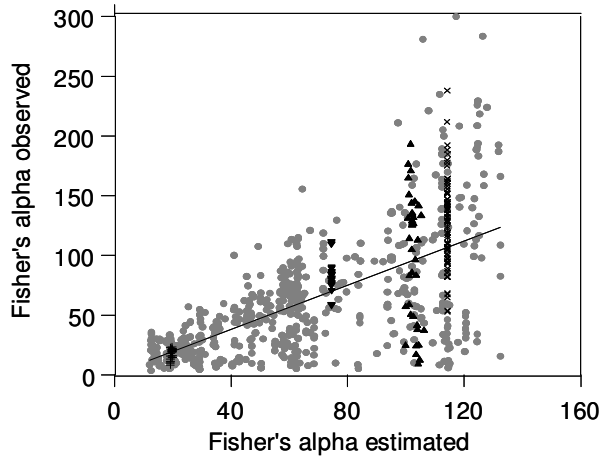


Figure 2.2: Relationship between observed tree alpha-diversity and estimated tree alpha-diversity for 752 1-ha plots in Amazonia, as modeled with a loess spatial regression ($R^2 = 0.38$). Plots located at the same geographical location show the full range of diversity for the value estimated in their 1 degree grid cell (● All plots; × Reserva Florestal Adolpho Ducke (central Amazonia); + Mabura Hill; ▼ Piste St. Elie (Guiana shield); ▲ Yasuní and surroundings (western Amazonia)).

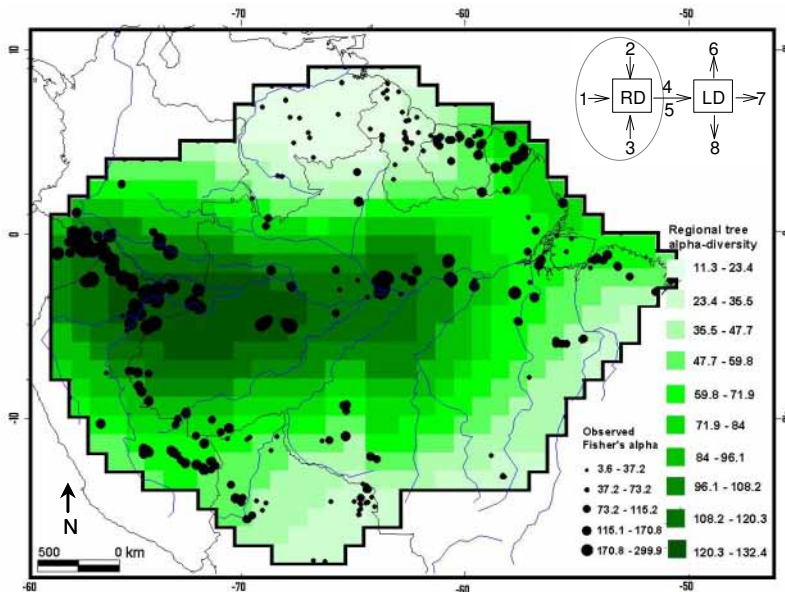


Figure 2.3: Regional variation of tree alpha-diversity (Fisher's alpha) based on a loess spatial regression. Tree alpha-diversity of 752 1-ha inventory plots modeled as a function of latitude and longitude and mapped on a one-degree grid cell scale for Amazonia. Inset on the upper right side represents Fig 2.1.

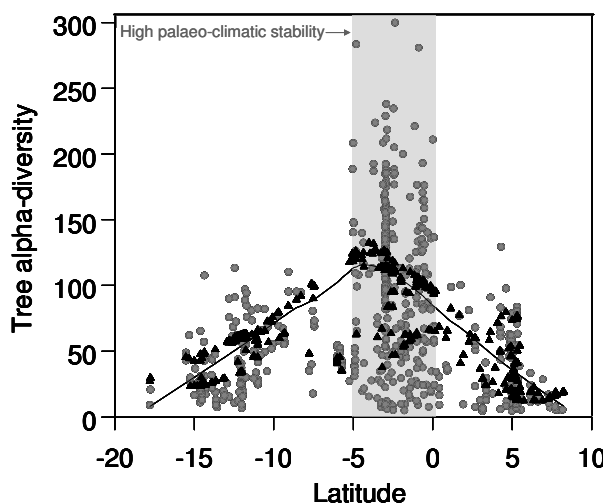


Figure 2.4: Relationship between tree alpha-diversity (● All data: observed value of Fisher's alpha for 752 tree inventory plots (ATDN 2008); ▲ RM: regional model (estimated values of Fisher's alpha as a function of latitude and longitude of each plot as obtained from the Loess regression model) and latitude used as a proxy for palaeo-climatic stability ($R^2 = 0.73$).

Local tree alpha-diversity and its interaction with regional tree alpha-diversity

The four forest types differed significantly in their LTD ($F_{[3,748]} = 89.91$; $p < 0.001$). We ascribe 28% of the variation in LTD, to environmental filtering (process 4 in Fig. 2.1). Local ecosystem dynamics, here analyzed as percentage of pioneer species in the RAINFOR plots (% of individuals with wood density $< 0.6 \text{ g cm}^{-3}$), showed a significant quadratic relationship with LTD ($R^2 = 0.17$). In the plots at 'Reserva Florestal Adolpho Ducke' (Volkmer and Magnusson, unpublished data), TAD had a similar relationship ($R^2 = 0.20$) with the percentage of pioneer trees (Fig. 2.5).

Table 2.2: Average and standard deviation of Fisher's alpha for 1-ha plots (ATDN 2008) for 4 main forest types on soils originating the Cratonic (Proterozoic and Palaeozoic) origin and Andean Cenozoic origin; the number of plots is given in brackets

Soil origin/Forest type	White-sand	Swamp	Floodplain	Terra-firme	Total
Protero/Palaeozoic	16.5±16.2 (34)	34.9±33.9 (14)	20.6±16.0 (41)	68.2±48.6 (402)	59.7±48.4 (491)
Cenozoic	62.0±49.0 (3)	33.0±20.4 (13)	51.9±32.0 (82)	106.5±58.6 (163)	85.2±57.2 (261)
Total	20.2±23.1 (37)	34.0±27.7 (27)	41.5±31.4 (123)	79.2±54.5 (565)	68.5±53.0 (752)

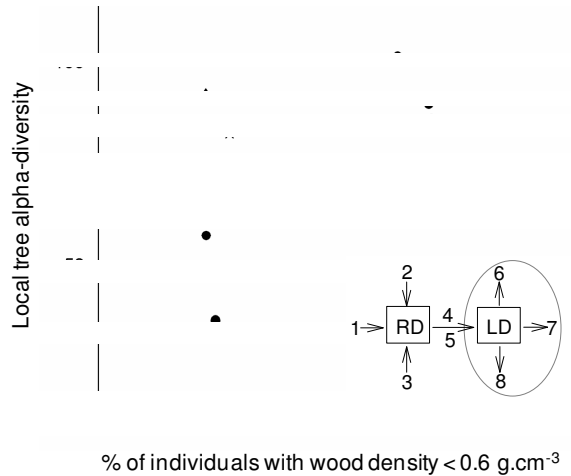


Figure 2.5: Relationship between variation in local tree alpha-diversity (residuals of Loess regression) and percentage of individuals with wood density lower than 0.6 g cm^{-3} (pioneer species) ($R^2 = 0.17$; $p < 0.01$), (● western Amazonia, × central Amazonia, and ▲ eastern Amazonia). Inset on the lower bottom side represents Fig 2.1.

DISCUSSION

Overview

Our analysis partitioned the variation of TAD in Amazonia into a regional and a local component. The proxies for palaeo-climatic stability (latitude and longitude) and bedrock age correlated significantly with the variation in RTD, but not in LTD. In contrast, LTD varied among forest types (i.e., ecological filters) and with local disturbance (Table 2.1). Our initial hypothesis that long-term and large-scale mechanisms mainly influence the RTD and short-term small-scale processes influence the LTD is therefore supported by these results. Regional drivers of TAD act mainly on the RTD, while local drivers act mainly on the LTD. It is important to point out that variables shaping RTD may also act at the local scale, whereas variables defined here as local, have typically only a minor influence on RTD (Ricklefs and Schluter, 1993). The classification of variables as either regional or local is hence a simplification, which however allows identification of the main drivers of tree alpha-diversity in Amazonia. In this section, we discuss how each of the palaeo-ecological and actual-ecological factors contributes to processes that shape tree alpha-diversity at each scale.

Regional tree alpha-diversity and regional processes

Forty-six percent of the total variation in TAD is explained by latitude and longitude. Latitude and longitude accounted for 73% and 20% for the variation of this model, respectively (Fig. 2.3). Actual rainfall seasonality explained just 19% of the total variation in

TAD. Because palaeo-climatic stability is probably closely related to latitude and longitude (see Introduction) and current climate is only a poor predictor for evolutionary drivers of regional diversity, we argue that variation in palaeo-climatic stability is the most likely cause for the variation in RTD. The correlation of TAD with latitude then reflects changes in forest area caused by orbitally forced climate change, while the correlation with longitude reflects persistent orographic rainfall in the western Amazonia due to the Andes. The use of latitude and longitude as a proxy for palaeo-climatic stability is obviously an oversimplification. Palaeo-vegetation simulation models, palynological records (Mayle et al., 2004), and the observation of southward shift of the ITCZ during glacial periods (Martin et al., 1997) suggest that central and western Amazonia experienced more stable climatic conditions than the northern and southern margins of the basin, providing a compelling argument to make use of such simple proxy.

The hypothesized stable palaeo-climate in central and western Amazonia favored persistence of tropical forest, whereas the more unstable palaeo-climate in south and north-eastern Amazonia forced shifts from open to dense forest (Mayle et al., 2004) and back. Such changes are still taking place as documented by recent forest increase on the southern edge of Amazonia in Bolivia (Mayle et al., 2000).

Climate change is thought to affect diversity because it may increase extinction rates (Araujo et al., 2008). In a period of climate change, species with poor dispersal ability and/or small ranges have lower chances to migrate to regions with suitable climate and are therefore more susceptible to extinction. As a result of this process, regions with historically instable climate have fewer species with small ranges (Dynesius and Jansson, 2000, Araujo et al., 2008). This phenomenon has been observed for reptiles, amphibians (Araujo et al., 2008), and trees in Europe (Svenning and Skov, 2007). Ter Steege et al. (2010) have shown a similar pattern for tree genera in Amazonia. The south-eastern Amazonia, with less stable palaeo-climate, has only half of the genera (257 genera in a sample of 52,182 trees) than western Amazonia (456 genera in 46,227 trees). The difference was mainly found in the rare genera. If their conclusion is correct, instable climate may have cost south-eastern Amazonia some 45% of its genera, either because they went extinct as they could not keep up with the forest decline, or failed to re-migrate either because low dispersal ability or species simply did not have enough time to spread their ranges (cf. Svenning and Skov, 2004, Svenning and Skov, 2008).

Fourteen percent of the variation in RTD is explained by bedrock age. Forests on young geological formations (Cenozoic, i.e., 66 Ma or younger) have higher tree diversity than forests on old geological formations (Proterozoic, i.e., 2,500 to 542 Ma). Soils originating from the Andes sedimentary bedrocks are considerably richer in nutrients than those originating from the Brazilian and Guiana crystalline shield bedrock (Sombroek, 2000). Ecosystems on rich soils are more dynamic than those on poor soils (Malhi et al., 2004, ter Steege et al., 2006). We suggest that the long-term large-scale ecosystem dynamics of these two contrasting landscapes (Andes foothill and Brazilian and the Guiana crystalline shields)

may have played a role in the evolutionary processes that shaped current diversity. Speciation is driven by a combination of processes such as evolutionary speed, reproductive isolation, and biotic interactions (Mittelbach et al., 2007). We argue here that the landscape evolution Amazonia had a remarkable impact on the evolutionary speed of tree species. Dynamic ecosystems experience high wood productivity (Malhi et al., 2004), forest turnover (Phillips et al., 2004), and abundance of pioneer species (ter Steege and Hammond, 2001, ter Steege et al., 2006). Tree species adapted to dynamic ecosystems have low wood density, small seed mass (ter Steege et al., 2006), short life span and, consequently, short generation time. Short generation time leads to faster evolution, thus higher speciation rates (Marzluff and Dial, 1991, Verdú, 2002, Allen et al., 2006). Based on this reasoning we suggest that the high diversity of forests on young western Amazonian geological formations could be the result of high speciation rates (Richardson et al., 2001, Erkens, 2007, Svenning et al., 2008). Species level phylogenies of families or genera occurring throughout Amazonia can be developed to test this hypothesis.

Local tree alpha-diversity and local processes

The reason why habitats differ in diversity and composition of tree species is partially explained by the fact that species are not drawn randomly from the regional species pool into the local species pool (Zobel, 1997). Environmental filters (Keddy, 1992, Zobel, 1997) and dispersal limitation (Hubbell, 2001, Zobel, 1997) determine *which* and *how many* species can occupy a local habitat. In our dataset we cannot test the effect of dispersal limitation which links the RTD and the LTD, as reliable broad-scale taxonomical information is not available for Amazonia (Hopkins, 2007) and there is a high number of morpho-species in our plots. The effect of environmental filtering, however, was quantified by analyzing local tree diversity in the four dominant forest types of Amazonia – terra-firme, white-sand, swamp and floodplain forests. The difference in local tree alpha-diversity is traditionally associated with differences in environmental conditions (Gentry, 1988, Tuomisto et al., 1998, Clark, 2004). There is little empirical evidence of a recurrent direct causal relationship between resource availability and local tree diversity, however (Pitman et al., 1999, Hubbell, 2001, Valencia et al., 2004). For white-sand forest, which occur on extremely poor soils, low frequency of disturbance events can explain part of the observed low tree alpha-diversity (see Molino and Sabatier, 2001, ter Steege and Hammond, 2001, Sheil and Burslem, 2003). Low frequency of disturbance, however, cannot explain the relatively low tree diversity in floodplains and swamps. We previously suggested (ter Steege et al., 2000) that alternative factor, shared by white-sand, swamp, and floodplain forests, namely their smaller area compared to terra-firme, could be responsible for their lower tree diversity. Hence, the cause for low diversity in these forest types could be the small and fragmented meta-populations of their constituent species, consistent with area (Terborgh, 1973, Rosenzweig, 1995, Fine and Ree, 2006) and neutral theory (Hubbell, 2001).

The variation of tree alpha-diversity at the local scale is enormous. It is surprising that different plots at one locality ('Reserva Florestal Adolpho Ducke' – central Amazonia) span almost the full range of alpha-diversity found in Amazonia (Fig. 2.2). A small percentage

(17% for the RAINFOR and 20% for 'Reserva Florestal Adolpho Ducke' plots) of the variation in local tree alpha-diversity could be explained by disturbance, here analyzed as percentage of individuals of pioneer species. This result is consistent with the Intermediate Disturbance Hypothesis (Connell, 1978). It is important to point out, however, that approximately 80% of the variation of LTD remains unexplained. Although perhaps disappointing, this is entirely consistent with the neutral theory of biodiversity and biogeography (Hubbell, 2001) and many previous findings (see e.g. Pitman et al., 1999, Valencia et al., 2004). As shown in Fig. 2.1, local tree alpha-diversity can be influenced by stochastic local extinction, predatory removal, and competitive exclusion. The effect of density-dependent mortality on local tree diversity could not be addressed by our dataset, but is clearly a candidate for promoting diversity (Connell, 1972). It may be both responsible for the higher local diversity in the wet western Amazonia (Givnish, 1999) and may also contribute to differences in tree composition between forest types (Fine et al., 2004).

Processes driving species diversity and their implication for conservation

Determining the relative contribution of long-term and large-scale as well as short-term and small-scale processes to the distribution of tree species diversity has important practical implications for biodiversity conservation. Modeling the impact of climate change on tree species diversity based on the relationship between tree species diversity and current climate can only be effective, if the distribution of tree species diversity is in equilibrium with current climate. However, as we suggest here, palaeo-climatic stability and palaeo-ecosystem dynamics are the main drivers regulating regional patterns of tree species diversity in Amazonia. Our results therefore suggest that only an approach which includes both evolutionary and current aspects of climate change will provide reliable predictions of the impacts of climate change on tree species diversity distribution in Amazonia (see Araujo et al., 2008).

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