Disentangling regional and local tree diversity in the Amazon

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We analyzed the most extensive data set of tree inventory plots spread over the complete Amazon basin and Guiana shield. We aimed to separate the regional and local tree alpha-diversity to investigate the drivers of diversity at the relevant scale. Our results are consistent with the partitioning of total tree alpha-diversity into regional and local components, which are controlled by evolutionary- and ecological processes, respectively. Regional diversity is correlated with palaeo-climatic stability (31%), and long-term large-scale ecosystem dynamics (14%), as represented by the age of the geological formation. Both mechanisms contribute to high diversity in the central to western Amazon. Actual rainfall seasonality is correlated with regional tree diversity to a certain extent (19%), but we argue that this is of little consequence for the evolutionary drivers of the regional species pool. Frequency of disturbance is the main process driving local diversity, although its explanatory power is relatively small (17%).

Large-scale patterns of biodiversity are often explained by current climate. A well know 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 the Amazon (ter Steege et al. 2006) has also mostly been explained in terms of annual rainfall (Clinebell et al. 1995), rainfall 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 the Amazon rain forest – viz the last ca 66 million yr (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 Amazon's history (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 patterns of diversity have to be interpreted in a proper historical perspective. Local diversity (here measured on 1-ha plots for large rainforest trees (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 and long-term processes, and a local species pool, which is regulated by small-scale and 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. 1). We therefore propose that an analysis of the Amazon's tree diversity should take evolutionary and ecological processes into account at the scale at which they are relevant.

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-know "Milanko-vitch cycles" (Gates 1993). Global temperature and rainfall regime has a major cycle related to the "eccentricity cycle" (ibid) with a periodicity of ca 100 000 yr. During warm and wet interglacial periods, tropical rain forest 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 23 000 yr causes shift changes southwards and northwards of the location of the Intertropical Convergence Zone (ITCZ) (Martin et al. 1993, 1997, Haug et al. 2001). As a consequence, the Amazon region experienced a more stable climate in its centre than at its edges. As the ITCZ on the South American continent shifts slightly southward (Martin
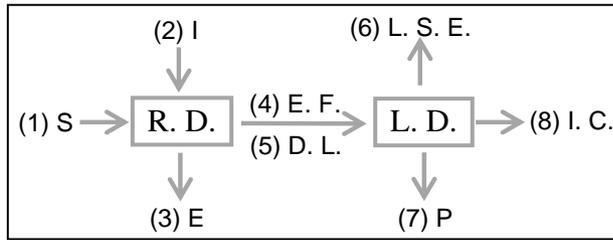
Figure 1. Diversity is influenced by regional and local processes (Ricklefs and Schluter 1993, Hubbell 2001, ter Steege and Zagt 2002). Regional diversity controlled by processes such as speciation (1), immigration (2), and extinction (3), whereas the local diversity is controlled by stochastic local extinction (6), interspecific competition (8), and predation (7). Regional and local diversity are linked via environmental filters (4) and dispersion limitation (5).

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 the western Amazon 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 (Araújo 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, Araújo et al. 2008).

Additionally, there is a sharp contrast in landscape evolution in the eastern and western Amazon (Sombroek 2000). In the western Amazon, 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 Guianese shield, respectively, soils developed on crystalline bedrock from the Proterozoic (∼2500 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 (Phillips et al. 1994, ter Steege and Hammond 2001, 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 the Amazon region (Oliveira and Nelson 2001, Pitman et al. 2002). Tree species diversity of 1-ha plots located very close together and thus, under similar climatic conditions, can exhibit huge differences in tree species diversity (ter Steege et al. 2003, Valencia et al. 2004). 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, 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. 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), commonly know as the "Janzen-Connell model". Frequency-dependent mortality reduces the potential of species to become dominant in ecosystems (for the Amazon, 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 paper, we apply a hierarchical approach to identify regional and local patterns and potential drivers of variation in tree species diversity in the Amazon. 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) database, which contains 781 tree inventory plots and spans the entire area of the Amazon basin and the Guiana shield (here collectively called "the Amazon"). 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 database (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 RAIN-FOR database (ver. FT29.06.06; Peacock et al. 2007). In total, we compiled data from 781 tree inventory plots spread across the Amazon 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 to 1 ha to our analysis. Plots >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 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 database) in the period of 1950–2000 with 30 arc-seconds resolution (∼1 km) from WORLD-CLIM (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 Amazon) 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 $< 0.6 \, \mathrm{g \, cm^{-3}}$. 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 data base. These percentages are considered to be proxies for disturbance in the plots (ter Steege and Hammond 2001).

Data analyses

Tree alpha-diversity was calculated with Fisher's alpha, which is relatively insensitive to sample size (Fisher et al. 1943, Rosenzweig 1995). To calculate tree alpha-diversity we used Fisher's alpha based on the total 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 under-estimate 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 very little (N. Pitman pers. comm.).

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, and local tree diversity (LTD) plus error (ε):

$$TAD = RTD + LTD + \varepsilon$$

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 very high local variation of TAD in locations with several plots (Fig. 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 the entire Amazon. 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 Amazon 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/Palaeozoic 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 (Introduction). The influence of current rainfall seasonality on RTD was also analysed with loess regression. The influence of bedrock age on RTD was determined with single factor ANOVA.

The next set of analyses focussed on local tree alpha-diversity and its interaction with regional tree alpha-diversity. We started by quantifying the contribution of forest 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.
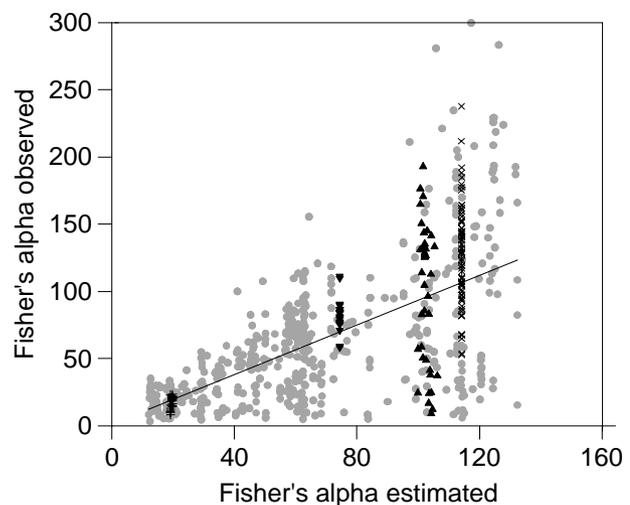

Figure 2. Relationship between observed tree alpha-diversity and estimated tree alpha-diversity for 752 1-ha plots in the Amazon, as modelled with a loess spatial regression ($r^2 = 0.38$). Plots located at the same geographical location show the full range of diversity for the value estimated in their 1 degree grid cell ($\bullet$ all plots; $\times$ Reserva Florestal Adolpho Ducke (central Amazonia); + Mabura Hill; $\blacktriangledown$ Piste St. Elie (Guiana shield); $\blacktriangle$ Yasuní and surroundings (western Amazonia)).

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 geographical Amazon regions and 72 plots are located at "Reserva Florestal Adolpho Ducke" (central Amazon). 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 $<0.6\,\mathrm{g\,cm^{-3}}$ for the 41 RAINFOR plots (our proxy for frequency of disturbance, see above). We analysed 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 72 plots, we analysed the relationship between the percentage of individuals of pioneer species and TAD with a quadratic regression model. All statistical analyses were performed in S-PLUS 2000 (Mathsoft).

Results

Regional tree diversity and regional processes

The loess regression explained 46% of the total variation in TAD (Table 1, Fig. 2), 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 was residual error (Table 1). The spatial interpolation reveals two rather simple gradients, related to 1) latitude and 2) 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 the Amazon and increases close to the western border of the study area (Fig. 3). Latitude accounted for 73% of the variation in this model and longitude 20% (Table 1, Fig. 4). Current rainfall seasonality explained 37% of the variation in RTD and 19% in variation of total TAD. Fitted values for TAD explained observed values of TAD well, but at locations with many plots variation in TAD encompassed nearly all variation present in the model (Fig. 2).

Average TAD differed among plots on the two different geological substrates (mean (Cenozoic) $= 85.2$; mean (Proterozoic) $= 59.7$) (Table 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 1), consistent with our expectation.

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

The four forest types differ significantly in their LTD ($F_{[3,748]} = 89.91$; $p < 0.001$), explaining 28% of the variation in LTD, which we ascribe to the process of environmental filtering (process 4 in Fig. 1).

Local ecosystem dynamics, here analyzed as percentage of pioneer species in the RAINFOR plots (% of individuals with wood density $<0.6\,\mathrm{g\,cm^{-3}}$), showed a significant quadratic relationship with LTD ($R^2 = 0.17$) (Fig. 5). In the plots at "Reserva Florestal Adolpho Ducke" (Volkmer and Magnusson pers. comm.), TAD had a similar relationship ($R^2 = 0.20$) with the percentage of pioneer trees.

Discussion

Our analysis partitioned the variation of TAD in the Amazon basin 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 LTD. By contrast, LTD varied among forest type (i.e. ecological filters) and with local disturbance (Table 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 the Amazon. 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.

Table 1. Contribution of regional and local drivers for variation of total, regional and local tree alpha-diversity in Amazon basin and 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	0.20	0.30		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, PZ, 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	0	**0.17**	**0.09**	QRM
Total						**0.64**	
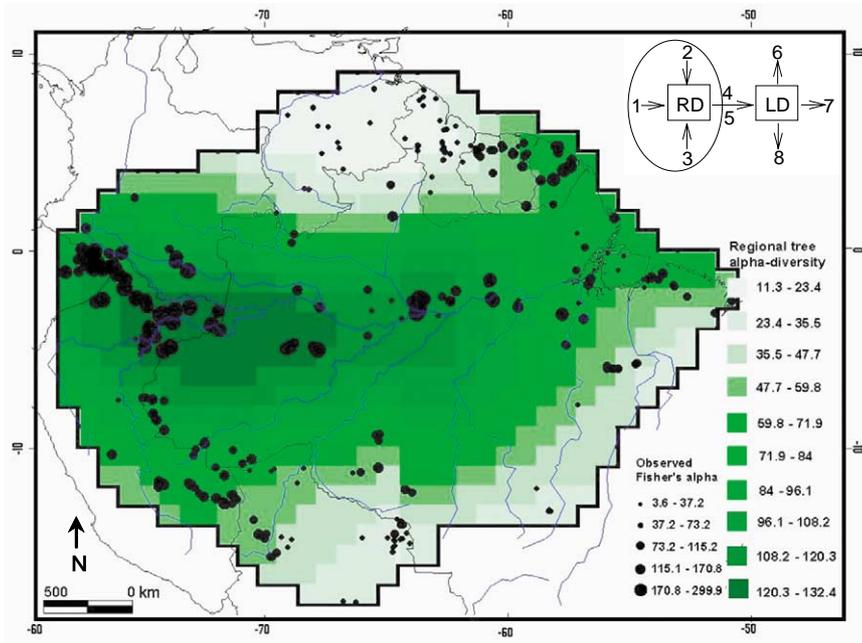
Figure 3. Regional variation of tree alpha-diversity (Fishers' alpha) based on a loess spatial regression. Tree alpha-diversity of 752 1-ha inventory plots modelled as a function of latitude and longitude and mapped on a one-degree grid cell scale to the entire Amazon region. Inset: scale and processes analysed, numbers as in Fig. 1.

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. 3). Actual rainfall seasonality explained just 19% of total variation of TAD. Because palaeo-climatic stability is probably closely related to latitude and longitude (Introduction) and current climate is not a good predictor for evolutionary drivers of regional diversity, we argue that
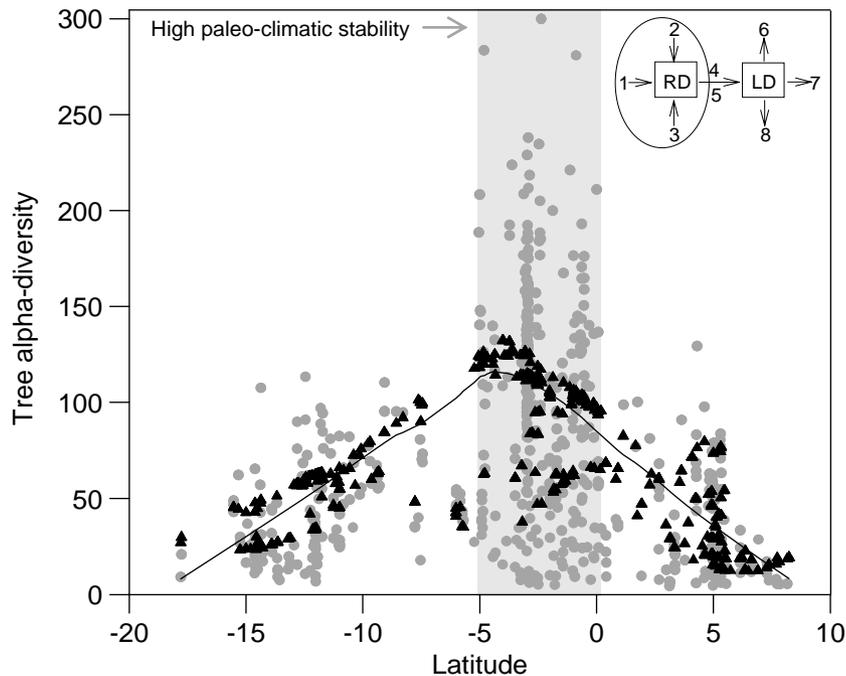

Figure 4. Relationship between tree alpha-diversity (● all data: observed value of Fisher's alpha for 752 tree inventory plots (ATDN 2008); ▲ RM: regional model (estimated values of Fisher's alpha as a function of latitude and longitude of each plot by Loess regression model)) and latitude used as a proxy for palaeo-climatic stability ($r^2 = 0.73$). Inset: scale and processes analysed numbers as in Fig. 1.
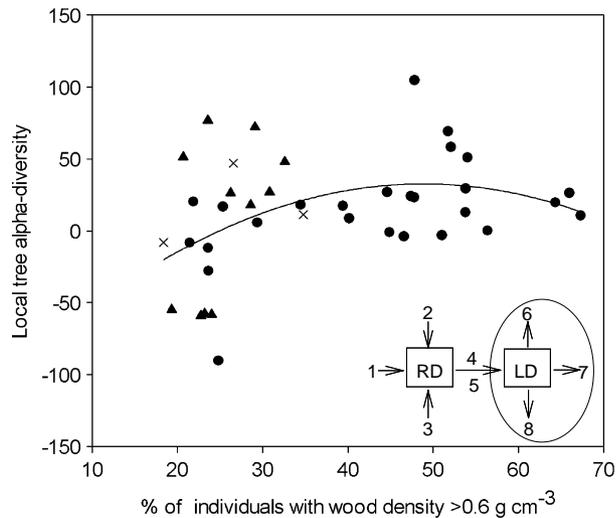
Figure 5. Relationship between variation in local tree alpha-diversity (residuals of Loess regression) and percentage of individuals with wood density lower 0.6 g cm^{-3} (pioneer species) ($r^2 = 0.17$; p < 0.01), ($\bullet$ western Amazon, $\times$ central Amazon and $\blacktriangle$ eastern Amazon plots). Inset: scale and processes analysed, numbers as in Fig. 1.

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 Amazon due to the Andes. The use of latitude and longitude as a proxy for palaeo-climatic stability is obviously an oversimplification. However, palaeo-vegetation simulation models, palinological records (Mayle et al. 2004), and the observation of southward shift of the ITCZ during glacials (Martin et al. 1997) suggest that central and western Amazon 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 hypothesised stable palaeo-climate in central and western Amazonia favoured persistence of tropical forest, whereas the more instable 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 Amazonian edge in Bolivia (Mayle et al. 2000).

Climate change is thought to affect diversity because it may increase extinction rates (Araújo 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, Araújo et al. 2008). This phenomenon has been observed for reptiles, amphibians (Araújo et al. 2008), and trees in Europe (Svenning and Skov 2007). ter Steege et al. (in press) have shown a similar pattern for tree genera in the Amazon. The south-eastern Amazon, with less stable palaeo-climate, has only half of the genera (257 genera in a sample of 52 182 trees) than the western Amazon (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 the south-eastern Amazon 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, 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. 2500 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. in press). We suggest that the long-term large-scale ecosystem dynamics of these two contrasting landscapes (Andes foothill and Brazilian and Guianese crystalline shields) may have played a role in the evolutionary processes that shaped current diversity levels. 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 of the Amazon had a remarkable impact on the evolutionary speed of tree species. Dynamic ecosystems experience high wood productivity (Malhi et al. 2004), forest turn-over (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 the Amazon can be developed to test this hypothesis.

Table 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)

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 (Zobel 1997, Hubbell 2001) 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 the Amazon (Hopkins 2007) and the 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 the Amazon – 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 (Molino and Sabatier 2001, ter Steege and Hammond 2001, Sheil and Burslem 2003). Low frequency of disturbance, however, can not 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 Amazon) span almost the full range of alpha-diversity found in the entire Amazon (Fig. 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 analysed 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 ca 80% of the variation of LTD remains unexplained. Although perhaps disappointing, this is entirely consistent with the neutral theory (Hubbell 2001) and many previous findings (Pitman et al. 1999, Valencia et al. 2004). As shown in Fig. 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 Amazon (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. Modelling 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 the Amazon. 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 the Amazon (Araújo et al. 2008).

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