A spatial model of tree α-diversity and tree density for the Amazon

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Abstract. Large-scale patterns of Amazonian biodiversity have until now been obscured by a sparse and scattered inventory record. Here we present the first comprehensive spatial model of tree α-diversity and tree density in Amazonian rainforests, based on the largest-yet compilation of forest inventories and bolstered by a spatial interpolation technique that allows us to estimate diversity and density in areas that have never been inventoried. These data were then compared to continent-wide patterns of rainfall seasonality. We find that dry season length, while only weakly correlated with average tree α-diversity, is a strong predictor of tree density and of maximum tree α-diversity. The most diverse forests for any given DSL are concentrated in a narrow latitudinal band just south of the equator, while the least diverse

forests for any given DSL are found in the Guayana Shield and Amazonian Bolivia. Denser forests are more diverse than sparser forests, even when we used a measure of diversity that corrects for sample size. We propose that rainfall seasonality regulates tree α-diversity and tree density by affecting shade tolerance and subsequently the number of different functional types of trees that can persist in an area.

Introduction

Biodiversity mapping and modelling is an increasingly useful tool for ecology and conservation, but it has not yet produced a reliable picture of diversity patterns in the world's most species-rich forest (Gentry 1988a, 1988b; Phillips et al. 1994; Gaston 2000; Myers et al. 2000; Condit et al. 2002).

The Amazon, which harbours a very significant portion of the world's diversity (Myers et al. 2000), is a perfect natural laboratory for the study of tree diversity because of its size and its bio-physical gradients. The number of plots has risen steadily over the years and is probably much greater than in any other tropical region. Most studies examining the patterns of plant diversity in the Neotropics, however, have relied heavily on plots in western Amazonia (Gentry 1988a, 1988b; Phillips et al. 1994; Clinebell et al. 1995; Terborgh and Andresen 1998; Givnish 1999; ter Steege et al. 2000). In western Amazonia species richness is found to be strongly correlated with total annual rainfall (Gentry 1988a, 1988b), often considered a proximate estimate of ecosystem productivity (Gentry 1988a, 1988b; Phillips et al. 1994; Clinebell et al. 1995). The rainfall–diversity relationship has been confirmed by other studies outside the Amazon (Hall and Swaine 1976; Huston 1980, 1994). In each of these studies fertility was negatively correlated with rainfall, which has complicated the search for single causal relationships. Ter Steege et al. (2000) showed that, when the whole of the Amazon was taken into account, rainfall was a poor estimator of tree α-diversity in 1-ha plots.

A closer inspection of the data of ter Steege et al. (2000) suggests that while rainfall and rainfall seasonality may not be good estimators of average tree α-diversity, they may be good estimators of maximum diversity. As many more factors may have an effect on tree α-diversity, these may obscure this relationship. If such factors interact rather than act in an additive manner, standard regression methods are not capable of detecting proper relationships. Recently, a more advanced method has become available for ecology (Cade et al. 1999) that has been pioneered in the field of econometrics (Koenker and Bassett 1978). With this technique, quantile regression, interacting factors may be studied even if not all such factors have been measured. Further details can be found in the Methods section.

Since our previous publication (ter Steege et al. 2000) much more plot data have become available and in this paper we have two main objectives:

1. Use a statistical model to generate an improved, most accurate spatial model to date, of tree α-diversity of the Amazon, including an error map that may assist to plan future plot establishment. The results of this model will be available on our website (see below) and regularly updated.
2. Describe the rainfall–diversity model as a model of limiting factors, whereby

rainfall seasonality is one of the main factors limiting tree α-diversity at a regional level, other factors being interactive with it.

We have no *a priori* assumptions what the most important other interacting factors might be, but by eliminating plots on 'special' soil types, such as white sands, floodplains and swamps, that generally have lower diversity than *terra firme* forest plots (ter Steege et al. 2000), we already eliminate some sources of variation. If the unknown factor(s) act at a regional level, mapping them should reveal a geographical pattern. Hence, we also map the other total of unknown limiting factors to discern this.

Methods

The total number of plots with data, presently known to us in the Amazon, which here includes the forest region of the Guayana Shield, is 425.[1] For the analyses we used forest plots on *terra firme* only, leaving out plots on white sands, floodplains and swamps, plots outside the Amazon, and plots with incomplete data. The final selection comprised 275 plots. This set mainly included 1-ha plots, but in areas of low plot density also smaller (plots that had more than 150 individuals of trees with a dbh $\geq$10 cm) or larger ones. Most (228) plots were 1 ha in size, 18 plots were between 0.25 and 1 ha, 20 plots were between 1 and 4 ha, and 9 were plotless line samples with 200–800 individuals (equivalent to ca. 0.4–1.6 ha). To standardize α-diversity we used Fishers's α (Fisher et al. 1943), which corrects well for variation in sample size (Taylor et al. 1976; Leigh 1995; Rosenzweig 1995; Condit et al. 1998).

Tree density was calculated on a hectare basis. For the plotless samples the tree density was extracted from the publications concerned, if this data was presented there. Otherwise the samples were omitted for the density estimates.

Mapping tree α-diversity

Because the plots over-sample some areas of Amazonia and under-sample others, we used a spatial model based on universal kriging (Burrough and McDonnel 1998; Kalunzy et al. 1998) to estimate diversity in 1° cells across the region. The theory and process is explained briefly below:

The regionalized variable theory assumes that the spatial variation of any variable Z at location x can be expressed as the sum of a structural component (m: a constant mean or a trend), a random but spatially correlated component (ε': the regionalized variable), and a residual error term (ε''), that is not spatially correlated (Burrough and McDonnel 1998):

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[1] This was the number when the analyses were carried out. During manuscript review a few more plots came to our knowledge. They are listed in the Appendix and will be used in the updated map on our website.

$$Z = m(x) + \varepsilon'(x) + \varepsilon''$$

We used a loess regression to detect the structural component (m). The loess regression explained 64% of the variation in Fisher's α. The residuals from the loess regression are equal to $\varepsilon'(x) + \varepsilon''$ and were analysed with variogram analysis (Burrough and McDonnel 1998; Kalunzy et al. 1998). In the residuals, a clear spatial structure was present, and this improved very much after the removal of two outlier plots. An exponential model fitted the variogram data well and showed autocorrelation up to ca. 2.2°. As a consequence, interpolation was carried out with the exponential variogram results and with inclusion of a spatial trend model. This is known as universal kriging.

The statistical model used by kriging also produces error estimates. These errors were also mapped for inspection and may serve as a useful tool for planning further exploration.

Estimates are only presented for the forest area of the region based on an interpretation of NOAA-AVHRR NDVI satellite data (http://terra.whrc.org/). This area includes 567 1° grid cells.

To examine the effect of spatial and ecological variables on diversity we used the kriging model predictions for each 1° grid cell. We took this course because several sites had many points close together, violating a main assumption of regression analysis – independence of data (this assumption is opposite to the requirement of kriging, which assumes and then estimates spatial dependence in the data). We tested the accuracy of the model's estimates by removing each single plot from the dataset, allowing the model to re-estimate the diversity of its cell with the remaining dataset, and then comparing the estimated diversity (for the grid cell) with the actual diversity of the removed plot. In this way the plot's own value has no influence on its estimated value. Thus, the complete interpolation process was carried out 275 times. We will call this the jackknifed estimation (a more correct term might be the studentized estimation – Venables and Ripley 1998).

Rainfall and tree α-diversity

To study the effect of rainfall on tree α-diversity we used dry season length (DSL), which was defined as the number of months with <100 mm of rain. DSL was extracted for every 1° grid cell in the region from a digitised map (data from Sombroek 2001; Figure 1). Sombroek (2001) did not distinguish between 0 and 1 month(s) of dry period and for calculations we classified both as zero.

Limiting factor theory assumes that factors influencing the dependent variable act heterogeneously (read: independently) over the landscape. Near the upper bound of the distribution, the factor under consideration is considered to be actively limiting the dependent variable. Variation below these maxima is caused by the interacting influence of other (often unmeasured) factors. We used quantile regression (Koenker and Bassett 1978; Cade et al. 1999) to examine whether DSL was correlated with maximum diversity and tree density (Cade et al. 1999). We used the module *regq*, written for S-plus (Cade et al. 1999). Two important assumptions of quantile
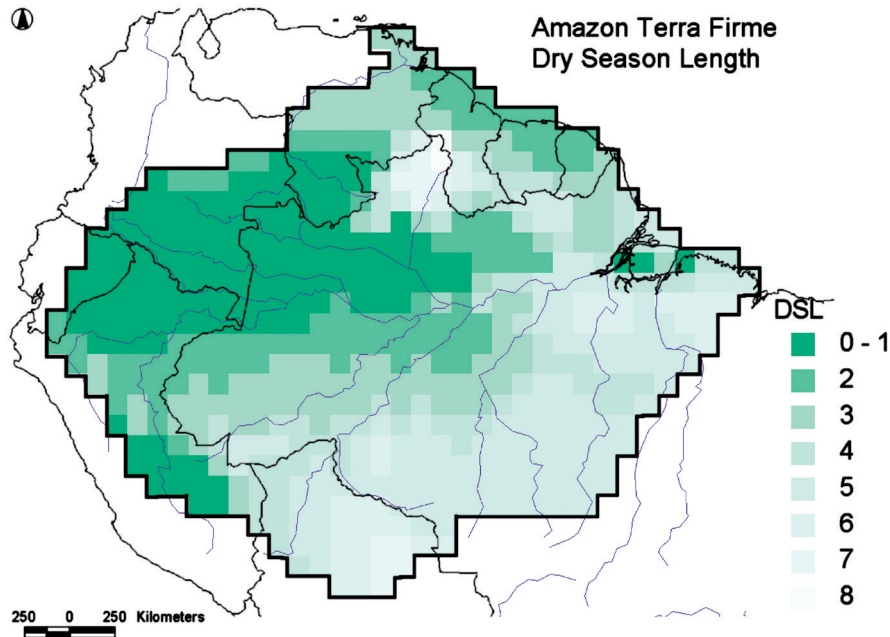
Figure 1. Map of DSL (data after Sombroek 2001), expressed as the number of months with <100 mm of rain.

regression are the existence of other interacting limiting factors and the fact that the dependent variable will attain its true maximum for the limiting factor (the measured independent variable) under investigation. While there are several factors that can be thought to influence diversity (disturbance, soil type (which was already eliminated)), we have no absolute proof of maximum tree α-diversity anywhere in the Amazon. However, it is difficult to imagine plots richer than some in western or central Amazonia where plots of ca. 600 individuals may contain ca. 300 species (e.g.: Gentry 1988a; de Oliveira and Mori 1999; Vasques-Martinez and Phillips 2000).

We used an interference interaction model (Cade et al. 1999), in linear form, where tree α-diversity (Z) is a linear (negative) function of DSL and its interaction with OIF:

$$Z = \alpha + \beta(1 - OIF)DSL + \varepsilon$$

If OIF = 0 (the upper bound of the distribution for DSL) this reduces to

$$Z_{max} = \alpha + \beta(DSL) + \varepsilon$$

This is equal to the maximum Z for a given DSL (in other words, it is the real relationship between DSL and average tree α-diversity for the grid cells). The parameters α and β were estimated by calculating the regression equation for the

90th percentile, where OIF approaches zero. To study whether OIF is either related to climatic factors or has an otherwise geographic pattern its estimated value was calculated as

$$OIF = (Z_{max} - Z)\beta DSL + \varepsilon'$$

Results

Mapping diversity and density

Both the raw and the interpolated plot data show the region's peak of average tree α-diversity as a large swath of mostly a-seasonal forest stretching along the equator from Ecuador, northern Peru, and southern Colombia into central Amazonian Brazil (Figure 2). *Terra firme* tree α-diversity is highest in the vicinity of Iquitos, Peru, and Manaus, Brazil and lowest in Bolivia and the Guayana Shield forests, with the exception of central-south French Guiana.

Average tree density for 1° grid cells in Amazonia varies from ca. 400 to 750 trees ha^{-1} and shows a distribution similar to that of tree α-diversity, but with a more pronounced peak in western Amazonia (Figure 3). Forests in western Amazonia are on average 150 stems ha^{-1} denser than those in eastern Amazonia.

The accuracy of the spatial model is high and the jackknifed estimation explains 80% of variance in the diversity of the removed plots ($n = 275$, data not shown).

The errors in the spatial model are largest where there are few plots in the 'neighbourhood' (Figure 4). These areas include the region in Pará below the Guianas, the Tapajós River basin, central Colombian Amazon, and the border region of northwestern Peru and Ecuador.

Rainfall, tree α-diversity and density

We find DSL to be negatively correlated with diversity and density. However, DSL is a much stronger predictor of estimated maximum diversity (Figure 5; $R^2 = 0.91$, $P \ll 0.001$ for the 90th quantile) than of estimated (average) diversity ($R^2 = 0.35$, $P \ll 0.001$, $n = 567$ grid cells). This same pattern is also present in the raw plot data (Figure 1, inset), the only difference being that very high local values have been smoothed out by the spatial interpolation.

The effect of the OIF is in fact of such magnitude that minimum tree α-diversity is almost equal for each DSL. The regression line for the 10th quantile is nearly horizontal, its slope still significantly different from zero, but more so very significantly different from the slope of the 90th percentile. This indeed supports the existence of interaction factors acting on tree α-diversity.

Average tree density is more strongly under control of seasonality than is tree α-diversity (Figure 6; $R^2 = 0.52$, $P \ll 0.001$). The higher and lower quantile regression lines are nearly parallel (Figure 6), suggesting that seasonality is the main effect, with other factors being mostly additive, rather than interacting.
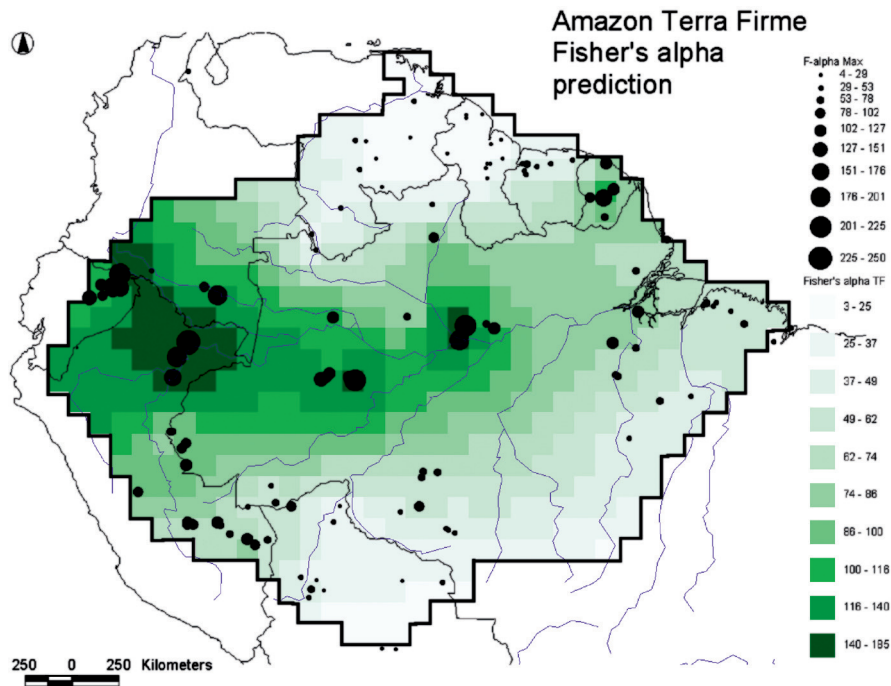
Figure 2. Map of average tree α-diversity (Fisher's α) based on 275 plots in *terra firme* forest in the Amazon and Guayana Shield rain forest area mapped on a 1° grid cell scale. The extent of tropical wet/moist and semi-deciduous forest area is based on NOAA-AVHRR NDVI satellite data (http://terra.whrc.org/). Diversity is highest in a narrow band from western Amazonia towards central Amazonia with peaks around Iquitos and Manaus. Dots indicate the maximum Fisher's α found at one location (*n* = 275). Because many plots may be in close proximity (and overlapping), much less than 275 dots are visible.

Even though Fisher's α values are standardized for density (at the plot level), we still find a relatively strong positive relationship between interpolated tree density and interpolated Fisher's α for the 567 grid cells (Figure 7; $R^2 = 0.46$, $P \ll 0.001$).

A spatial null-hypothesis is that grid cells with average Fisher's α above the 90th quantile and those below the 10th (Figure 5) are randomly distributed over the spatial gradient of DSL (cf. Figure 1). When we map these grid cells, those with the highest diversity for any DSL regime (OIF = 0) are found within a single band in central Amazonia, just south of the equator. The least diverse grid cells, where seasonality is only of limited influence on tree α-diversity (OIF = maximum) are concentrated in two geographically distinct areas: the northwestern Guayana Shield and Bolivia. In Figure 8 this is shown is a slightly different manner as the strength of the OIF between 0 and 100%. The band where the OIF are of little influence is clearly visible below the Amazon River.

The OIF have a strong unimodal relationship with latitude, peaking at 5° S (Figure 9). This unimodal pattern is obvious with and without the data related to the
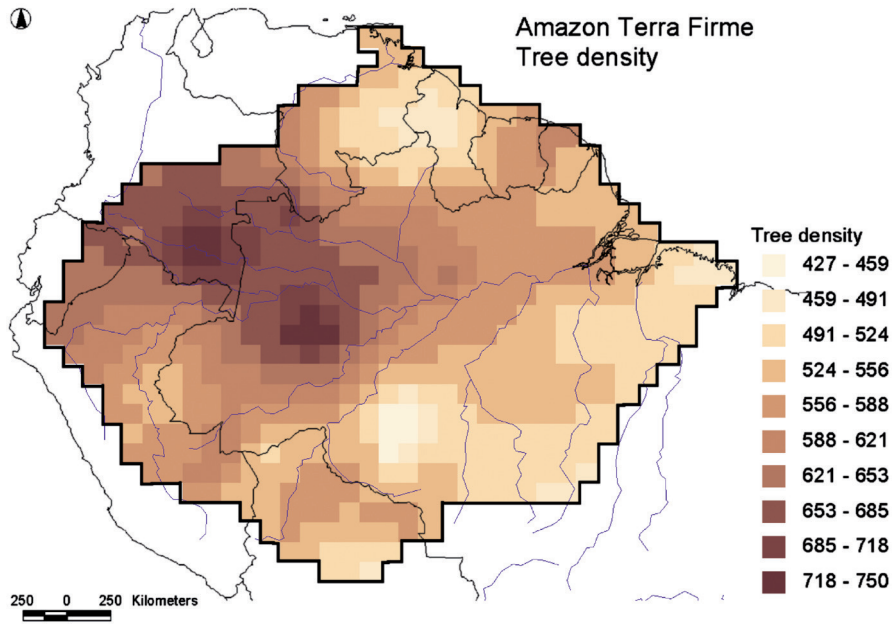
Figure 3. Map of average tree density (trees $\geq$10 cm dbh ha^{-1}) across the Amazon. Forests in western Amazonia have on average 150 more stems per ha than those in eastern Amazonia.
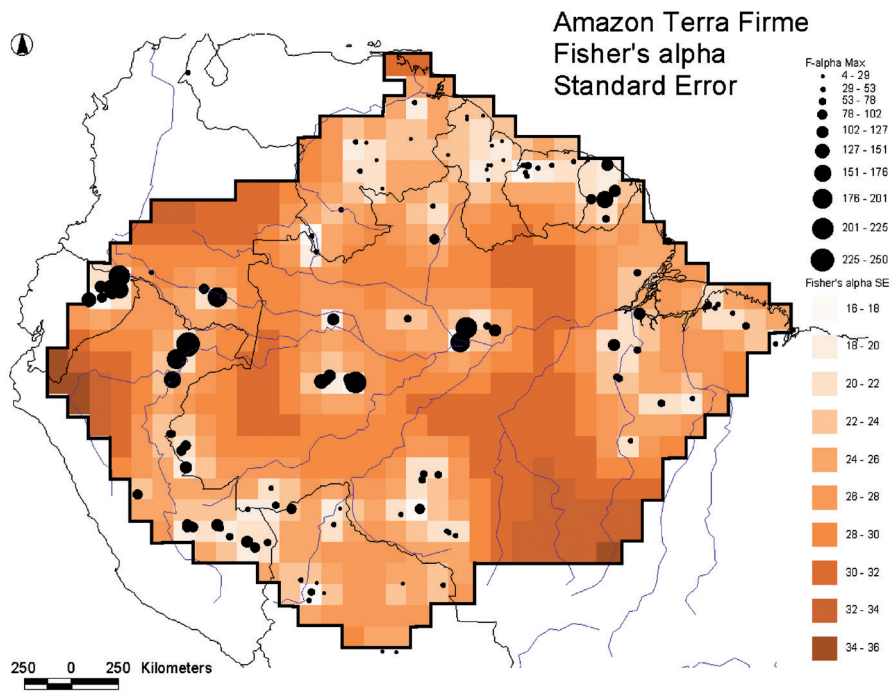

Figure 4. Map of standard errors in tree α-diversity (Fisher's α) as produced by the spatial model obtained by universal kriging (Figure 2).
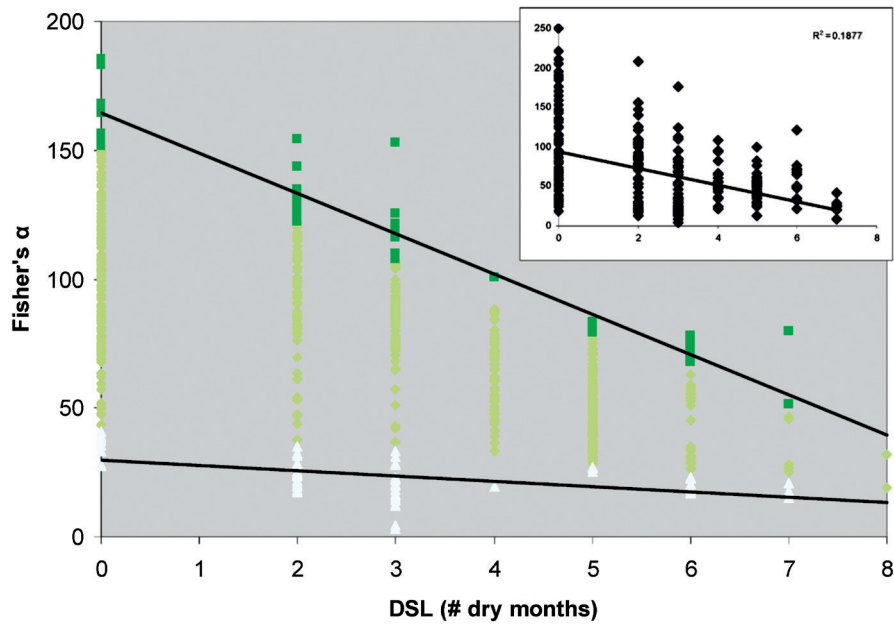
Figure 5. Modelled Fisher's α as a function of DSL. An increase in dry months strongly limits the average maximum tree α-diversity found at a site. Dark green: grid cells with Fisher's α over the 90th quantile (rainfall seasonality is the main limiting factor to tree α-diversity); light green: grid cells with Fisher's α below the 10th quantile (rainfall seasonality has no marked effect on tree α-diversity in these grid cells). The slopes of the two regression lines differ significantly. The inset shows the same relationship for actual plot data with least squares regression to show a weak overall relation between DSL and tree α-diversity.

10th quantile (Figure 9) and also if data is plotted for each DSL value separately (data not shown). In other words, even if rainfall has been corrected for (correlation between OIF and DSL is non-existent – $R^2 = 0.003$), there is still a very strong regional spatial pattern in tree α-diversity, peaking at 5° S.

Discussion

Mapping tree α-diversity and tree density in the Amazon

As the accuracy of the spatial model, tested with the jackknifed estimation was high, this suggests that the tree α-diversity of unmeasured areas can be estimated with a fairly high level of accuracy. The same pattern as shown in Figure 2 was also apparent in an earlier diversity map (based on inverse distance weighting) drawn with data from >100 fewer plots (ter Steege et al. 2000), also suggesting that the pattern may be robust despite the immense areas still unexplored by botanists and ecologists in Amazonia. New data not yet included in the map (Henkel (in press); D. Sabatier et al., unpublished data; J. Schulz and J. Lindeman, unpublished data; A. Duque, unpublished data) also correspond well to the modelled pattern.
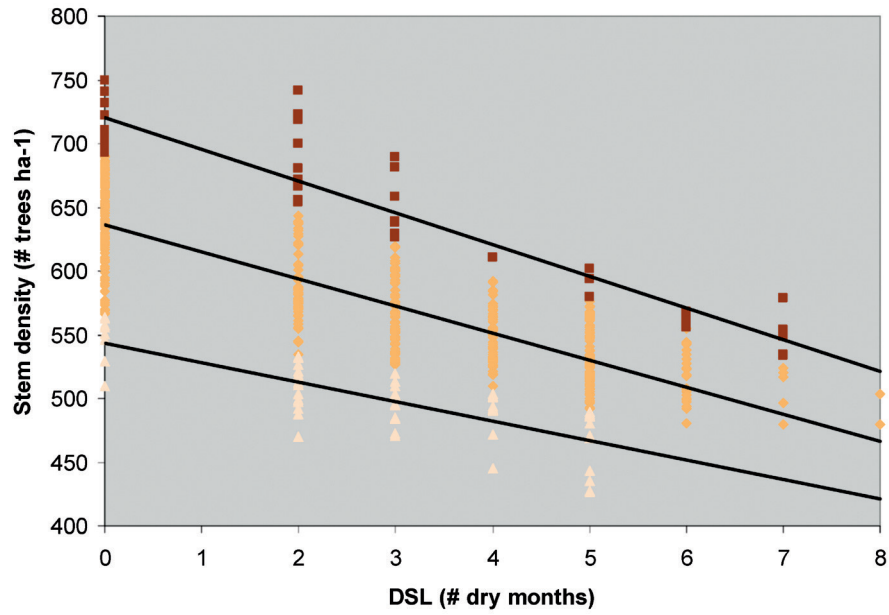
Figure 6. Average tree density (trees ha^{-1}) of Amazonian 1° grid cells as a function of DSL. Dark brown: grid cells with density higher than the 90th quantile; light brown: grid cells with density below the 10th quantile. Although the slopes of the 90th and 10th quantile differ significantly, they are practically similar in absolute value, suggesting that seasonality is a main factor influencing tree density in the Amazon.
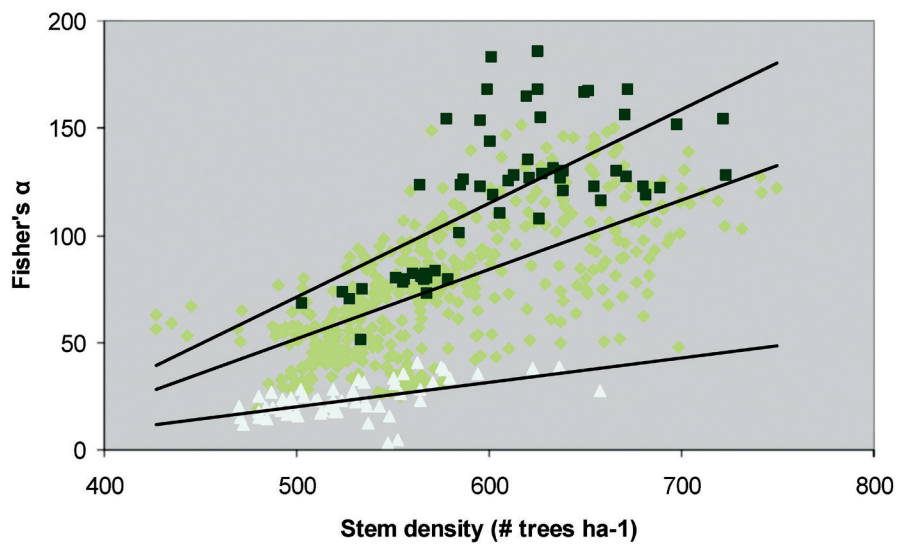
Figure 7. Fisher's α is still influenced by average tree density in 1° grid cells, suggesting that density has a regional effect of diversity. This effect is present in the high, medium and low quantile data (see Figure 4).
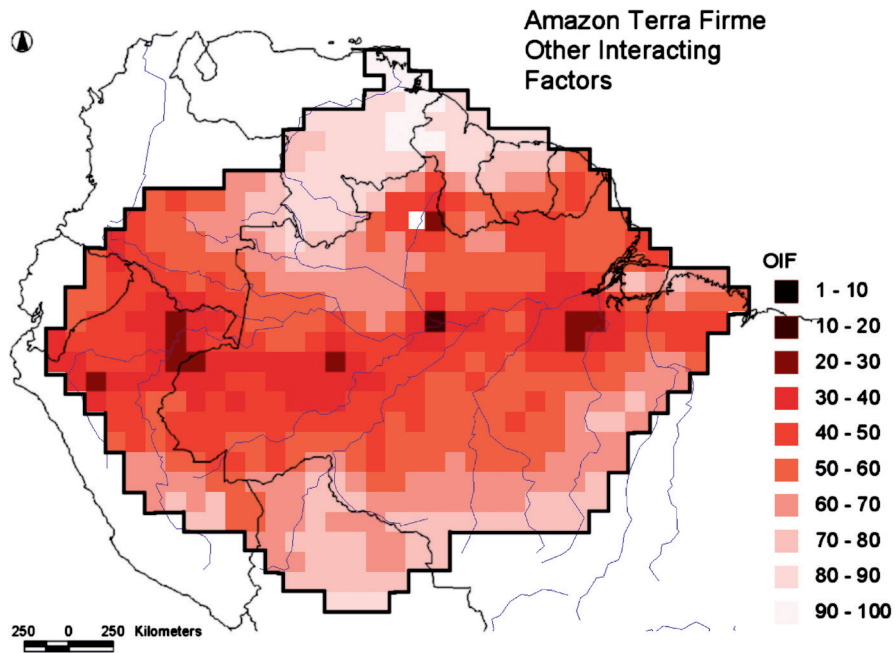
Figure 8. Spatial distribution of the OIF. OIF is displayed as a percentage of its maximum: 100 indicates interacting factors at maximum and rainfall not important in determining tree α-diversity; 0 indicates that rainfall is the major limiting factor for tree α-diversity.
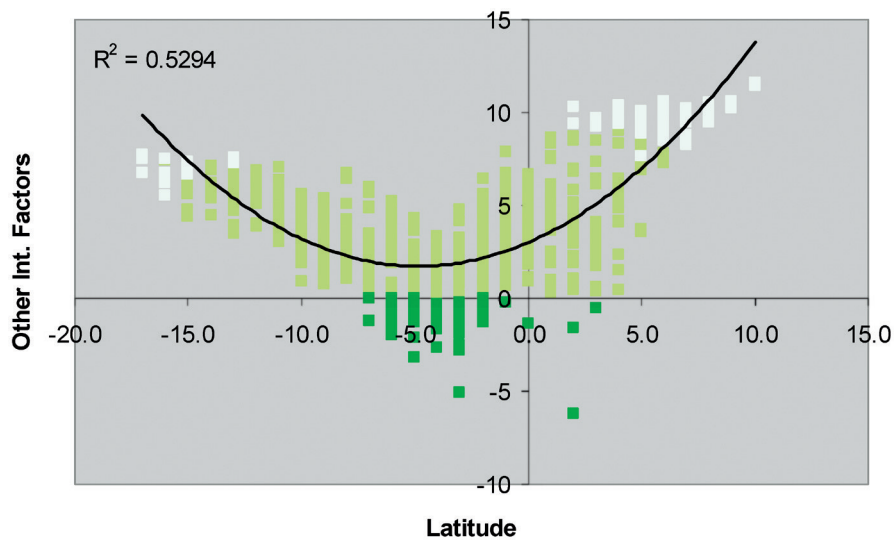
Figure 9. Latitude vs. OIF. OIF are least limiting (most positive) around 5° S, the central band of the Amazon forest region.

The pattern is in stark contrast, however, with previous maps of diversity in the Amazon (Prance 1982; Conservation International 1990) and suggests that the main diversity pattern in the Amazon may be much more simple in its spatial configuration, with consequences for inferred forest history (see also Bush 1994).

Errors are useful for planning

Although the general prediction of tree α-diversity of excluded plots by the model was quite accurate, errors are not equally distributed over the map. Errors in the spatial model are largest where there are few plots in the 'neighbourhood' (Figure 4). As mentioned above, these areas include the region in Pará below the Guianas, the Tapajós River basin, central Colombian Amazon, and the border region of northwestern Peru and Ecuador. Mapping of diversity in the Amazon would benefit most from new plots in these areas. In the southern part of Colombia (Leticia) and adjacent Brazil, errors are slightly smaller and, in addition to that, new plots have already been established there (A. Duque, personal communication).

The main pattern: drought is limiting diversity but what is cause and what is correlation?

DSL was a much stronger predictor of estimated maximum diversity than of estimated (average) diversity on the modelled and raw data (Figure 5), as predicted by limiting factor theory. Based on the results of the quantile regression we suggest that DSL has a strong (linear) effect on diversity, an effect that is masked by OIF in the full dataset. The effect of the OIF is in fact of such magnitude that minimum tree α-diversity is almost equal for each DSL.

While our results are in general agreement with previous studies (Hall and Swaine 1976; Huston 1980; Phillips et al. 1994; Clinebell et al. 1995), the strong relationship between maximum tree α-diversity and DSL and potential interacting limiting factors demonstrates why researchers see such contrasting results when they compare rainfall regime and tree diversity – they look at mean diversity, not maximum potential diversity. Secondly, our results support hypotheses that consider the effect of the length of the growing season and number of potential co-existing functional types, which can be considered a proxy measure for diversity. Recently, two such mechanistic models have shown that, at a global level, the length of the growing season may indeed determine the number of functional types, and hence species, that can exist (Kikuzawa 1996; Kleidon and Mooney 2000).

We suggest that, in the Amazon, density and diversity may be driven by the same ecological factor (see also Pitman 2000): DSL. High constant moisture is thought to increase shade tolerance, higher densities, and subsequently a higher number of functional guilds in the understorey (Huston 1994). Indeed, in western Amazonia the higher density (of individuals ≥ 10 cm dbh) is a result of higher density of smaller understorey trees (Pitman 2000) and this effect may even be stronger for yet smaller size classes (Givnish 1999 – who did *not* find the effect in the size classes ≥ 10 cm dbh in the 'Gentry dataset', however! If our thoughts are correct, these

'extra' individuals should, at least for a significant part, consist of other species and of other functional guilds, increasing diversity more than if they would consist of seedlings and saplings of the overstorey trees alone. This would also explain that even when we correct for density by using Fisher's α there is still an effect of average tree density on tree α-diversity (Figure 7).

We do not have complete data for all plots (individual trees and their diameters) but propose a simple test for this hypothesis. If indeed an increased diversity in western Amazonia is caused by the higher diversity of small individuals, calculating Fisher's α separately for individuals <20 cm and for trees ≥20 cm should reveal a difference when carried out for eastern, central and western Amazonia.

One other causal factor that is in accordance with the results, are insect and fungal pressure, which are both thought to increase strongly with (more predictable, constant) moisture and mediate tree diversity through species-specific density-dependent mortality (Givnish 1999; E.G. Leigh, personal communication; but see Hille Ris-Lambers et al. 2000; ter Steege and Zagt 2002). This prediction should also lead to testable hypotheses in dry and wet areas with maximum diversity.

Other spatial causes

The OIF have a strong unimodal relationship with latitude (Figures 8 and 9), peaking at 5° S, and this unimodel relationship is not related to rainfall. We suggest that at present this maximum diversity (for any given seasonality) in greater Amazonia is best explained by a stochastic null-model (Colwell and Lees 2000) which predicts that even in the absence of an environmental gradient, the highest number of species will be found in the central portion of a geographical domain, which for the Amazon forest coincides largely with a band around 5° S. This higher 'regional species pool' results in higher potential tree α-diversity in plots as well, which is our measure used.

In addition to that, we hypothesise that the consistently low diversity in the Guianas may also be the result of the small size of this area, compared to the major Amazon forest block (see Terborgh 1973; Rosenzweig 1995; ter Steege et al. 2000). The Bolivian area includes many wet savannahs and may have become forested only very recently in geological time (Mayle et al. 2000), which may also contribute to its low diversity and high abundance of well-dispersed families with several fast growing species, such as Moraceae (ter Steege et al. 2000).

A caution for conservation planning

While the data presented increase our insight into potential factors influencing tree α-diversity, we caution the use of diversity maps as a single source of data for conservation planning. Although the Guayana Shield and the Bolivian area have much lower diversity than central and western Amazonian areas, their species are not just a sub-sample of the latter area. In addition to that, within the areas of equal diversity, gradients in species composition (β-diversity) are continuously present (western Amazonia and Panama: see Condit et al. 2002; Guayana Shield: D.

Sabatier, unpublished data; H. ter Steege, unpublished data). Such information is also crucial if a representative portion of the area's diversity is to be protected.

A bit about the future

The map and some associated data will be published on the website of our Amazonian Plot Network, accessible through: http://www.bio.uu.nl/~herba/research.html.

It is our intention to update this web-based map regularly as newly published plot data become available. Some of us and colleagues have already started with the establishment of new plots in areas where coverage is low (Pitman et al., Peru, Ecuador) or are planning to do so (C. Peres, Tapajós and other Brazilian parts; B. Hoffman, South Suriname). We would also welcome and acknowledge plot data sent to us by others.

As there are much fewer plots on floodplains (64) and even fewer in swamps (20) and on white sand podzols (14), maps for these plots are not well feasible (for some information see ter Steege et al. 2000). On our website a preliminary map of floodplain diversity will be present. We especially encourage the establishment of plots in these less diverse ecosystems.

Further research plans include the role of neutral models and ecology in patterns of β-diversity, especially in western Amazonia and the Guayana Shield, two areas for which the comparative taxonomy for a great number of plots can be resolved with the least difficulties. To further resolve the role of ecology in shaping tree composition of forest communities (and plots therein) it is also necessary to establish plots in the various forest systems found.

For more information please visit: http://www.bio.uu.nl/~herba/research.html.

Appendix.   References to plot data in the Amazon.

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