

# The odd man out? Might climate explain the lower tree $\alpha$ -diversity of African rain forests relative to Amazonian rain forests?

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## Summary

1. Comparative analyses of diversity variation among and between regions allow testing of alternative explanatory models and ideas. Here, we explore the relationships between the tree  $\alpha$ -diversity of small rain forest plots in Africa and in Amazonia and climatic

variables, to test the explanatory power of climate and the consistency of relationships between the two continents.

2. Our analysis included 1003 African plots and 512 Amazonian plots. All are located in old-growth primary non-flooded forest under 900 m altitude. Tree  $\alpha$ -diversity is estimated using Fisher's alpha calculated for trees with diameter at breast height  $\geq 10$  cm. Mean diversity values are lower in Africa by a factor of two.

3. Climate-diversity analyses are based on data aggregated for grid cells of  $2.5 \times 2.5$  km. The highest Fisher's alpha values are found in Amazonian forests with no climatic analogue in our African data set. When the analysis is restricted to pixels of directly comparable climate, the mean diversity of African forests is still much lower than that in Amazonia. Only in regions of low mean annual rainfall and temperature is mean diversity in African forests comparable with, or superior to, the diversity in Amazonia.

4. The climatic variables best correlated with the tree  $\alpha$ -diversity are largely different in the African and Amazonian data, or correlate with African and Amazonian diversity in opposite directions.

5. These differences in the relationship between local/landscape-scale  $\alpha$ -diversity and climate variables between the two continents point to the possible significance of an array of factors including: macro-scale climate differences between the two regions, overall size of the respective species pools, past climate variation, other forms of long-term and short-term environmental variation, and edaphics. We speculate that the lower  $\alpha$ -diversity of African lowland rain forests reported here may be in part a function of the smaller regional species pool of tree species adapted to warm, wet conditions.

6. Our results point to the importance of controlling for variation in plot size and for gross differences in regional climates when undertaking comparative analyses between regions of how local diversity of forest varies in relation to other putative controlling factors.

*Key-words:* Africa, Amazonia, biodiversity, biogeography, climate, comparative analysis, diversity theory, Fisher's alpha, tree alpha diversity, tropical forest

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## Introduction

Tropical rain forests host the highest levels of biodiversity on earth. Nevertheless, our understanding of the determinants of rain forest diversity is relatively poor and the causes of the differing diversity levels inside and between the world's main rain forest areas remain uncertain (Richards 1973; Gentry 1988; Sheil 1996; Givnish 1999; Leigh *et al.* 2004; Wills *et al.* 2006). In a comparative study of the main tropical forest ecosystems of the world, Richards (1973) concluded that whenever differences are found, it is Africa that is the 'Odd man out': African rain forests always seem to differ from American and Asian rain forests more than they do from each other. One of the major differences is the relative poverty of the African rain forest flora. In this paper, our goal is to present a comparative analysis of tree alpha ( $\alpha$ ) diversity patterns within the rain forest biome of West and central Africa and South America.

The broad pattern of geographical gradients in species richness of terrestrial ecosystems from low in Polar Regions to high in the tropical rain forest biome is long established, and recent work has demonstrated that it is

largely attributable to climate (O'Brien 1998; Francis & Currie 2003; Hawkins *et al.* 2003; Field *et al.* 2005). It is therefore sensible to start a comparative diversity analysis by testing contemporary climatic models of diversity variation (Richards 1973; O'Brien 2006). We therefore focus herein on the relationships between climate variables and a metric of diversity, basing our analyses on a large data set derived from small forest plots from both continents.

Patterns of diversity at one spatial scale can be distinct from, and have distinct drivers from, patterns at other (coarser or finer) spatial scales (Whittaker *et al.* 2001). Besides contemporary climate, sources of rain forest diversity variation have been ascribed notably to historical factors (varying from centennial to geological time scales), soil fertility, constraints related to species pool size, the intermediate disturbance hypothesis, animal disturbances, the mid-domain effect, anthropogenic influence and extreme disturbances (Connell 1978; Phillips *et al.* 1994; Sheil 1996, 2001; Givnish 1999; Colwell & Lees 2000; Morley 2000; Plotkin *et al.* 2000; Willis & Whittaker 2002; Newbery *et al.* 2004; Rangel & Diniz-Filho 2005; ter Steege *et al.* 2006).

Spatial patterns of plant diversity within the rain forest areas of Africa and Amazonia are not known with high precision because the underlying species range data are largely incomplete and highly dependent on the sampling intensity (Kier *et al.* 2005; Kuper *et al.* 2006; Schulman *et al.* 2007). ter Steege *et al.* (2006) gathered data from large-scale inventories in Amazonia ( $4^\circ \times 6^\circ$  blocks) that they analysed at the genus level. They distinguished two dominant gradients in composition and function of trees with diameter at breast height (d.b.h.)  $\geq 30$  cm: a major gradient in soil fertility and a gradient in dry season length. These gradients were also correlated with tree diversity.

At the community level, Gentry (1988) concluded that equatorial forests are more diverse than tropical forests further from the equator, that woody plant diversity varies little up to 1500 m elevation, and that local species richness generally increases with soil fertility and precipitation. Clinebell *et al.* (1995) reanalysed Gentry's 0.1-ha Neotropical data set and showed that annual rainfall and rainfall seasonality were the most important variables for explaining species richness, independent of soil quality. With a larger set of typically 1-ha forest plots (trees d.b.h.  $\geq 10$  cm), ter Steege *et al.* (2003) reported that dry season length is a strong predictor of tree density and of 'maximum' tree  $\alpha$ -diversity in Amazonia. The metric they used for tree  $\alpha$ -diversity was Fisher's  $\alpha$  (Fisher *et al.* 1943), the properties of which are discussed below. Hence, their work suggests that while climate may provide reasonable statistical models for 'maximal'  $\alpha$ -diversity variation within Amazonia, it is not the only factor influencing  $\alpha$ -diversity.

To permit a proper comparison with these findings, we have assembled tree diversity data from small plots in the African rain forests. By selecting plots from both continents that meet given criteria, we attempt what is to our knowledge the first systematic comparative analysis of  $\alpha$ -diversity variation between African and Amazonian

rain forests. We aim to answer the following questions:

- 1 Do African and Amazonian rain forests exhibit comparable levels of  $\alpha$ -diversity of trees?
- 2 What are the main climatic differences between the rain forest areas of Amazonia and Africa?
- 3 Can climate variables explain  $\alpha$ -diversity variation within and between the two areas and are the climatic relationships for Africa consistent with those reported by ter Steege *et al.* (2003) for Amazonia?
- 4 Additionally, is tree  $\alpha$ -diversity correlated in the same way with the climatic variables in both continents?
- 5 Does dry season length covary with 'maximal'  $\alpha$ -diversity in African rain forest?

## Methods

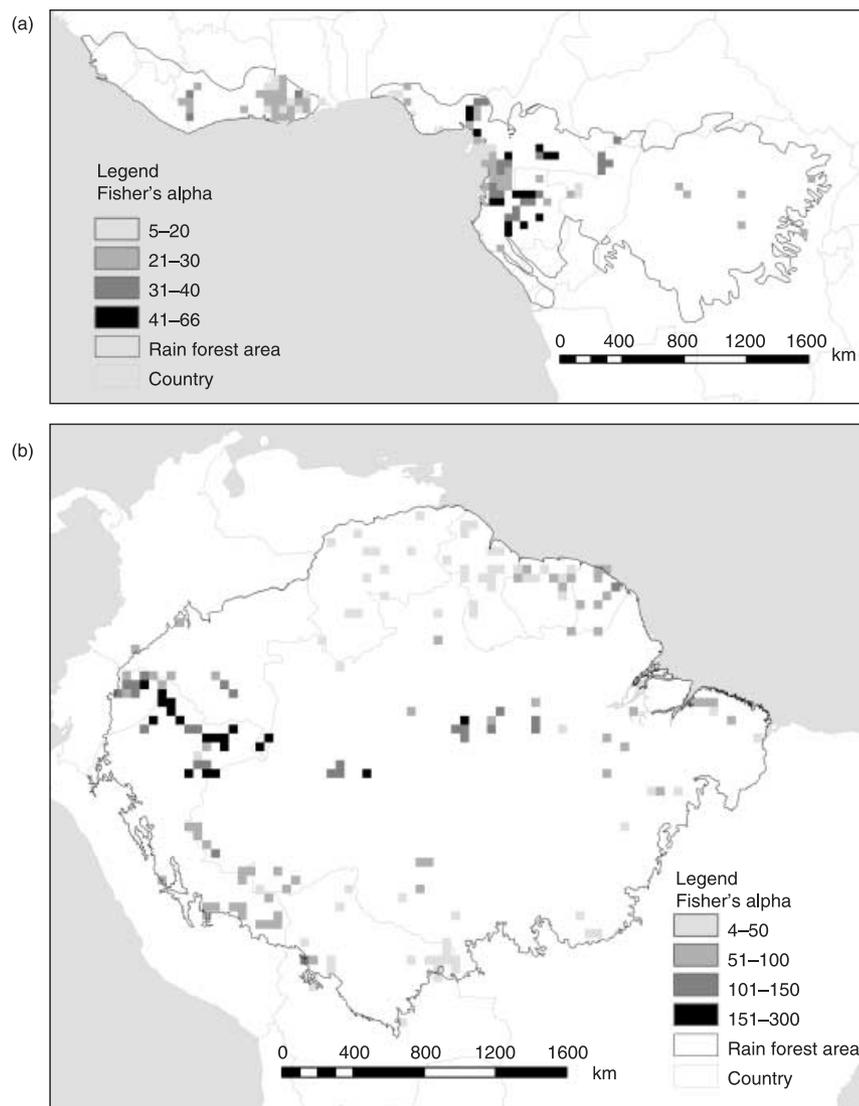
### DATA

The Amazon Tree Diversity Network database provided the Amazonian data (512 plots and transects, [http://www.bio.uu.nl/~herba/Guyana/Amazon\\_plot\\_network/Index.htm](http://www.bio.uu.nl/~herba/Guyana/Amazon_plot_network/Index.htm)). The African  $\alpha$ -diversity data were compiled from literature and unpublished data (1003 plots and transects). References for the African data points are listed in Appendix S1 in Supplementary material. The data points selected for this study are located in old growth terra firme rain forest below 900 m altitude (above this altitude tropical montane influences appear increasingly in forest plots). Their minimum and maximum sizes and stem numbers are as shown in Table 1. Following the recommendations of Condit *et al.* (1998), the minimum acceptable number of individual trees in a plot was set to 50. In Africa, plots in monodominant and swamp forests were excluded. In Amazonia, plots on white sands, floodplains and swamps were excluded. Data points are unequally distributed in both continents (Fig. 1).

For each data point, Fisher's  $\alpha$  values were calculated from the number of species and the number of individuals of trees d.b.h.  $\geq 10$  cm. Plots and transects

**Table 1.** Area, number of trees, Fisher's  $\alpha$  values and altitude for the four data sets (non-aggregated data). full: all plots; 1 ha: c. 1-ha data sets including only plots with area 1–1.5 ha and maximal length = 500 m. Af = Africa, Am = Amazonia.

	Area (ha)	Number of trees	Fisher's $\alpha$	Altitude (m)
Af-full ( $n = 1003$ )				
Minimum	0.044	50	1.6	7
Maximum	7.600	2900	85.6	900
Mean $\pm$ SD	$0.286 \pm 0.45$	$137 \pm 200$	$27.7 \pm 13.3$	$305 \pm 205$
Af-1 ha ( $n = 63$ )				
Minimum	1.000	246	7.8	9
Maximum	1.486	781	66.1	814
Mean $\pm$ SD	$1.023 \pm 0.104$	$475 \pm 91$	$40.4 \pm 13.8$	$456 \pm 237$
Am-full ( $n = 512$ )				
Minimum	0.250	144	3.6	0
Maximum	5.000	3251	299.9	841
Mean $\pm$ SD	$0.968 \pm 0.442$	$571 \pm 277$	$82.4 \pm 54.8$	$193 \pm 156$
Am-1 ha ( $n = 144$ )				
Minimum	1.000	324	3.6	9
Maximum	1.500	860	211.0	650
Mean $\pm$ SD	$1.021 \pm 0.100$	$585 \pm 99$	$74.6 \pm 45$	$153 \pm 137$



**Fig. 1.** Tree  $\alpha$ -diversity patterns in the rain forests of (a) Africa and (b) Amazonia. The focus of the analyses presented in the paper is a 2.5-km size squared pixel. On these maps, pixel size is 50 km for display. The 50-km<sup>2</sup> pixel's value is the mean Fisher's  $\alpha$  value resulting from the aggregation of the 2.5-km<sup>2</sup> pixels. The potential rain forest area considered for this study is around 249 million ha in Africa vs. 668 million ha in Amazonia. Note that intervals used are not the same in both continents.

varied greatly in size and shape, and although area was known for each plot, the  $x - y$  dimensions were unknown for 46% of the Amazonian data set. To control for the possible influence of plot area, number of trees and of plot dimensions (shape) on Fisher's  $\alpha$  values, results are presented for those reduced data sets that met stricter selection criteria, as well as for each full data set. The criteria for the reduced data set are that plot area is between 1.0 and 1.5 ha and that plot length is  $\leq 500$  m. For convenience, we refer hereafter to these data sets as the full and *c.* 1-ha data sets using the following codes: Af-full, Af-1 ha, Am-full, Am-1 ha (where Af = African, Am = Amazonian).

Climatic data were extracted from the WorldClim database (<http://www.worldclim.org>, Hijmans *et al.* 2005), which provided globally interpolated values for 19 bioclimatic variables (see Table 2).

In addition, dry season length (DSL) was calculated from the mean monthly rainfall values (DSL = number of months  $< 100$  mm). We refer hereafter to the 19 original WorldClim variables plus the calculated dry season length as '20 climatic variables'. WorldClim also provided an elevation layer based on the Shuttle Radar Topography Mission (SRTM). We extracted the elevation of each data point from this SRTM layer. WorldClim is based on data from 1950 to 2000, and has a spatial resolution of 30 arc s (approximately 1 km), although it must be remembered that in the tropics these data were derived from a very sparse network of climatological observations.

Our definition of Amazonia follows Eva & Huber (2005), including lowland Amazonia, the Guyanas, and the Tocantins and Gurupi regions to the east of the Brazilian Amazon Basin (Fig. 1b). The boundaries of the Western and central African rain forest areas were

**Table 2.** Correlations of 20 climatic variables and altitude to tree  $\alpha$ -diversity in the rain forests of Africa and Amazonia for the full data sets and for the *c.* 1-ha data sets (plots with area 1–1.5 ha and maximal length 500 m, aggregated data). Af: Africa, Am: Amazon. p: \*ordinary *t*-test  $\leq 0.05$ , \*\**t*-test with Dutilleul correction  $\leq 0.05$ . Mean diurnal  $T^\circ$  range = mean of monthly (maximum  $T^\circ$  – minimum  $T^\circ$ ); isothermality = mean diurnal range/ $T^\circ$  annual range;  $T^\circ$  seasonality =  $SD \times 100$ ;  $T^\circ$  annual range = maximum  $T^\circ$  warmest month – minimum  $T^\circ$  coldest month; P seasonality = coefficient of variation. A quarter is a period of three successive months

Variable		Af-full		Am-full		Af-1 ha		Am-1 ha	
		Corr.	p	Corr.	p	Corr.	p	Corr.	p
Mean annual $T^\circ$	mT	-0.35	**	0.21	*	-0.44	**	NS	
Mean diurnal $T^\circ$ range	mdrT	0.20	**	-0.29	*	NS		NS	
Isothermality	isoT	0.29	**	0.39	**	NS		0.32	*
$T^\circ$ seasonality	Tsea	-0.27	*	-0.31	*	NS		-0.25	*
Maximum $T^\circ$ warmest month	Twm	-0.32	**	-0.18	*	-0.41	**	NS	
Minimum $T^\circ$ coldest month	Tcm	-0.38	**	0.29	*	NS		0.25	*
$T^\circ$ annual range	Tar	NS		-0.36	*	NS		-0.26	*
Mean $T^\circ$ wettest quarter	Tweq	-0.37	**	0.16	*	-0.50	**	NS	
Mean $T^\circ$ driest quarter	Tdq	-0.39	**	0.21	*	-0.40	**	0.23	*
Mean $T^\circ$ warmest quarter	Twaq	-0.37	**	0.15	*	-0.44	**	NS	
Mean $T^\circ$ coldest quarter	Tcq	-0.32	**	0.25	*	-0.46	**	0.24	*
Annual precipitation	aP	0.23	*	0.40	**	NS		0.36	*
P wettest month	Pwm	0.22	*	-0.09		NS		NS	
P driest month	Pdm	NS		0.55	**	NS		0.34	*
P seasonality	Psea	0.25	**	-0.59	**	NS		-0.33	*
P wettest quarter	Pweq	0.24	*	NS		NS		NS	
P driest quarter	Pdq	-0.09	*	0.53	**	NS		0.31	*
P warmest quarter	Pwaq	0.34	**	0.31	*	0.32	*	NS	
P coldest quarter	Pcq	-0.08	*	0.30	*	NS		0.46	**
Dry season length	dsl	NS		-0.47	**	NS		-0.22	*
Altitude	alt	0.37	**	-0.22	*	0.34	*	NS	

digitized from the land-cover map presented by Mayaux *et al.* (2004). The external boundaries of the original cover of the rain forest were estimated from the present extent of the closed evergreen lowland forest, degraded evergreen lowland forest and mosaic forest/croplands (Fig. 1a).

#### ANALYSES

Following ter Steege *et al.* (2003), tree  $\alpha$ -diversity was estimated with Fisher's  $\alpha$  calculated for trees d.b.h.  $\geq 10$  cm. Fisher's  $\alpha$  is a constant that represents diversity in a logarithmic series estimating the number of species  $S$  within  $N$  observed individuals (Magurran 2004):  $S = \alpha \ln(1 + N/\alpha)$ . It has been shown elsewhere that Fisher's alpha is a good approximation of the theta index in the neutral theory of biogeography and biodiversity (Etienne & Alonso 2005). Theta is interpreted as the diversity of the species pool, of which the plot is but one sample. Condit *et al.* (1998) compared the values of several diversity indices between different plots as a function of the number of individuals sampled. In their study, Fisher's  $\alpha$  gave fairly invariant estimates of diversity ratios between plots in all samples of  $> 50$  individuals. Nevertheless, they recommend that comparisons be based on samples of approximately standardized numbers of stems, and that samples of fewer than 50 stems (or in very diverse forests, of fewer than 100 stems) should be excluded from analysis.

Plot area and number of stems were variable in our full data sets (Table 1), which, as just indicated, can bias diversity estimates. In the *c.* 1-ha data sets, we controlled for size and dimensions, and consequently, we also limited the variation in number of stems, with the smallest sample being 246 trees, well above the 50 and 100 thresholds identified by Condit *et al.* (1998). Fisher's  $\alpha$  was calculated for each plot, but, to reduce concerns about spatial autocorrelation within the data (Lennon 2000; Diniz-Filho *et al.* 2003), data points have been aggregated to a pixel size of 2.5 km. Each 2.5-km pixel was given the mean  $\alpha$  value of plots included inside the pixel area. We made no interpolation; many pixels inside each rain forest area included no plot and remained as no data. The focal scale of the analysis *sensu* Whittaker *et al.* (2001) is thus the mean  $\alpha$  of small plots inside a 2.5-km size square. After aggregation, the full and *c.* 1-ha data sets included, respectively, 698 and 38 pixels for Africa and 307 and 84 pixels for Amazonia. We further refer to these 2.5-km size pixels as the aggregated data. Except in Table 1, all diversity results presented are for the aggregated data. The values of the climatic variables and altitude were extracted for the centre of the pixel. Geographical data were manipulated with ArcGIS® 9.1 (ESRI, Redlands, CA, USA).

We used Pearson's correlation coefficient to measure the relationship of Fisher's  $\alpha$  with the 20 climatic variables and altitude. The *t*-tests of these correlations were corrected to take spatial autocorrelation into account

(Dutilleul 1993) using PASSaGE version 1.1 (<http://www.passagesoftware.net/>, Rosenberg 2001).

As a first step in understanding any differences in  $\alpha$ -diversity between the two continents, we needed to establish whether the climate regimes of the two rain forest regions are comparable. This we did at two levels: first, comparing the climate space of the entire rain forest biome, and second, comparing the climate space of the pixels for which we had diversity data. In order to compare the complete climatic space of the two rain forest areas, the WorldClim pixels within each rain forest region were systematically subsampled with a similar intensity (~1.5%) in the two continents (Africa,  $n = 45\,844$ ; Amazonia,  $n = 112\,986$ ). Subsampling was required because analysis of every pixel in the climate space was too burdensome on computer processing power.

Principal components analysis (PCA) of the 20 climatic variables was applied to extract the main climatic gradients in (i) the subsample of the WorldClim pixels of each rain forest area separately, and (ii) the combined diversity data sets of the two continents. This allowed us to assess (i) how well each diversity data set represents the climate space of each rain forest region (i.e. either Africa or Amazonia), and (ii) the climatic similarity between the two diversity data sets. PCA was performed for the full and for the *c.* 1-ha data sets.

In the interaction model proposed by ter Steege *et al.* (2003) for the  $\alpha$ -diversity of Amazonian forests, tree  $\alpha$ -diversity ( $Z$ ) is a linear function of the dry season length and a variety of undefined 'other interacting factors' (OIFs):

$$Z = \alpha + \beta(1 - \text{OIF}) \text{DSL} + \epsilon$$

where  $\alpha$  and  $\beta$  are constants and  $\epsilon$  is an error term. If  $\text{OIF} = 0$  (the upper bound of the distribution for DSL) this reduces to

$$Z = \alpha + \beta (\text{DSL}) + \epsilon.$$

This is equal to the maximum  $Z$  for a given DSL. This model was efficient in predicting the 'maximal' diversity for a given DSL in Amazonia. Here, we tested this model on the African data set. The parameters  $\alpha$  and  $\beta$  were estimated by applying quantile regression (Cade *et al.* 1999) for the 90th percentile, where OIF approaches zero.

## Results

### DIVERSITY PATTERNS

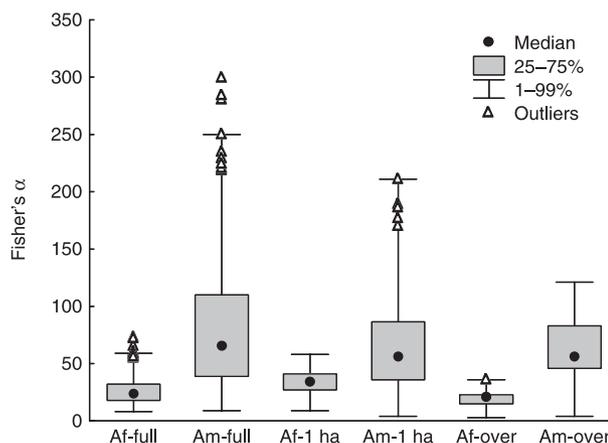
In both continents, there is great variation in  $\alpha$ -diversity of forest stands, and this can apply at very local scales: pixels with low Fisher's  $\alpha$  values are found almost everywhere. In Africa, pixels with high diversity values are clustered in the Western portion of central Africa (Fig. 1a). In Amazonia, the most diverse stands are located in a narrow latitudinal band just south of the equator, with the highest concentration of very high diversity values in the western part of this band (Fig. 1b).

Mean  $\alpha$ -diversity in Amazonia is much greater than in Africa (Mann–Whitney  $U$ -test:  $P < 0.001$ , mean  $\alpha$  Africa = 26, mean  $\alpha$  Amazonia = 81). Low diversity values are present in both continents but high diversity values ( $\alpha > 100$ ) are absent from Africa (Fig. 2). This result is maintained in the *c.* 1-ha data sets ( $P < 0.001$ , mean  $\alpha$  Africa = 36, mean  $\alpha$  Amazonia = 69, Fig. 2).

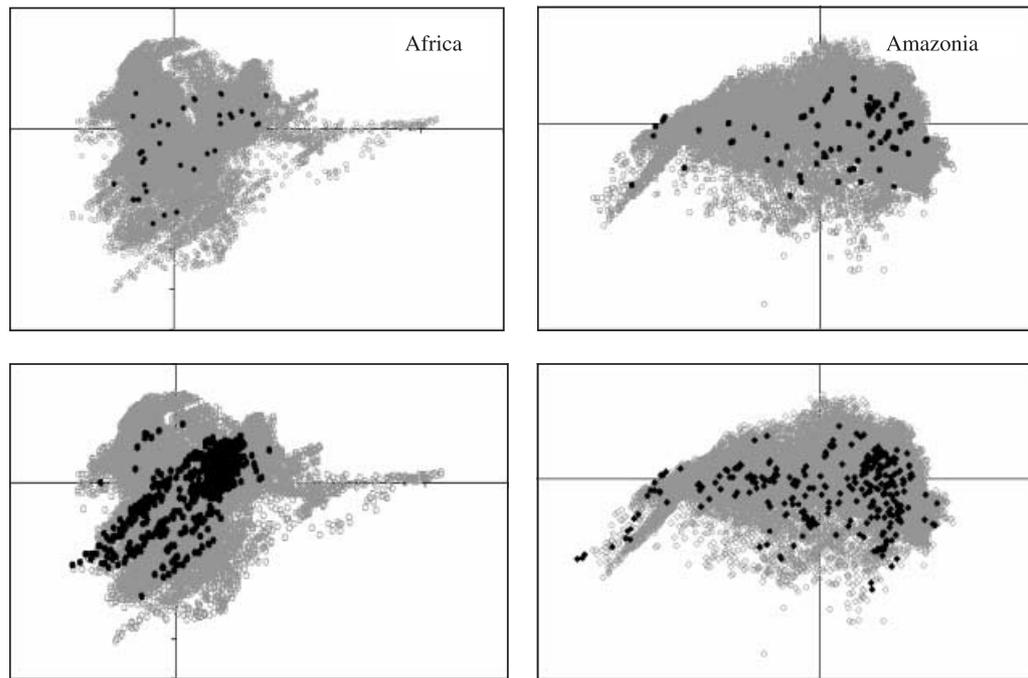
### CLIMATE COMPARISONS

The rain forest region in Africa features lower mean values for most precipitation variables. It also has higher mean elevation, lower mean temperature and higher mean temperature seasonality than the Amazonian rain forest region (see Appendix S2).

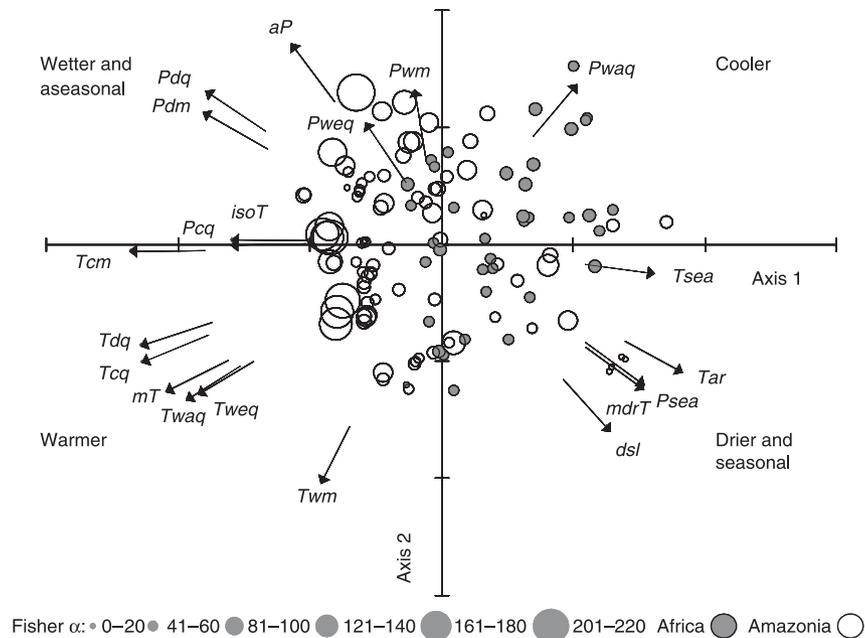
The position of the four diversity data sets inside the climatic space of the corresponding rain forest area is presented in Fig. 3. The diversity data set for Amazonia spans the climate space of Amazonia very well. The



**Fig. 2.** Tree  $\alpha$ -diversity of small forest plots in terra firme forest (< 900 m altitude) in Africa (Af) and Amazonia (Am), aggregated data: full-data sets ( $n$  Af = 698,  $n$  Am = 307), *c.* 1-ha data sets ( $n$  Af = 38,  $n$  Am = 84) and points that are inside the climatic overlap between the two *c.* 1-ha data sets (over,  $n$  Af = 34,  $n$  Am = 35).



**Fig. 3.** Climatic position of the diversity pixels (aggregated data) in relation to the climate of their respective rain forest area. The PCA axes are the two main climatic gradients in each rain forest area and are thus not comparable between the two rain forest areas (PCA of 20 climatic variables, Africa  $n = 45\,844$ , Amazonia  $n = 112\,986$ , Axis 1: horizontal, Axis 2: vertical). These axes represent 60% of the total climatic variance in Africa and 66% in Amazonia. For the significance of these axes, see Appendix S3. Black points are the position of the diversity data points inside that climatic space (up: *c.* 1-ha data sets, down: full data sets). Shaded points are a random selection of ~1-km pixels inside the rain forest area (only 30 000 pixels are displayed for each rain forest area, but these represent fairly the pattern of the whole rain forest pixel sample).



**Fig. 4.** Principal components analysis of 20 bioclimatic variables for the two *c.* 1-ha diversity data sets (Africa,  $n = 38$ ; Amazonia,  $n = 84$ , aggregated data). Axis 1 represents 43% of the climatic variance, and axis 2 represents 22%. Symbol sizes are proportional to the Fisher's  $\alpha$  value of the pixel (class interval is 20). Details on the variables are provided in Table 2 and details on the PCA in Appendix S4. The scaling factor between the scores of the climatic variables and the scores of the pixels is 0.26. The arrows representing the climatic variables should continue to the origin; we suppressed their basal part to increase the readability of the figure. Results for the full data sets are presented in Appendix S6.

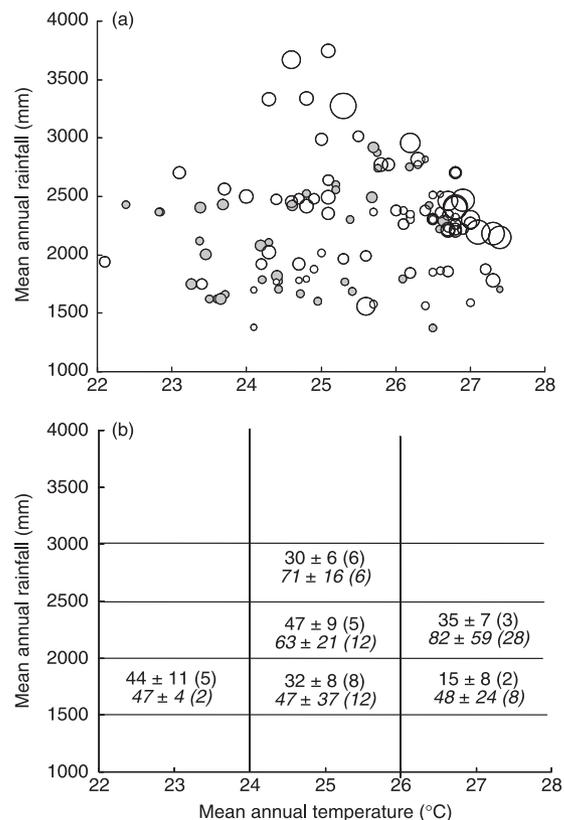
African diversity data set coverage appears less complete, lacking extreme values on the two main climatic gradients. Note that the main climatic axes are different in the two continents. PCA details and loadings of the 20 climatic variables on the PCA axes for each continent are given in Appendix S3. Mean values of the climatic variables for the diversity data sets are presented in Appendix S2, where they can also be compared with those of each rain forest region.

The two *c.* 1-ha diversity data sets (Amazon and Africa) are presented in a common PCA climate space in Fig. 4 (for details see Appendix S4). The first two PCA axes represent 65% of the climatic variability. The climate variables cluster into three main groups: in the top left are variables associated with high precipitation and isothermality, in the bottom right are variables associated with low precipitation and high seasonality, and in the bottom left are variables associated with high temperatures. Note that in this data set the precipitation and seasonality variables are largely orthogonal to the temperature variables, and in particular that total annual precipitation (*aP*) is almost exactly orthogonal to mean annual temperature (*mT*). Hence, we can rotate the PCA axes in Fig. 4 and adequately describe the climate space covered by the first two PCA axes by plotting annual precipitation against annual temperature. As these two fundamental climatic variables are more intuitive than the PCA axes and more readily available worldwide, we adopt them as our main axes of climate variability in our subsequent analysis.

There is only a partial climatic overlap between the *c.* 1-ha diversity data sets in Amazonia and in Africa (Fig. 4). In Amazonia, the main climatic gradient is related to precipitation variables and to precipitation and temperature seasonality (top left to bottom right). In Africa, the main climatic gradient is mainly related to temperature variables (top right to bottom left). The African pixels are generally drier than the Amazonian pixels.

#### DIVERSITY–CLIMATE RELATIONSHIPS

Correlations of the 20 climatic variables and altitude with the tree  $\alpha$ -diversity are presented in Table 2 (results for untransformed data). The *t*-tests of these correlations were corrected to take spatial autocorrelation into account. We did not apply Bonferroni corrections for multiple testing. Nevertheless, except for the Amazonian *c.* 1-ha data set, the number of significant correlations is largely greater than would be expected by chance. Results for transformed data (improving the normality of the distribution of the diversity data and/or the other variable) are in accordance with those for the untransformed data (see Appendix S5). The climatic variables that are best correlated with tree  $\alpha$ -diversity differ between the two continents or are correlated in opposite directions. The most significant correlations with  $\alpha$ -diversity in Africa are negative with temperature and positive with altitude and precipitation of the warmest

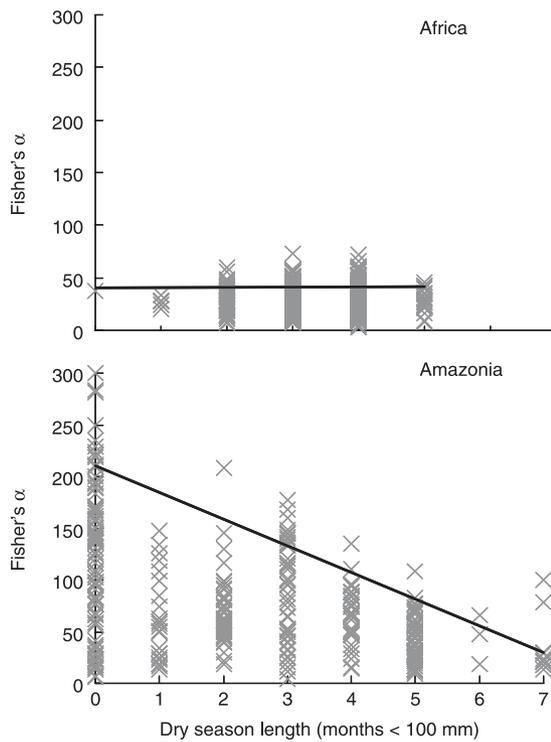


**Fig. 5.** Mean annual precipitation and temperature for the *c.* 1-ha diversity data sets (aggregated data). Circles sizes are proportional to the Fisher's  $\alpha$  value of the pixel (open circles: Amazonian, shaded circles: Africa). The graph has been divided into sections. Numbers indicate the mean Fisher's  $\alpha$  value and standard deviation in each section, the number of pixels is given in parentheses (Amazonia values are italicized). Results for the full data sets are presented in Appendix S6.

quarter. In Amazonia, the best correlations are positive with precipitation and isothermality and negative with precipitation seasonality.

The highest  $\alpha$ -diversity values are found in Amazonian pixels in the wet and aseasonal regions, climatic regimes scarcely represented in the African data (top left of Fig. 4). Indeed, most African pixels are on the dry and seasonal side of the graph. As these climatic differences between the two data sets might explain the diversity differences, we calculated the mean diversity values for the pixels within the PCA (axes 1 and 2) ordination of the combined *c.* 1-ha diversity data sets where there was overlap between the African and Amazonian data (Appendix S4). Even within this subset,  $\alpha$ -diversity is much greater in Amazonia than in Africa (Mann–Whitney *U*-test:  $P < 0.001$ , mean Africa = 20, mean Amazonia = 61, Fig. 2).

As the mean annual precipitation and mean annual temperature gradients are orthogonal (above, Fig. 4), these two variables are good candidates for a further climate-controlled comparison of  $\alpha$ -diversity across the two data sets (Fig. 5 and Appendix S6). For low values of temperature and precipitation, African diversity is



**Fig. 6.** Tree  $\alpha$ -diversity (full data sets, aggregated data) as a function of the dry season length. Lines are the quantile regressions (quantile 0.9, Africa  $P = 0.419$ , Amazonia  $P < 0.0001$ ). Results for the *c.* 1-ha data set are presented in Appendix S7.

similar to (*c.* 1-ha data sets) or higher than (full data sets) Amazonian diversity. For wetter and warmer climates, the difference between the diversity values of the two continents widens (Fig. 5).

In Amazonia, DSL is negatively correlated with the upper quantile of  $\alpha$ -diversity ( $P < 0.0001$ , Fig. 6). In Africa, the highest diversity values correspond to intermediate DSL values and no significant linear relationship is observed between 'maximal'  $\alpha$ -diversity and DSL ( $P = 0.971$ , Fig. 6). Results for the *c.* 1-ha data sets are similar for Africa. In Amazonia, the negative correlation of DSL with the upper quantile of  $\alpha$ -diversity is weaker (see Appendix S7).

## Discussion

### DATA SET LIMITATIONS

This analysis is focused on a diversity index, Fisher's  $\alpha$ , calculated for trees  $\geq 10$  cm d.b.h. for small rain forest plots, with greatest weight placed on the analysis of data for plots of area between 1 and 1.5 ha (the *c.* 1-ha data sets). Our analyses are thus of a measure of within-community (local scale) diversity. Although the results presented here might differ from those we would obtain if analysing coarse-scale diversity data (e.g. Field *et al.* 2005), it is always the case that comparisons of diversity should be made with reference to scale (Whittaker *et al.* 2001). Furthermore, there are insufficient data

currently available for a reliable comparison at substantially larger plot sizes than detailed herein.

There are significant data gaps for both continents, owing to a paucity of inventories from large areas, in particular within tropical Africa. The superposition of our data set with the distribution of closed evergreen lowland forest in Africa (Mayaux *et al.* 2004) indicates that we lack data primarily from Liberia and for the large forest areas of D. R. Congo. Significant gaps occur also in the Brazilian regions adjacent to the Guyanas, the central Colombian Amazon and large tracts of the (dry and seasonal) southern Brazilian Amazon (ter Steege *et al.* 2003).

The accuracy of the climate data (WorldClim) is mainly dependent upon the density of weather stations and on the quality of the interpolation. The accuracy of interpolated precipitation data in mountainous areas is not particularly good, because of extreme local rainfall gradients. Areas with low population density such as Amazonia have few weather stations and most of these are located at the periphery of or along rivers. In Africa, the distribution of the weather stations is quite good, except in some parts of D. R. Congo. This country also has very few climate data after 1960. Although these weaknesses in the climatic data certainly may affect the values of the climatic variables for individual points, we do not consider that they seriously undermine the analyses presented. Our analysis is further limited by the climatic variables we used. We included the 19 variables provided by WorldClim and added the dry season length to aid comparison with ter Steege *et al.* (2003). These 20 variables are calculated from monthly rainfall and temperature variables. There is no doubt these are key climatic variables, although others could have been selected (cf. O'Brien 1998).

We arbitrarily selected the plots under 900 m a.s.l. in order to limit the elevational variation between Africa and Amazonia and to exclude submontane forest. However, it is well known that the lower elevational limit of submontane forest is highly variable (Richards 1996; Ashton 2003; Senterre 2005). A selection of similar forest types between the two continents based on the forest structure, functional types, or the presence or absence of indicator species would have been more rigorous but was not possible here because we lack detailed data for most of the current data points.

The quality of the diversity data is variable. The number of individuals that will be identified or attributed to a morpho-species is dependent upon the experience of the botanist who made the inventory as well as on the time spent on taxonomic analysis and the degree of specimen vouchering. Additional uncertainties arise from the fact that for some data points it is not known whether lianas were also included in the number of individuals with d.b.h.  $\geq 10$  cm and how multitemmed individuals were considered (number of stems d.b.h.  $\geq 10$  cm vs. numbers of individuals).

We selected plots in old-growth terra firme forest. In compiling the African data set, we obtained data for

some plots that were known to have been selectively logged more than 15 years before the plot was recorded. We discarded these plots from the c. 1-ha data set. Nevertheless, it is very difficult to be certain that a forest has never been logged in the past.

Plot shape and dimensions are also well known to influence diversity data: a long and narrow transect is likely to include more species than a short and wide plot of similar area (Condit *et al.* 1996; Laurance *et al.* 1998). We also know that Fisher's  $\alpha$  is sensitive to the number of individuals (Condit *et al.* 1998). We presented two series of results: for our full data set and for a subset limited to plots of 1–1.5 ha that did not exceed 500 m in length (c. 1-ha data set). As both series of results are comparable, our analyses seem fairly robust to the sampling variation involved.

#### DIVERSITY–CLIMATE RELATIONSHIPS

Within each continent, tree  $\alpha$ -diversity is correlated with climatic variables. However, the explanatory power of contemporary climatic controls is questioned by the substantial differences in the form of the climate– $\alpha$ -diversity relationships in Africa and Amazonia (Table 2, Fig. 6). This might indicate that either the contemporary climate cannot provide a fundamental explanation for the diversity patterns in both continents, or that our simple empirical approach to determining these relationships has failed to recognize the real form of the underlying relationships to climate (for a theoretically grounded approach, see O'Brien 1998, 2006; Field *et al.* 2005). We also have to remember that there is only a partial climate overlap between the two diversity data sets (Fig. 4), which limits direct comparison of the diversity–climate relationships between the two continents.

There are many theoretical arguments and empirical observations for the variation in different facets of diversity phenomena across and within the world's rain forests (Givnish 1999; Leigh *et al.* 2004). Drivers of environmental change relate to several time frames, and heterogeneity in contemporary environment may be differentially evident at different spatial scales of analysis (Willis & Whittaker 2002). It is very difficult to confidently link analyses of  $\alpha$ -diversity variation to deterministic environmental factors and/or stochastic and historical factors. We cannot evaluate the applicability of most ideas and theories that have been put forward in a meaningful way. The discussion that follows is therefore necessarily speculative in nature.

Animals have an effect on tree  $\alpha$ -diversity and forest structure: they disperse the seeds of some tree species, and predate others, while some mega-fauna (e.g. African elephant) are known to cause stem damage and mortality (Silman *et al.* 2003; Sheil & Salim 2004). Regional variations in the composition, density and distribution of the fauna might therefore influence tree diversity patterns.

A positive correlation between soil fertility and tree diversity has been demonstrated in other studies (e.g.

Dubbin *et al.* 2006; ter Steege *et al.* 2006). Phillips *et al.* (1994) showed that mean annual tree mortality and recruitment (i.e. stem turnover) is a good correlate of species richness. We did not test for the correlations of these two factors with  $\alpha$ -diversity in our data set because for most of the points, we lack soil fertility data and multicensus data.

The mid-domain effect argument (Colwell & Lees 2000; Rangel & Diniz-Filho 2005) proposes that species richness gradients may arise by stochastic processes combined with geometrical constraints imposed by the edges of the domain in which species are embedded, and by the cohesion of the species' geographical ranges. This line of argument appears of little relevance to patterns in the alpha-scale diversity metric analysed herein and hence we do not consider it further.

There is some evidence that the Pleistocene and Holocene histories of climate and vegetation of the two rain forest areas have been quite different and might have a relevance to understanding variation in diversity at a variety of scales. Whilst Pleistocene climate change clearly impinged on Amazonia, recent palaeo-ecological analyses indicate that the rain forests persisted without large-scale simultaneous reduction in their extent across the basin (Morley 2000; Colinvaux *et al.* 2001; Bush & Silman 2004; Cowling *et al.* 2004; Mayle *et al.* 2004; Maslin *et al.* 2005). It is therefore reasonable to postulate that macro-scale species richness patterns across Amazonia should correspond to expectations of water-energy theory: highest diversity where globally optimal temperatures, high precipitation and low seasonality are combined (O'Brien 1993, 1998, 2006; Field *et al.* 2005). By comparison, the African tropics are thought to have experienced more dramatic vegetation changes during the Pleistocene and Holocene (Dupont *et al.* 2000; Morley 2000; Elenga *et al.* 2004). During the driest and coolest periods of the Pleistocene (0.6–0 Ma), African rain forests are thought to have been restricted to refuges from which they subsequently spread during the Holocene (Maley 1996; Morley 2000). Most authors agree on the location of the African Pleistocene forest refuges but there is controversy concerning their extent (Colyn *et al.* 1991; Robbrecht 1996; Sosef 1996; Leal 2001). Our African data set presents a concentration of data points of high  $\alpha$ -diversity in proximity to or within the proposed locations of the Pleistocene forest refuges. This might indicate that high  $\alpha$ -diversity values are favoured by long-term suitability of the area for tropical lowland forest taxa and thus by a large regional species pool size.

Recent studies analysing palaeo-ecological data from both marine and terrestrial signals suggest that climate changes also occurred in the equatorial region of West Africa during the late Holocene around 4–3.8 kyr BP (Marret *et al.* 2006) and around 3 kyr BP (Vincens *et al.* 1999). Maley (2002) describes a catastrophic destruction of African forests about 2500 years ago. These Pleistocene and Holocene events could possibly still exert an influence on present-day vegetation.

For instance, some part of the rain forest species pool may not have had enough time since these events to reach all the areas that are forested today, yielding a dispersal limitation gradient from the forest refugia to those areas that were covered in savanna. The correlations of tree  $\alpha$ -diversity with the climatic variables and altitude we describe here for the African data set might therefore reflect a greater degree of departure of species distributions from equilibrium with current climate than pertains in Amazonia. Such imbalances as a consequence of slow post-glacial spread from ice age refuges are well described in Europe (e.g. Araújo & Pearson 2005; Giesecke *et al.* 2007), but our current understanding of such phenomena in the tropics remains tantalisingly uncertain.

#### LOWER DIVERSITY OF AFRICAN RAIN FORESTS

The lower overall floristic diversity of tropical Africa when compared with tropical America and Asia is well documented (Richards 1996; Primack & Corlett 2005). However, at the local or community level, Reitsma (1988) and Gentry (1988) showed that a hectare of African rain forest may contain the same level of  $\alpha$ -diversity as many equivalent areas in Southeast Asia and tropical South America. Here we provide a formal comparison of tree  $\alpha$ -diversity between the African and Amazonian rain forests that has been calibrated for climate. For low values of mean annual temperature and mean annual rainfall, the tree  $\alpha$ -diversity of small plots in Africa is equivalent, or even superior, to that in Amazonian rain forests, but when both mean annual temperature and mean annual precipitation increase, the difference between the diversity values increases (Fig. 5). Gentry (1988), using a much smaller data set, obtained similar results for all species with d.b.h. > 2.5 cm: the Central African rain forests may be as diverse as their Neotropical equivalents for sites with precipitation of 1600–2000 mm. In our data set, for combined higher values of precipitation and temperature, it may be argued that African forests were not able to fill up the ‘species holding capacities’ that the climate provides, possibly because there are insufficient species in the regional pool that are adapted to warm, wet conditions. Indeed, the regional species-pool theory relates local species richness to the richness of the regional species pool from which the local community was presumably assembled (Fox & Srivastava 2006). The regional pool of species adapted to cool, dry conditions may be quite large in Africa, however, because of its palaeoclimatic history, explaining why in cool, dry conditions African plots seem to have similar or possibly higher diversity than Amazonian plots.

We expect a smaller regional species pool of tree species adapted to warm and wet conditions in Africa than in Amazonia due to the contrasting history of climate and vegetation of the two rain forest areas. At the end of the Middle Miocene, savanna expanded over much

of the African tropics, at the expense of rain forests, and large areas of the continent underwent uplift, preventing many lowland rain forest taxa from dispersing into suitable low-altitude habitats. This resulted in widespread extinction in the rain forest flora from the Late Miocene into the Pliocene (Morley 2000). In contrast, palaeoclimate and palaeoecological records suggest that tropical forests were established in the lowlands of Amazonia at least by the end of the Miocene and have been continuously maintained since then (Willis & McElwain 2002; Maslin *et al.* 2005). This prolonged environmental constancy may have minimized extinction rates in Amazonia (Morley 2000; Colinvaux & De Oliveira 2001). Extinction processes are also likely to be stronger in Africa than in Amazonia because of the smaller African rain forest area. Smaller area is associated with smaller population sizes, which in turn enhances extinction risk. According to the rain forest limits used in this study, the potential rain forest area corresponding to the current climate is around 249 million ha in Africa vs. 668 million ha in Amazonia. As speciation and extinction are processes that operate over millions of years, an adequate test of area’s contribution to diversity patterns must take into consideration the fact that biome areas have changed through time in response to climate. Both the size and the age of a biome are important factors in explaining its current species richness, but only when an integrated measure of both factors is included (Fine & Ree 2006). Such an analysis has not been performed for the tropical rain forests of the two continents.

A simple way to evaluate the regional species pool hypothesis would be to compare the number of wet-affiliated trees in the flora of the two rain forest areas. As far as we know, such figures have not yet been calculated. Fine & Ree (2006) provide estimates of the number of tree species for the Neotropics (22 500) and African tropics (6500). Although their definition of ‘tropics’ is very large (areas that never experience 0 °C temperature) and also includes dry forest and miombo, it is likely that a similar proportion applies also for the number of rain forest tree species. We would predict that tropical Africa and Amazonia have similar regional pool sizes of dry-affiliate rain forest tree species (possibly with Africa having a slightly larger pool), but that Africa has a greatly reduced pool of wet-affiliate rain forest tree species.

It has also been speculated that the lower diversity of the African vs. the Amazonian rain forest could result from a stronger anthropogenic impact in Africa (Richards 1973). This theory is based mainly on the discovery of charcoal and pottery below mature forests (White & Oates 1999) and on the fact that many of the large tree species that dominate the African rain forests are found to recruit poorly within the forest (especially the light-demanding species; van Gernerden *et al.* 2003). The presence of canopy gaps is insufficient for the regeneration of these trees: they might need larger-scale disturbances such as those produced by shifting cultivation. However, our knowledge of the extent and intensity of

the long-term human occupation of the rain forests is limited, especially in Amazonia (Heckenberger *et al.* 1999, 2003), as is our understanding of its effects on forest diversity. It is therefore difficult to evaluate the historical anthropogenic impacts on rain forest  $\alpha$ -diversity within the two continents.

### Conclusion and perspectives

Analysis of large data sets (i.e. A.H. Gentry's work, Slik *et al.* 2003) and the existence of extended scientific networks (ATDN, RAINFOR, CTFS) have strongly improved our knowledge of rain forest diversity variation, providing a basis for intensive and efficient research. Such coordinated efforts are insufficiently developed in Africa, and as a consequence the literature about rain forest diversity often lacks reference to African data. Our comparison of the tree  $\alpha$ -diversity of small plots in the African and Amazonian rain forests has highlighted the large differences in one facet of diversity–climate relationships between the two continents: that pertaining to the alpha diversity values of small blocks of forest. In the future, understanding of the lower species richness and diversity of African rain forests relative to Amazonian and South-East Asian rain forests will certainly benefit from phylogenetic studies of the African forest's component species (Pennington *et al.* 2004; Plana 2004) and from further intercontinental comparative analyses of the structure and dynamism of rain forest communities.

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## Supplementary material

The following Supplementary material is available for this article:

**Appendix S1** References and details for the African tree  $\alpha$ -diversity data set.

**Appendix S2** Mean and standard deviations of 20 climatic variables and altitude within (i) the whole rain forest area, (ii) the full diversity data sets and (iii) the c. 1-ha diversity data sets.

**Appendix S3** Loadings of the PCA of the values of 20 climatic variables for a systematic sampling inside the rain forest area of Africa and of Amazonia and correlations between the climatic variables.

**Appendix S4** Loadings of the PCA of the values of 20 climatic variables for the combined diversity data sets, PCA graph for the full data sets, PCA graph with the limits of the climatic overlap for the c. 1-ha data sets.

**Appendix S5** Correlations of 20 climatic variables and altitude to the tree  $\alpha$ -diversity in the rain forests of Africa and Amazonia: transformed data.

**Appendix S6** Mean annual precipitation and temperature for the full diversity data sets (aggregated data) with circles sizes proportional to the Fisher alpha value of the pixel.

**Appendix S7** Tree  $\alpha$ -diversity as a function of the dry season length (c. 1-ha data sets, aggregated data) and quantile regression.

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