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ORIGINAL ARTICLE

Tree species composition and diversity gradients in white-water forests across the Amazon Basin

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ABSTRACT

Aim Attention has increasingly been focused on the floristic variation within forests of the Amazon Basin. Variations in species composition and diversity are poorly understood, especially in Amazonian floodplain forests. We investigated tree species composition, richness and α diversity in the Amazonian white-water (várzea) forest, looking particularly at: (1) the flood-level gradient, (2) the successional stage (stand age), and (3) the geographical location of the forests.

Location Eastern Amazonia, central Amazonia, equatorial western Amazonia and the southern part of western Amazonia.

Methods The data originate from 16 permanent várzea forest plots in the central and western Brazilian Amazon and in the northern Bolivian Amazon. In addition, revised species lists of 28 várzea forest inventories from across the Amazon Basin were used. Most important families and species were determined using importance values. Floristic similarity between plots was calculated to detect similarity variations between forest types and over geographical distances. To check for spatial diversity gradients, α diversity (Fisher) of the plots was correlated with stand age, longitudinal and latitudinal plot location, and flood-level gradient.

Results More than 900 flood-tolerant tree species were recorded, which indicates that Amazonian várzea forests are the most species-rich floodplain forests worldwide. The most important plant families recorded also dominate most Neotropical upland forests, and *c.* 31% of the tree species listed also occur in the uplands. Species distribution and diversity varied: (1) on the flood-level gradient, with a distinct separation between low-várzea forests and high-várzea forests, (2) in relation to natural forest succession, with species-poor forests in early stages of succession and species-rich forests in later stages, and (3) as a function of geographical distance between sites, indicating an increasing α diversity from eastern to western Amazonia, and simultaneously from the southern part of western Amazonia to equatorial western Amazonia.

Main conclusions The east-to-west gradient of increasing species diversity in várzea forests reflects the diversity patterns also described for Amazonian terra firme. Despite the fine-scale geomorphological heterogeneity of the floodplains, and despite high disturbance of the different forest types by sedimentation and erosion, várzea forests are dominated by a high proportion of generalistic, widely distributed tree species. In contrast to high-várzea forests, where floristic dissimilarity increases significantly with increasing distance between the sites, low-várzea forests can exhibit high floristic similarity over large geographical distances. The high várzea may be an important transitional zone for lateral immigration of terra firme species to the floodplains, thus contributing to

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comparatively high species richness. However, long-distance dispersal of many low-várzea trees contributes to comparatively low species richness in highly flooded low várzea.

Keywords

Alpha diversity, Amazonia, floodplain forest, high várzea, low várzea, species distribution, species richness, species similarity, várzea.

INTRODUCTION

Amazonian várzea forests cover an area *c.* 100,000 km^2 (Junk, 1997), and are affected by periodic floods of sediment-loaded, nutrient-rich white-water rivers including the Solimões-Amazon, the Purus and Madeira Rivers (Prance, 1979). The water-level fluctuations result in an aquatic and a terrestrial phase during the year (Junk *et al.*, 1989). The average extent of flooding depends on precipitation, discharge and topography of the floodplains, and varies along the river course. Thus it can reach up to 16 m in western Amazonia, 10 m in central Amazonia, and 6 m in eastern Amazonia (Junk, 1989; Lamotte, 1990).

Amazonian floodplain forests normally contain fewer tree species than their non-flooded counterparts of the same region (Prance, 1979; Balslev *et al.*, 1987). This is because the duration and height of flooding influence the ecophysiology of trees, and result in the trees adapting to the periodically anoxic site conditions. A zonation of tree communities is thus created along the flood-level gradient, with trees exhibiting a variety of adaptations (Junk, 1989; Ayres, 1993; Cattanio *et al.*, 2002; Wittmann *et al.*, 2002, 2004). The different várzea forest types are characterized according to inundation height and length (highly flooded 'low restinga', 'chavascal' and 'bajeal'; low flooded 'high restinga': Lamotte, 1990; Ayres, 1993; Queiroz, 1995; Cattanio *et al.*, 2002). Wittmann *et al.* (2002) classified central Amazonian várzea forests as low várzea or high várzea. Low-várzea forests become established where the annual water column has an average height of > 3 m (inundation period > 50 days year^{-1}). Due to the high geomorphological variations and frequent habitat disturbance by sedimentation and erosion (Salo *et al.*, 1986; Kalliola *et al.*, 1991; Campbell *et al.*, 1992), low-várzea forests are characterized by a patchwork of microhabitats. Forest succession starts with species-poor stands on ridges, which experience frequent deposition, point bars and channel bars (Salo *et al.*, 1986; Kalliola *et al.*, 1991). In subsequent successional stages, trees reach maximum ages of between 200 and 400 years (Worbes *et al.*, 1992; Worbes, 1997), and species richness increases to a maximum of *c.* 90 species ha^{-1} (trees ≥ 10 cm diameter at breast height, d.b.h.; Nebel *et al.*, 2001; Wittmann *et al.*, 2002; Schöngart, 2003). An inventory based on remote sensing revealed that the different low-várzea forest types cover an area *c.* 85–90% of the forested area in the western Brazilian várzea (Wittmann *et al.*, 2002). Definitions of low-várzea successional stages are described by Worbes *et al.* (1992) and Schöngart (2003). Early successional colonization and interactions between succession and the geomorphological variation are described by Salo *et al.* (1986), Kalliola *et al.* (1991), Terborgh & Petren (1991), Campbell *et al.* (1992) and Wittmann *et al.* (2004). High-várzea forests become established where the annual water column averages less than 3 m in height (< 50 days year^{-1}), and consist of late successional forests that occupy the transitional zone between flooded and non-flooded sites (Ayres, 1993; Wittmann *et al.*, 2002). Frequency of geomorphological habitat disturbance is comparatively low, because these forests are normally located at a distance from the main river channels, where the river water energy is reduced when it reaches these more elevated sites (Wittmann *et al.*, 2004). In western Brazilian Amazonia, high-várzea forests cover an area *c.* 10–15% of the forested white-water floodplains (Wittmann *et al.*, 2002).

Most attempts to explain the geographical variation in floristic composition and tree species diversity within the Amazon are based on correlations between floristic parameters at different sites and on environmental variables, such as precipitation and soil fertility (Whitmore, 1975; Gentry, 1988; Leigh, 1999; Ter Steege *et al.*, 2000; Pitman *et al.*, 2002). Other studies use historical and evolutionary interpretations to explain variations in tree species composition, dividing Amazonia into phytogeographical provinces or regions (Mori, 1991; Prance, 1994; de Oliveira & Daly, 1999). In várzea forests, the application of correlations between environmental variables and patterns of floristic composition and diversity is difficult because the amount of precipitation in most parts of the Amazon Basin is not synonymous with the height and duration of annual inundations (Junk *et al.*, 1989), and because soil fertility is in general higher than in upland forests (Prance, 1979; Furch & Klinge, 1989). Moreover, processes in floodplain forest evolution differ from those on terra firme, even where interactions and species exchange between floodplains and the uplands have occurred since the beginning of the Andean orogeny (Kubitzki, 1989).

In recent efforts to determine patterns of tree species composition and diversity in Amazonian forests, much emphasis has been placed on the determination of diversity gradients across Amazonian terra firme (Condit *et al.*, 2000, 2002; Ter Steege *et al.*, 2000, 2003; Pitman *et al.*, 2001; Tuomisto *et al.*, 2003). There has been comparatively little emphasis on Amazonian floodplains. Previous studies on species distribution and diversity patterns in Amazonian várzea have mostly concentrated on central Amazonia (Junk, 1989; Worbes *et al.*, 1992; Ayres, 1993; Wittmann *et al.*, 2002). In this study, we examine tree species composition, richness and α diversity in várzea forests across the Amazon Basin. A survey of floristic inventories in the Amazonian várzea is presented. The number of tree species in the Amazonian várzea and the dependence of floristic and diversity patterns on flooding and stand age (stage of succession) are addressed. We also investigate how species composition, floristic similarity and species diversity change over geographical distance, and whether diversity gradients exist along the geographical locations of the inventoried forests.

METHODS

Sites studied and plot characteristics

The data used are from our inventories of 16 permanent plots established in the Mamirauá Sustainable Development Reserve, western Brazilian Amazon (11 plots, 9.25 ha: Queiroz, 1995; Wittmann *et al.*, 2002; Schöngart, 2003); near the city of Manaus, central Brazilian Amazon (two plots, 1.8 ha: Wittmann *et al.*, 2002); and in the northern Bolivian Amazon (three 1-ha plots: J.C.M., unpubl. data). In addition, 28 várzea forest inventories compiled by other authors and distributed across the Amazon Basin were used (Table 1).

Floristic analysis focuses on these 44 tree inventories, which cover a 62.34-ha area scattered over 10 regions along the Amazonian várzea river system (Table 1; Fig. 1). All plots sampled are subject to a monomodal, predictable inundation depending on the dry and rainy seasons in the catchment area (Junk *et al.*, 1989), and thus are comparable in terms of periodic waterlogging of the trees.

More than the half of all the plots are located in equatorial central Amazonia, and are distributed over three regions along the Solimões and Japurá Rivers (Fig. 1). Inventories from only one eastern Amazonian region with several forest inventories near the mouth of the Amazon (Guamá River) are available. Western Amazonia is comparatively well represented, with two inventoried regions in Peru (Ucayali and Manu Rivers), and one each in Brazil (Juruá River), Colombia (Caquetá River), Bolivia (Orthon, Madre de Diós and Tahuamanu Rivers) and Ecuador (Napo River) (Table 1; Fig. 1). Only inventories that met the following criteria were considered: (1) minimum inventoried area of 1 ha per region; (2) minimum d.b.h. of 5 cm for inventoried trees (although the majority of inventories used 10 cm); (3) information on the number of individuals and species in the plots available; and (4) identification of individual trees at species level.

Data analysis

All data from the plots were entered at family, genus and species levels, resulting in an overall species list. The species were carefully verified in the herbarium of the National Institute for Amazon Research, Manaus, and using databases of other herbaria (Missouri Botanical Garden; New York Botanical Garden; Royal Botanic Gardens, Kew). Morphospecies, unidentified species, synonymous species, and species not documented in these herbaria were excluded.

Some authors argue that information focusing on the species level in Neotropical forests is often imprecise and contains too much noise to produce interpretable results (Terborgh & Andresen, 1998; Ter Steege *et al.*, 2000). We focused on the species rather than the generic level because: (1) species richness in the várzea is expected to be lower than in terra firme forests, and many species occur in high abundance, and (2) most várzea species can be found in the herbaria mentioned above, mostly with good taxonomic descriptions.

To avoid unequal individual and species numbers per plot, owing to different plot sizes and tree diameters, the importance value index (IVI, Curtis & McIntosh, 1951) for each species in each plot was calculated. The IVI incorporates relative frequency, relative abundance and relative dominance (basal areas) of the trees, and species are therefore equally weighted. However, for five plots no information on the basal areas was available (Table 1). In these plots, relative species abundance was used and standardized to an area of 1 ha. Overall, the most important species were determined using the overall importance value (OIV), which represents the sum of relative IVI (rIVI) and the relative frequency (rF) ($n = 44$ plots).

Alpha-diversity was quantified with Fisher's α-diversity coefficient (Fisher *et al.*, 1943), using all individuals and species per plot, including distinguishable morphospecies. Fisher's α is relatively insensitive to sample size and performs well on tropical forest plot data (Leigh, 1995; Ter Steege *et al.*, 2000). Floristic similarity between plots was calculated using Sørensen's (1948) index (SI), but only with reference to the identified species. Thus similarity values must be considered as relative values. Similarity variations were determined by correlations between the plots (km) and Sørensen's coefficient.

To check for spatial diversity gradients, Fisher's α was correlated (Pearson) with stand age, plot location and flood-level gradient. The forests were classified as follows:

1. várzea successional stages (early, secondary and late) according to Worbes *et al.* (1992),
2. low-várzea forests (mean tree inundation height > 3 m; mean inundation period > 50 days year^{-1}) and high-várzea forests (mean tree inundation height < 3 m; mean inundation period < 50 days year^{-1}) according to Wittmann *et al.* (2002), and
3. forests located in the eastern Amazonia (region 1), central Amazonia (regions 2–4), equatorial western Amazonia (regions 5–8), and the southern part of western Amazonia (regions 9 and 10) (Fig. 1).

Information on stand ages and/or successional stages in most of the inventoried forests was incomplete, therefore stand-age analyses were restricted to 11 permanent plots in regions 2 and 4 (Fig. 1), where dendrochronological data for

Table 1 References and site characteristics of tree inventories in Amazonian várzea

Reference	Map point	Region	Country	River	Latitude/longitude	Forest type	Size (ha)	Minimum d.b.h. (cm)	No. of trees	Basal area ($m^2\ ha^{-1}$)	No. of species	Fisher's alpha
Black *et al.* (1950)	1	EA	Brazil	Guamá	01°20′ S/48°30′ W	LV	1	10	564	–	62	17.8
Pires & Koury (1959)	1	EA	Brazil	Guamá	01°20′ S/48°30′ W	LV	3.8	10	1837	–	107	24.8
Pires & Koury (1959)	1	EA	Brazil	Guamá	01°20′ S/48°30′ W	LV	1	5–8	539	–	53	14.6
Cattanio *et al.* (2002)	1	EA	Brazil	Guamá	01°20′ S/48°30′ W	LV	1	10	588	29.5	84	26.8
Cattanio *et al.* (2002)	1	EA	Brazil	Guamá	01°20′ S/48°30′ W	HV	0.2	5	238	30.3	67	31.0
Cattanio *et al.* (2002)	1	EA	Brazil	Guamá	01°20′ S/48°30′ W	LV	0.2	5	504	36.9	45	12.0
Wittmann *et al.* (2002)	2	CA	Brazil	Solimões	03°15′ S/59°58′ W	LV	1	10	466	47.8	35	8.8
Klinge *et al.* (1996)	2	CA	Brazil	Solimões	03°15′ S/59°58′ W	LV	0.9	5	980	45.0	43	9.2
Revilla (1991)	2	CA	Brazil	Solimões	03°15′ S/59°58′ W	LV	1	5	947	71.9	48	10.7
Worbes *et al.* (1992)	2	CA	Brazil	Solimões	03°15′ S/59°58′ W	LV	0.76	5	925	41.0	35	7.2
Worbes *et al.* (1992)	2	CA	Brazil	Solimões	03°15′ S/59°58′ W	LV	0.21	5	168	60.0	30	10.6
Wittmann *et al.* (2002)	2	CA	Brazil	Solimões	03°20′ S/60°00′ W	HV	0.8	10	380	31.0	68	24.2
Worbes *et al.* (1992)	2	CA	Brazil	Solimões	03°08′ S/59°40′ W	LV	0.4	10	224	45.0	41	14.7
Worbes *et al.* (1992)	2	CA	Brazil	Solimões	03°08′ S/59°45′ W	LV	0.4	10	298	17.0	27	7.21
Worbes *et al.* (1992)	3	CA	Brazil	Solimões	03°25′ S/60°46′ W	LV	1	5	627	33.0	89	28.3
Revilla (1991)	3	CA	Brazil	Solimões	03°23′ S/60°40′ W	LV	5	5	3650	33.0	129	26.1
Revilla (1991)	3	CA	Brazil	Solimões	03°25′ S/60°46′ W	LV	10	5	9010	41.3	187	33.4
Schöngart (2003)	4	CA	Brazil	Japurá	02°53′ S/64°53′ W	LV	0.05	10	62	13.8	5	1.3
Schöngart (2003)	4	CA	Brazil	Japurá	02°47′ S/65°04′ W	LV	0.2	10	107	52.2	37	20.0
Schöngart (2003)	4	CA	Brazil	Japurá	02°53′ S/64°53′ W	LV	1	10	838	30.5	30	6.1
Schöngart (2003)	4	CA	Brazil	Japurá	02°54′ S/64°53′ W	LV	1	10	487	50.5	45	12.1
Schöngart (2003)	4	CA	Brazil	Japurá	02°47′ S/65°04′ W	LV	1	10	504	26.9	87	30.3
Schöngart (2003)	4	CA	Brazil	Japurá	02°51′ S/64°55′ W	LV	1	10	462	27.3	111	46.4
Wittmann *et al.* (2002)	4	CA	Brazil	Japurá	02°51′ S/64°55′ W	LV	1	10	641	30.1	45	11.0
Wittmann *et al.* (2002)	4	CA	Brazil	Japurá	02°51′ S/64°55′ W	LV	1	10	434	37.7	91	35.1
Wittmann *et al.* (2002)	4	CA	Brazil	Japurá	02°51′ S/64°55′ W	HV	0.9	10	416	31.9	142	76.1
Queiroz (1995)	4	CA	Brazil	Japurá	02°58′ S/64°55′ W	LV	1	10	443	263.1	37	9.6
Queiroz (1995)	4	CA	Brazil	Japurá	02°58′ S/64°55′ W	LV	1	10	430	78.5	68	22.8
Ayres (1993)	4	CA	Brazil	Japurá	02°58′ S/64°55′ W	LV	1	10	460	32.6	109	45.1
Ayres (1993)	4	CA	Brazil	Japurá	02°58′ S/64°55′ W	HV	1	10	580	49.8	135	55.3
Urrego (1997)	5	WAe	Colombia	Caquetá	00°30′ S/71°30′ W	HV	1.7	10	684	–	301	80.9
Urrego (1997)	5	WAe	Colombia	Caquetá	00°30′ S/71°30′ W	LV	3	10	1074	–	104	16.7
Balslev *et al.* (1987)	6	WAe	Ecuador	Napo	00°32′ S/76°27′ W	HV	1	10	417	35.5	149	83.0
Nebel *et al.* (2001)	7	WAe	Peru	Ucayali	04°55′ S/73°44′ W	HV	3	10	1367	24.7	146	41.4
Nebel *et al.* (2001)	7	WAe	Peru	Ucayali	04°55′ S/73°44′ W	HV	3	10	1697	22.6	202	59.7
Nebel *et al.* (2001)	7	WAe	Peru	Ucayali	04°55′ S/73°44′ W	LV	3	10	1560	27.7	195	58.8
Campbell *et al.* (1992)	8	WAe	Brazil	Juruá	07°38′ S/72°40′ W	LV	1	10	777	25.7	20	3.8
Campbell *et al.* (1992)	8	WAe	Brazil	Juruá	07°38′ S/72°40′ W	HV	1	10	420	27.0	73	25.6
Campbell *et al.* (1992)	8	WAe	Brazil	Juruá	07°38′ S/72°40′ W	HV	1	10	523	25.5	106	40.1
Dallmeier *et al.* (1996)	9	WAs	Peru	Manu	11°45′ S/71°30′ W	HV	1	10	610	37.2	157	68.5
Dallmeier *et al.* (1996)	9	WAs	Peru	Manu	11°45′ S/71°30′ W	LV	1	10	688	30.0	73	20.7
J.C.M., unpubl. data	10	WAs	Bolivia	Madre de Diós	11°10′ S/67°20′ W	HV	1	10	649	45.0	92	27.0
J.C.M., unpubl. data	10	WAs	Bolivia	Orthon	11°02′ S/67°10′ W	HV	1	10	649	58.0	85	24.4
J.C.M., unpubl. data	10	WAs	Bolivia	Tahuamanu	11°07′ S/68°25′ W	HV	1	10	579	43.0	98	32.3

EA, eastern Amazonia; CA, central Amazonia; WA, western Amazonia; WAe, equatorial western Amazonia; WAs, southern part of western Amazonia; LV, low várzea; HV, high várzea.

the trees were available (Schöngart, 2003; F.W., unpubl. data), and to three plots in region 8 with known tree ages (Campbell *et al.*, 1992). Only 25 inventories yielded information on height and/or duration of the annual inundations of the plots. Most of these inventories, however, restricted this information to 'low-positioned' or 'high-positioned' sites, often using local estimates of the fluvial landscape as mentioned earlier. Correlations between α diversity and the location of trees along the flood-level gradient were therefore restricted to the categories of low várzea and high várzea. The application of more detailed multivariate ordinations and/or gradient analyses of tree species along the flood-level gradient were not

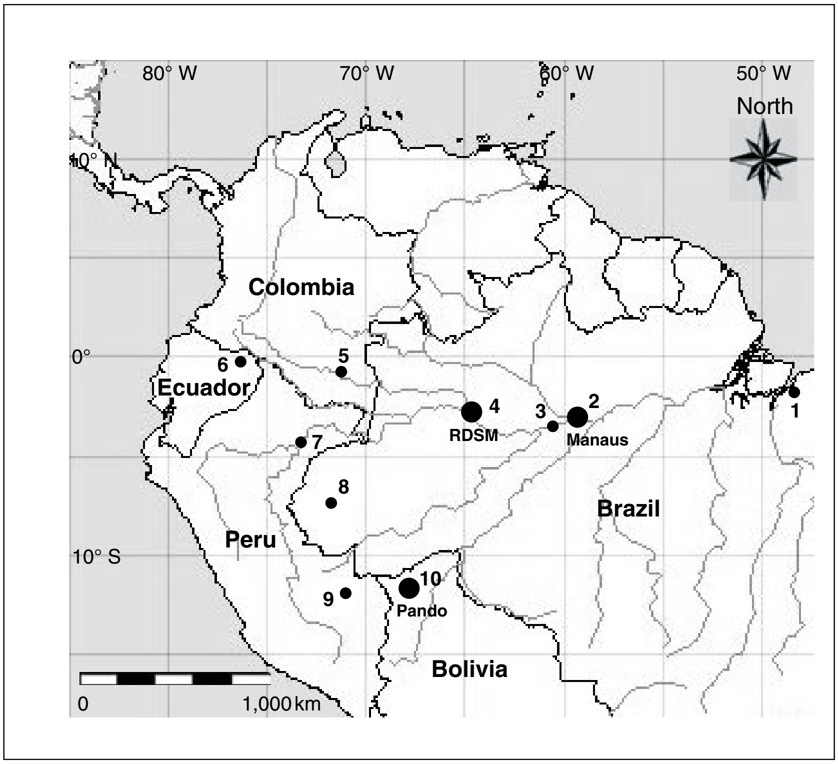

Figure 1 Selected tree inventories in the Amazonian várzea. Large circles represent our own study sites. 2, Solimões River near Manaus, Brazil; 4, Japurá River in the Mamirauá Sustainable Development Reserve, Brazil; 10, Orthon, Madre de Diós and Tahuamanu Rivers in Pando, Bolivia.

possible. Moreover, most of the inventories lack information about the geomorphological conditions of the plots, as well as the distance of plots to the main river channels. Thus, relationships between floristic patterns and fluviodynamics and/or the geomorphological situation of the plots could not be analysed in this study.

RESULTS

Floristic patterns at the family level

A total of 39,497 trees were registered, belonging to *c.* 1900 morphospecies. After the exclusion of all morphospecies, 918 identified species remained, belonging to 320 genera and 73 families. The 16 most important families totalled *c.* 77% (IVI) of all listed individuals. The most important family overall was the Leguminosae, which totalled *c.* 11.2% of all individuals, followed by Euphorbiaceae (7.7%), Bombacaceae (7.5%), Moraceae (7.5%) and Arecaceae (7.4%).

Distribution among the 16 most important families differed significantly between low-várzea and high-várzea forests. Leguminosae and Euphorbiaceae were important families in both forest types, whereas Bombacaceae, Flacourtiaceae, Cecropiaceae, Capparaceae and Lauraceae showed a distinctly higher importance in the low várzea. Arecaceae, Moraceae, Annonaceae and Meliaceae were more important in the high várzea (Table 2).

The floristic composition at the family level also differed along the geographical gradients. The Leguminosae and Euphorbiaceae were important in all regions, but their

Table 2 Family distribution of the 16 most important families along vertical and geographical gradients

		Vertical distribution		Longitudinal distribution			Latitudinal distribution in WA	
	Family	LV	HV	EA	CA	WA	WAe	WAs
1	Arecaceae	5.1	12.3	5.6	0.7	11.4	9.4	14.5
2	Leguminosae	12.5	8.4	7.6	12.2	8.8	10.1	6.9
3	Moraceae	5.7	11.4	5.7	5.5	11.8	9.4	15.3
4	Euphorbiaceae	7.3	8.5	4.4	8.4	7.3	8.5	5.6
5	Bombacaceae	9.0	4.3	25.3	10.9	2.8	2.3	3.6
6	Flacourtiaceae	6.7	2.0	11.9	6.6	4.1	3.5	5.1
7	Cecropiaceae	5.2	2.5	4.6	5.7	3.2	4.7	1.0
8	Meliaceae	1.4	5.1	1.0	0.5	5.0	3.7	7.0
9	Sapotaceae	3.0	4.0	1.6	3.1	3.7	3.2	4.4
10	Annonaceae	3.0	5.5	1.4	4.0	4.2	4.7	3.5
11	Lecythidaceae	3.1	2.0	2.9	2.3	3.5	5.4	0.5
12	Rubiaceae	1.7	2.3	1.6	1.8	2.4	2.9	1.5
13	Myristicaceae	0.9	4.8	1.7	1.1	3.8	4.6	2.6
14	Sterculiaceae	0.6	2.5	3.1	0.1	2.1	0.9	4.0
15	Lauraceae	3.9	1.2	2.2	4.7	1.2	1.6	0.5
16	Capparaceae	5.1	0.2	4.0	6.2	0.1	0.1	0.1
$\sum$17–73		25.8	23.0	15.4	26.2	24.6	25.0	23.9

Numbers represent percentages of total importance values (TIV, Curtis & McIntosh, 1951). LV, low várzea; HV, high várzea; EA, eastern Amazonia; CA, central Amazonia; WA, western Amazonia; WAe, equatorial western Amazonia; WAs, southern part of western Amazonia.

importance was highest in central Amazonia. The importance of Bombacaceae and Flacourtiaceae decreased from east to west, whereas the importance of Sapotaceae, Annonaceae, and Rubiaceae showed an opposite trend. The Arecaceae were most frequent in western Amazonia and, to a lesser extent, in eastern Amazonia, but were nearly absent in central Amazonia (Table 2). The variation in family importance between equatorial western Amazonia and the southern part of western Amazonia was comparatively low. Leguminosae, Euphorbiaceae, Cecropiaceae and Lecythidaceae were more important in equatorial, western Amazonia than in the southern part of western Amazonia, whereas Arecaceae, Moraceae, Flacourtiaceae and Meliaceae were more important in the southern part of western Amazonia (Table 2).

Floristic patterns at the species level

Tree species distribution and richness differed significantly between the low-várzea and high-várzea forests. Out of all the listed species, 232 (25.3%) occurred exclusively in the low várzea ($n = 30$ plots, 44.94 ha); 297 (32.3%) in the high várzea ($n = 14$ plots, 17.4 ha); and 389 (42.4%) in both habitats. Accordingly, species richness of trees ≥ 10 cm d.b.h. averaged 56.9 species ha^{-1} in the low-várzea forests ($n = 21$ plots, 24.87 ha), with 100.8 species ha^{-1} in the high-várzea forests ($n = 13$ plots, 17.2 ha).

The 30 most important low-várzea species accounted for 42.3% of overall importance (OIV, Table 3a). The most important species was *Pseudobombax munguba* (Mart. & Zucc.) Dugand, followed by *Laetia corymbulosa* Spruce ex. Benth. and *Crataeva benthamii* Eichler. In the high-várzea forests, the 30 most important species accounted for 24.9% of the OIV [especially *Brosimum lactescens* (S. Moore) C. C. Berg, *Theobroma cacao* L. and *Hura crepitans* L.]. The most important species occurring in both forest types were *Pseudobombax munguba*, *Euterpe oleracea* Mart. and *Astrocaryum chonta* Mart.

The overall floristic similarity (SI; Sørensen, 1948) between the low-várzea inventories averaged 33.2 ± 23.6%, with the highest between the early and secondary stages and between adjacent plots (max. SI, 70%). In the high-várzea inventories, the SI averaged 12.4 ± 6.2%, and exceeded 30% only in one analysis in two neighbouring plots. In both forest types, floristic similarity decreased linearly with increasing distance between plots. Nevertheless, floristic similarity between low-várzea forest plots > 1,000 km apart still averaged *c.* 20%, and exceeded 40% in several cases (Fig. 2a). In high-várzea forests, floristic similarity between plots > 1,000 km apart averaged *c.* 10%, and exceeded 20% in only one analysis (Fig. 2b).

The SI between eastern Amazonia and the western regions was *c.* 20%. The SI increased to *c.* 32% between central Amazonia and equatorial western Amazonia; to *c.* 31% between central Amazonia and the southern part of western Amazonia; and reached the highest percentage between the western Amazonian regions (*c.* 36%). The 30 most important species in this study (OIV, low-várzea + high-várzea forests) accounted for 30.4 and 46.0% of all species recorded in eastern and central Amazonia, respectively, but only for 13.5% in equatorial western Amazonia and 20.0% in the southern part of western Amazonia (Table 4). This indicated that the floristic composition in western Amazonian várzea is distinctly different from that in the eastern regions. Species richness (≥ 10 cm d.b.h.) of low-várzea forests was lowest in eastern Amazonia and highest in the southern part of western Amazonia (Fig. 3). The species richness of high-várzea forests was highest in central Amazonia. For eastern Amazonia, no comparable data were available.

Diversity gradients

Alpha-diversity (Fisher) of the plots ranged from 1.3 (early successional forests, low várzea) to 83.0 (late successional forest, high várzea) (Table 1). Within the plots with available dendrochronological data, α diversity was strongly correlated to stand age (Fig. 4a), indicating that tree species diversity increased continuously with proceeding forest succession. Fisher's coefficient was simultaneously correlated with the mean height of inundation (Fig. 4b). In low-várzea and high-várzea forests, Fisher's alpha averaged 19.7 ± 13.7 and 47.8 ± 22.2, respectively.

Alpha-diversity and the longitudinal location of plots were significantly correlated, indicating a trend of increasing diversity from east to west. This trend was especially pronounced in the high-várzea forests, and to a lesser extent in the low-várzea forests (Fig. 5a,b). Within western Amazonian várzea forests, α diversity decreased from equatorial western Amazonia to the southern part of western Amazonia. Again, this trend was more pronounced within the high-várzea forests ($n = 10$, $R^2 = 0.4898$, $P < 0.001$) than in the low-várzea forests ($n = 4$, $R^2 = 0.0223$, $P < 0.05$).

DISCUSSION

Comparison of várzea forests with other floodplains and the uplands

The 918 tree species registered in our study belong to 73 families, which correspond to about 52% of all Neotropical plant families containing tree species (Maas & Westra, 1993; Ter Steege *et al.*, 2000). The most important families recorded in the várzea, including Leguminosae in eastern Amazonia and Arecaceae, Moraceae and Myristicaceae in western Amazonia, also dominate most Neotropical upland forests (Gentry, 1988, 1992; Terborgh & Andresen, 1998; Ter Steege *et al.*, 2000). Bombacaceae, Flacourtiaceae and Capparaceae, however, are especially important families in the low-várzea forests of the eastern and central Amazon. Comparison of our species list with those of terra firme inventories scattered over the Amazon Basin (de Oliveira & Mori, 1999; Ribeiro *et al.*, 1999; Pitman *et al.*, 2001; Duque *et al.*, 2002; Rudas *et al.*, 2002; de Oliveira & do Amaral, 2004; Peñaherrera & Asanza, 2004) shows that 286 (31%) of the tree species listed in the várzea also occur in upland forests. From these species, 193 (67.5%) were restricted to the high várzea.

Table 3 Overall importance of the 30 most important species in (a) low várzea and (b) high várzea

	Family	Species	rIVI	rF	OIV
(a) Low várzea					
1	Bombacaceae	*Pseudobombax munguba* (Mart. & Zucc.) Dugand	8.48	1.47	9.95
2	Flacourtiaceae	*Laetia corymbulosa* Spruce ex Benth.	5.33	1.18	6.51
3	Capparaceae	*Crataeva benthamii* Eichler	5.13	0.97	6.10
4	Cecropiaceae	*Cecropia latiloba* Miq.	4.51	1.19	5.70
5	Leguminosae	*Pterocarpus amazonum* (Mart. ex Benth.) Amshoff	3.23	1.26	4.49
6	Verbenaceae	*Vitex cymosa* Bert. ex Spreng.	3.76	0.56	4.32
7	Lauraceae	*Nectandra amazonum* Nees	3.11	1.05	4.16
8	Euphorbiaceae	*Piranhea trifoliata* Baill.	2.73	0.98	3.71
9	Tiliaceae	*Luehea cymulosa* Spruce ex Benth.	2.90	0.70	3.60
10	Arecaceae	*Euterpe oleracea* Mart.	2.67	0.56	3.23
11	Moraceae	*Ficus trigona* L. f.	2.40	0.42	2.82
12	Polygonaceae	*Triplaris surinamensis* Cham.	1.46	0.70	2.16
13	Bignoniaceae	*Tabebuia barbata* (E. Mey.) Sandwith	1.16	0.98	2.14
14	Leguminosae	*Macrolobium acaciifolium* (Benth.) Benth.	1.16	0.91	2.07
15	Aquifoliaceae	*Ilex inundata* Poepp. ex Reissek	1.67	0.29	1.96
16	Lecythidaceae	*Eschweilera albiflora* (DC.) Miers	1.37	0.56	1.93
17	Leguminosae	*Vatairea guianensis* Aubl.	1.13	0.77	1.90
18	Moraceae	*Maclura tinctoria* (L.) D. Don ex Steud.	1.20	0.63	1.83
19	Arecaceae	*Astrocaryum chonta* Mart.	1.18	0.42	1.60
20	Euphorbiaceae	*Mabea nitida* Spruce ex Benth.	0.96	0.56	1.52
21	Sapotaceae	*Pouteria elegans* (DC.) Baehni	1.02	0.42	1.44
22	Euphorbiaceae	*Hevea spruceana* (Benth.) Müll. Arg.	0.98	0.42	1.40
23	Rubiaceae	*Duroia duckei* Huber	0.83	0.56	1.39
24	Bignoniaceae	*Crescentia amazonica* Ducke	0.96	0.42	1.38
25	Lecythidaceae	*Eschweilera parvifolia* Mart. ex DC.	0.90	0.42	1.32
26	Lecythidaceae	*Gustavia augusta* L.	0.40	0.91	1.31
27	Myrtaceae	*Calyptranthes crebra* Mc Vaugh	0.85	0.35	1.20
28	Clusiaceae	*Calophyllum brasiliense* Cambess	0.63	0.56	1.19
29	Flacourtiaceae	*Casearia aculeata* Jacq.	0.61	0.56	1.17
30	Myristicaceae	*Virola surinamensis* (Rol. ex Rottb.) Warb.	0.48	0.63	1.11
$\sum$			63.20	21.41	84.61
$\sum$31–617			36.80	78.59	115.39
Total			100	100	200
(b) High várzea					
1	Moraceae	*Brosimum lactescens* (S. Moore) C.C. Berg	2.56	0.80	3.36
2	Sterculiaceae	*Theobroma cacao* L.	1.83	0.65	2.48
3	Euphorbiaceae	*Hura crepitans* L.	1.65	0.58	2.23
4	Meliaceae	*Trichilia septentrionalis* C. DC.	1.82	0.29	2.11
5	Anacardiaceae	*Spondias lutea* L.	1.59	0.51	2.10
6	Moraceae	*Maquira coriacea* (H. Karst.) C.C. Berg	1.53	0.51	2.04
7	Arecaceae	*Astrocaryum chonta* Mart.	1.64	0.36	2.00
8	Boraginaceae	*Cordia nodosa* Lam.	1.20	0.73	1.93
9	Arecaceae	*Iriartea deltoidea* Ruiz & Pav.	1.46	0.44	1.90
10	Euphorbiaceae	*Drypetes amazonica* Steyerm.	1.49	0.36	1.85
11	Arecaceae	*Euterpe oleracea* Mart.	1.04	0.65	1.69
12	Euphorbiaceae	*Alchornea triplinervia* (Spreng.) Müll. Arg.	1.49	0.15	1.64
13	Bombacaceae	*Ceiba samauma* (Mart.) K. Schum.	1.24	0.36	1.60
14	Dichapetalaceae	*Tapura acreana* (Ule) Rizzini	1.36	0.22	1.58
15	Myristicaceae	*Otoba parvifolia* (Markgr.) A.H. Gentry	1.40	0.15	1.55
16	Meliaceae	*Guarea macrophylla* Vahl	1.07	0.44	1.51
17	Rubiaceae	*Calycophyllum spruceanum* (Benth.) Hook.	1.06	0.44	1.50
18	Arecaceae	*Attalea phalerata* Mart. ex Spreng.	1.23	0.22	1.45
19	Moraceae	*Ficus maxima* Mill.	1.00	0.44	1.44
20	Euphorbiaceae	*Sapium marmieri* Huber	0.79	0.65	1.44
21	Arecaceae	*Astrocaryum jauari* Mart.	0.98	0.44	1.42
22	Annonaceae	*Unonopsis floribunda* Diels	0.73	0.58	1.31

Table 3 *continued.*

	Family	Species	rIVI	rF	OIV
23	Arecaceae	*Scheelea brachyclada* Burret	1.23	0.07	1.30
24	Polygonaceae	*Coccoloba densifrons* C. Mart. ex Meisn.	0.79	0.51	1.30
25	Bombacaceae	*Ceiba pentandra* (L.) Gaertn.	0.81	0.44	1.25
26	Myristicaceae	*Virola calophylla* (Spruce) Warb.	0.72	0.51	1.22
27	Violaceae	*Leonia glycycarpa* Ruiz & Pav.	0.64	0.58	1.22
28	Myristicaceae	*Virola cuspidata* (Spruce ex Benth.) Warb.	0.60	0.58	1.18
29	Myristicaceae	*Virola surinamensis* (Rol. ex Rottb.) Warb.	0.81	0.36	1.17
30	Moraceae	*Pseudolmedia laevis* (Ruiz & Pav.) J. F. Macbr.	0.73	0.44	1.17
$\sum$			36.49	13.46	49.94
$\sum$31–686			63.51	86.54	150.06
Total			100	100	200

rIVI, relative importance value index (Curtis & McIntosh, 1951); rF, relative frequency (a, $n = 34$ plots; b, $n = 18$ plots); OIV, overall importance value (see text).

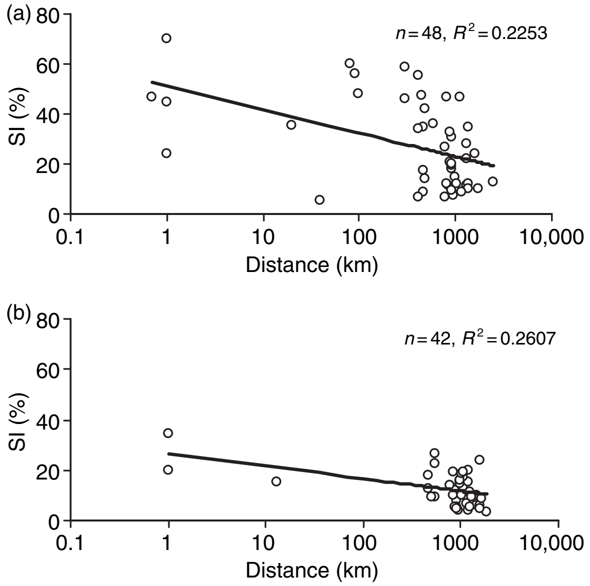

Figure 2 Floristic similarity (SI = Sørensen's Index) between low-várzea forests (a) and high-várzea forests (b) over geographical distance.

Species richness in equatorial Amazonian upland forests ranges from 117 to 120 species ha^{-1} in eastern Amazonia; from 179 to 285 species ha^{-1} in central Amazonia (summarized by de Oliveira & Nelson, 2001; see also Ter Steege *et al.*, 2003); and up to 300 species ha^{-1} in western Amazonia (Gentry, 1987; see also Ter Steege *et al.*, 2003). Species richness in high-várzea forests is comparatively low: maximally 84 species ha^{-1} in eastern Amazonia (Cattanio *et al.*, 2002); 142 species ha^{-1} in central Amazonia (Wittmann *et al.*, 2002); 157 species ha^{-1} in the southern part of western Amazonia (Dallmeier *et al.*, 1996); and 149 species ha^{-1} in equatorial western Amazonia (Balslev *et al.*, 1987). However, the results of this study indicate that Amazonian várzea forests are the most species-rich floodplain forests worldwide. With more than 900 identified flood-tolerant tree species, species richness is at least 20 times higher than in the floodplains of the European temperate zone (Schnitzler *et al.*, 2005), and *c.* 10 times higher than in subtropical bottomland forests of North America (Johnson & Little, 1967; Clark & Benforado, 1981; Schnitzler *et al.*, 2005). In comparison with tropical floodplains, species richness in the Amazonian várzea is *c.* 10 times higher than in forests of Cambodia (Tonle Sap: Campbell *et al.*, in press), and *c.* three times higher than in the Brazilian Pantanal (Junk *et al.*, in press). Furthermore, Amazonian floodplains also consist of black-water inundation forests (igapó *sensu* Prance, 1979), which are characterized by a species composition distinctly different from that of the várzea (Prance, 1979; Worbes, 1997; Ferreira, 2000).

The comparatively high tree species richness in várzea forests is the result of the coexistence of species well adapted to flooding together with generalist species that also occur in the uplands. Some of these generalists (e.g. *Pseudobombax munguba*, *Leonia glycycarpa* Ruiz & Pav. and *Duroia duckei* Huber) are distributed widely throughout the Neotropics, and occur particularly in semi-deciduous forests and savannas (Prance, 1979). Junk (1989) and Worbes (1997) assume that these species are not primarily adapted to flooding, but are generally tolerant of seasonal poor-growth conditions. Thus this study confirms that Amazonian várzea forests reflect the high diversity generally characterizing the Neotropics.

Floristic patterns along the flood-level gradient and interactions with landscape dynamics and forest succession

The results of this study confirm that the height and the duration of the annual inundations appear to be the most important factor in explaining tree species distribution, richness and α diversity in várzea forests. Low-várzea forests are less diverse than high-várzea forests, as a result of higher and more prolonged inundations that require special adaptations

Table 4 Distribution of important tree species in the classified regions of the Amazon Basin

	Overall importance				
Region	EA	CA	WAe	WAs	∑
Species number	158	295	556	219	918
Euterpe oleracea Mart.	26.12	–	1.65	2.82	30.95
Astrocaryum chonta Mart.	12.93	0.13	1.59	2.78	17.43
Pseudobombax munguba (Mart. & Zucc.) Dugand	2.35	12.73	0.34	–	15.42
Laetia corymbulosa Spruce ex Benth.	–	7.23	0.12	5.23	12.58
Brosimum lactescens (S. Moore) C.C. Berg	0.75	0.25	1.4	6.98	9.38
Cecropia latiloba Miq.	–	6.61	2.32	0.41	9.34
Theobroma cacao L.	3.40	0.12	0.9	4.91	9.33
Spondias lutea L.	4.90	0.90	0.96	1.80	8.56
Hura crepitans L.	3.30	0.87	0.68	3.34	8.19
Pterocarpus amazonum (Mart. ex Benth.) Amshoff	1.11	5.46	0.63	0.83	8.03
Crataeva benthamii Eichler	–	7.94	0.09	–	8.03
Luehea cymulosa Spruce ex Benth.	–	3.93	0.61	2.50	7.04
Vitex cymosa Bert. ex Spreng.	–	5.46	–	0.83	6.29
Virola surinamensis (Rol. ex Rottb.) Warb.	2.95	0.63	1.94	0.38	5.90
Calophyllum brasiliense Cambess	0.34	0.65	0.30	4.33	5.62
Triplaris surinamensis Cham.	–	2.53	2.00	1.00	5.53
Nectandra amazonum Nees	–	5.49	–	–	5.49
Piranhea trifoliata Baill.	–	5.30	–	–	5.30
Macrolobium acaciifolium (Benth.) Benth.	1.30	2.82	0.41	0.38	4.91
Eschweilera albiflora (DC.) Miers	–	1.44	3.24	–	4.68
Maclura tinctoria (L.) D. Don ex Steud.	–	1.81	1.86	0.98	4.65
Ficus trigona L. f.	0.63	3.04	0.09	0.56	4.32
Tabebuia barbata (E. Mey) Sandwith	–	3.20	0.39	–	3.59
Vatairea guianensis Aubl.	0.73	1.97	0.69	–	3.39
Eschweilera parvifolia Mart. ex DC.	–	1.27	2.18	–	3.45
Astrocaryum jauari Mart.	–	1.42	1.59	–	3.01
Ilex inundata Poepp. Ex Reissek	–	2.48	–	–	2.48
Mabea nitida Spruce ex Benth.	–	1.94	0.51	–	2.45
Pouteria elegans (A. DC.) Baehni	–	2.18	–	–	2.18
Hevea spruceana (Benth.) Müll. Arg.	–	2.16	–	–	2.16
∑	60.81	91.96	26.49	40.06	219.32
OI of other species	139.19	108.04	173.51	159.94	580.68
Total	200	200	200	200	800

Numbers represent overall importance values (see text). EA, eastern Amazonia; CA, central Amazonia; WAe, equatorial western Amazonia; WAs, southern part of western Amazonia.

of trees to the periodic anoxic conditions. The most important adaptive mechanism is a reduced metabolism during the aquatic phase, which often triggers tree phenology and leads to periodic reduced wood increment in many floodplain trees, resulting in the formation of annual growth rings in the wood (Worbes, 1989, 1997; Schöngart *et al.*, 2002; Schöngart, 2003). Other adaptations are reduced chlorophyll content in leaves and consequently reduced photosynthetic activity during flooding (Waldhoff *et al.*, 1998; Piedade *et al.*, 2000); the ability to maintain green leaves below the water surface (Waldhoff *et al.*, 1998); the formation of adventitious roots and lenticels (Kozlowski, 1984); a high potential for sexual and vegetative reproduction (Puhakka & Kalliola, 1993; Worbes, 1997); and hydrochoric or ichthyochoric seed dispersal (Goulding, 1983; Pires & Prance, 1985).

In addition to the limiting factor of the annual inundations, the fluviodynamic geomorphology and related, small-scale changes in soil texture are crucial factors influencing species richness and diversity in várzea forests (Salo *et al.*, 1986; Lamotte, 1990; Kalliola *et al.*, 1991; Campbell *et al.*, 1992; Wittmann *et al.*, 2004). Species composition in floodplains varies widely, depending on the frequency of river disturbance (Oliveira-Filho *et al.*, 1994). The periodic deposition and removal of litter and thus seed banks affects seed and seedling recruitment, and therefore the selection of species able to survive in these areas (Metzger *et al.*, 1997). In highly inundated low várzea, the evolution of the fluvial landscape, which is characterized by sedimentation and erosion, determines the comparatively low tree species richness, especially next to the highly dynamic riverbanks (Kalliola *et al.*, 1991;

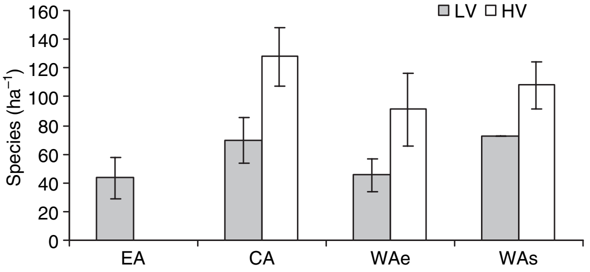

Figure 3 Species richness (trees ≥ 10 cm d.b.h.) of low-várzea (LV) and high-várzea (HV) forests in classified regions of the Amazon Basin. Error bars, SD. No data were available for high-várzea forests in eastern Amazonia. In the southern part of western Amazonia, only one low-várzea inventory was available. EA = eastern Amazonia; CA = central Amazonia; WAe = equatorial western Amazonia; WAs = southern part of western Amazonia. Data derive from sites of variable area (Table 1), which may influence the estimates of species richness per hectare due to nonlinearity of species-accumulation curves.

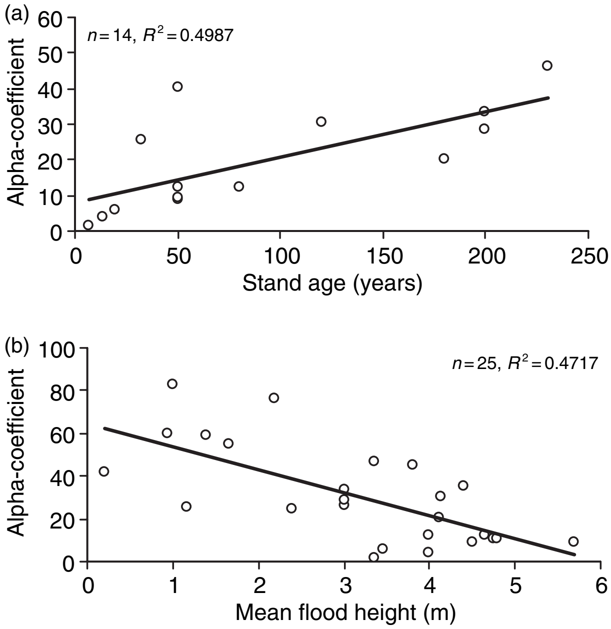

Figure 4 Fisher's α-diversity coefficient (Fisher *et al.*, 1943) plotted against stand age (a) and mean flood height (b) of forest plots.

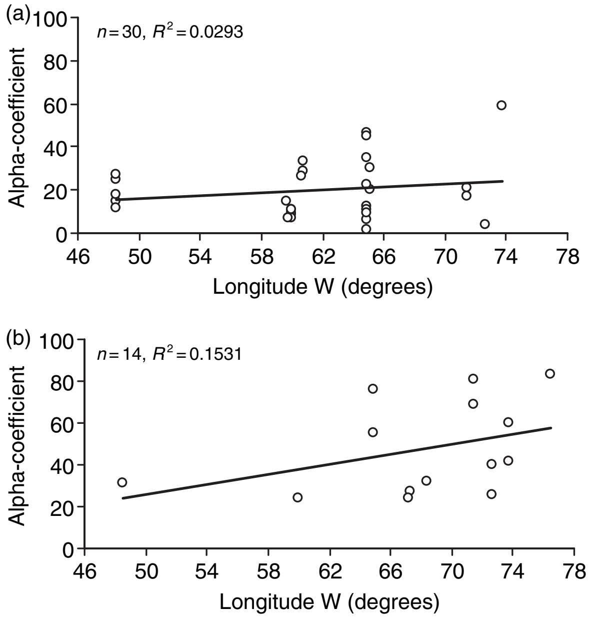

Figure 5 Fisher's α-diversity coefficient (Fisher *et al.*, 1943) plotted against longitudinal location of plots in low várzea (a) and high várzea (b).

Terborgh & Petren, 1991). Tree pioneers colonizing these sites, such as *Salix martiana* Leyb., *Alchornea castaneifolia* (Humb. & Bonpl. ex Willd.) A. Juss. and *Tessaria integrifolia* Ruiz & Pav. often form monospecific stands (Kalliola *et al.*, 1991; Worbes *et al.*, 1992; Parolin *et al.*, 2002). They normally develop deep primary roots, which offer good mechanical support against the relatively high water velocity during the aquatic phases. Moreover, these species form a new secondary root layer every year, which develops above the sediment freshly deposited during the aquatic phases (Kalliola *et al.*, 1991; Wittmann & Parolin, 2005). In ancient, silted-up river meanders, swales and floodplain lakes, which are generally found at a distance from the main river channels, trees of the 'chavascal' or 'bajeal' establish on fine-grained soils that are poorly drained. Tree species richness in these depressions is low, because the colonizing trees must tolerate extreme anoxic conditions at the root level, which persist for most of the year (Wittmann *et al.*, 2004; Wittmann & Parolin, 2005).

In várzea forests, increasing species diversity correlated with the decreasing impact of flooding and the decreasing dynamics of geomorphology has been described by several authors (Junk, 1989; Lamotte, 1990; Campbell *et al.*, 1992; Ayres, 1993; Puhakka & Kalliola, 1993; Cattanio *et al.*, 2002; Parolin *et al.*, 2002; Wittmann *et al.*, 2002, 2004). Forest succession and the changing environmental conditions along the vertical gradient are strongly interlinked. Forest succession starts with the presence of light-demanding, species-poor pioneer stands in the areas with the highest flood levels. With high stand densities, pioneer species favour the deposition of sediment, which leads to more elevated stands in subsequent successional stages. Species of late successional stages develop dense crowns, which result in reduced solar radiation intensity on the forest floor (Wittmann & Junk, 2003). Pioneer regeneration is impeded, and competition for light results in high-várzea late successional forests.

Depending on the position along the flood-level gradient, the mean inundation period in high-várzea forests sometimes barely reaches more than 2 months year^{-1}, and may fail completely during exceptionally dry years (e.g. during El Niño events: Schöngart *et al.*, 2004). The decreasing impact of flooding leads to comparatively high species richness in high-várzea forests. Gap regeneration might also increase species richness in the high várzea to a greater extent than in the low várzea, because mortality of late-succession canopy trees with partially extensive crowns creates a mosaic of light-regeneration niches (Wittmann & Junk, 2003).

Kubitzki (1989) stated that many várzea tree species can be considered as ecotypes originating from the surrounding terra firme. Occasional low inundations might be of crucial importance for the establishment of terra firme species in the várzea (Wittmann & Junk, 2003). The immigration of tree species not primarily adapted to flooding from the uplands to the high várzea increases species richness exponentially (Wittmann *et al.*, 2002). In this study, the comparatively high floristic similarity found between the high-várzea forests and the terra firme confirms this floristic relationship at the transitional zone between Amazonian flooded and non-flooded ecosystems.

Diversity patterns along geographical gradients

Tree species diversity in várzea forests increased from eastern to western Amazonia. This trend was especially pronounced in high-várzea forests, but was also documented for equatorial Amazonian terra firme, where α diversity appears to be linked to tree density and rainfall seasonality (Ter Steege *et al.*, 2003). In an investigation of floristic composition patterns in 48 forest plots across the Neotropics, Terborgh & Andresen (1998) have concluded that geographical position is the most important driver of floristic dissimilarity in alluvial floodplain forests. The authors found that the mean dissimilarity between terra firme and flooded forests, within each region, was barely larger than the mean dissimilarity in pairwise cross-comparisons between the two forest types within regions. Thus tree communities of inundated forests tend to resemble those of terra firme forests within the same geographical region more closely than those of inundation forests in adjacent regions. We generally agree with these conclusions from comparisons of high-várzea and terra firme forests of the same region, which strengthen the hypothesis that the high várzea acts as a transitional zone for tree immigration from the uplands to the floodplains, and which therefore also explains the east-to-west increase in α diversity. The high floristic resemblance between high-várzea and terra firme forests is especially pronounced in western Amazonia, because of the more accentuated topography compared with the relief of floodplains further east. Inundations in western Amazonia are higher, but are shorter than those in central and eastern Amazonia (Terborgh & Andresen, 1998). Therefore trees without specific adaptations to flooding might establish more easily in western Amazonian várzea.

Our data do not support the finding of Terborgh & Andresen (1998) with respect to floristic differences in remote low-várzea forests. We found that species composition in the low várzea differed significantly from that of upland forests, and that low-várzea forests greatly resemble each other, even if separated by large distances. Godoy *et al.* (1999) mentioned that the Amazon and the Orinoco basins show marked similarities in both habitats and tree species, which they interpreted as the result of the high connectivity between the riparian corridors of both basins and the effective operation of dispersal mechanisms. Long-distance dispersal by currents and fish is especially common for many low-várzea trees (Gottsberger, 1978; Goulding, 1983; Pires & Prance, 1985; Ziburski, 1991; Kubitzki & Ziburski, 1994; Lopez, 2001; Scarano *et al.*, 2003), and thus contributes to randomly distributed tree species that dominate several thousand km^2 in Amazonian low várzea. Despite the small-scale heterogeneity of the alluvial landscape, the high connectivity of the riparian corridors leads to similar vertically arranged ecological niches across remote várzea forests, and consequently to a restricted number of highly dominant tree species in low-várzea forests across the Amazon Basin.

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