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The várzea forests in Amazonia: flooding and the highly dynamic geomorphology interact with natural forest succession

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Abstract

Although flooding and the highly dynamic geomorphology influence ecophysiology of trees in Amazonian white-water forests (várzea), information about the extent of these environmental conditions on distribution and richness of tree species is scarce. To better understand dynamic of natural forest succession and the development of different várzea forest types, we inventoried structure and floristic composition of trees ≥ 10 cm DBH in a total area of 5.24 ha in várzea forests near Tefé and near Manaus, Brazilian Amazon. The forests were of different successional stages and situated on different sites along the flood-level gradient. Topography and average inundation of all inventoried trees was measured with a theodolite. Sedimentation was recorded during the aquatic phase 2000 and the soil texture in each site determined.

The low-várzea forests were composed of different successional stages subjected to annual floods between 7 and 3 m. Stand density per hectare averaged 490 individuals in the early successional stage, up to 1000 individuals in the early secondary stage and 434 individuals in the late successional stage, species richness amounted to 4, 45 and 91 tree species, respectively. The high-várzea forests were late successional stages subjected to annual inundations above 3 m. Stand density per hectare averaged 407 individuals and species richness amounted to 68 species in a frequently exploited forest near Manaus and to 172 species in a undisturbed forest near Tefé.

Species richness and distribution along the gradients of flooding and sedimentation was well defined. Only 2.6% of 222 recorded tree species occurred over the whole flood-level gradient. Sedimentation was highest in the early successional stages near the slip-off slopes of the main-river channels, and decreased with increasing topographic level of the forested sites and proceeding succession, reaching lowest rates in the high-várzea forests. Simultaneously, soil texture changed from coarse-grained soils in early stages to fine-grained soils in subsequent stages. Thus, natural succession in várzea forests is linked to the biogenical induced silting up of the sites, because dunes and large stems building trees slow down water energy and favour the deposition of fine grained sediment. A special vegetation unit within the low várzea is the 'chavascal', a species-poor swamp forest, which establishes in the marginal zone of lakes or in ancient silted up river arms. Since it is located off the direct influence of the main-river channels, it seems to be characterised by longstanding stable environmental conditions, and therefore cannot rank with the successional sequence near the highly dynamic river systems.

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Keywords: Várzea; Succession; Sedimentation; Soil texture; Species richness; Species equitability

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1. Introduction

Amazonian várzea forests cover an area of about 60000–100 000 km² (Goulding, 1996; Junk, 1997). They are influenced by periodic floods of sediment loaded, nutrient-rich white-water rivers (Prance, 1979), such as the Solimões, the Madeira and the Japurá Rivers. The annual water-level fluctuations result in the existence of an aquatic and a terrestrial phase during the year (Junk et al., 1989). In central Amazonia, average amplitude of flooding is about 10 m, corresponding to a submersion of trees of up to 230 days per year (Junk, 1989).

Due to its high nutrient status, the várzea is one of the most influenced ecosystems by human activities in Amazonia (Junk, 2000; Ohly, 2000). Forests are cleared to enable the agricultural use of the várzea soils, particularly in a large scale near the centres of human concentration. However, the forests are the habitat of several endemic plant and animal species and many trees offer food resources for fish and other organisms. Furthermore, the forests are rich in fibre and timber products extracted by the local population (Klenke and Ohly, 1993; Parolin, 2000). Therefore, the preservation of várzea forests by the introduction of sustainable management plans is strongly recommended (Ayres et al., 1999; Junk, 2000; Worbes et al., 2001; Wittmann and Junk, 2003).

A sustainable management of várzea forest resources needs information about floristic composition and structure of the different forest types, including the detailed knowledge about the environmental site conditions influencing richness and distribution of tree species. Amazonian floodplain forests normally contain fewer species than their non-flooded counterparts of the same region (Prance, 1979; Balslev et al., 1987; Junk, 1989). Worbes (1997) and Parolin (2000) estimated overall tree species richness in the central Amazonian várzea to 250–300 species. The distribution of species is strongly linked to the flood-level gradient (Junk, 1989; Ayres, 1993), because duration and height of flooding influences ecophysiology of trees and therefore requires special adaptations of trees to the periodically anoxic site conditions. Wittmann et al. (2002) distinguished between forests of the low várzea and forests of the high várzea. Low-várzea forests establish where the annual water column averages heights >3 m (inundation period >50 days

per year), whereas high-várzea forests establish where it averages <3 m. Within the low várzea, structure and species composition depends on the successional stage of the forests. However, the number of low-várzea tree species is restricted due to the impact caused by the high and prolonged inundations. In the high várzea, inundation is reduced to that way that many species of the surrounding terra firme can establish. Thus, species richness in undisturbed high-várzea forests can be up to 150 species ha⁻¹ (≥ 10 cm diameter at breast height—DBH), which is almost similar to non-flooded terra firme forests (Ribeiro et al., 1999; Nebel et al., 2001; Wittmann et al., 2002).

Without taking the flood gradient into consideration, Worbes et al. (1992) described the successional sequence in várzea forests, from the first establishment of early successional stages on fresh deposited sand bars until late successional forests, with trees reaching ages between 100 and 300 years. With proceeding succession, species richness increases from monospecific stands to stands with about 100 species ha⁻¹ ≥ 10 cm DBH. Tree density declines from a maximum of some 1000 stems ha⁻¹ in early stages to about 500 stems ha⁻¹ in subsequent stages. Growth height of upper canopy trees increases from 10 to 15 m in early stages to about 30–35 m in subsequent stages and forests develop from mono-layered to multi-layered and well stratified stands (Wittmann et al., 2002). Besides flooding and natural forest succession, sedimentation, erosion and the physical soil features are determinant environmental factors for the development of várzea forests (Salo et al., 1986; Terborgh and Petren, 1991). The low inclination of the Amazonian rivers in combination with the high content of sediments and suspended material causes the development of a highly dynamical landscape, characterized by the formation of depressions, levees, lakes and river-channels (Gibbs, 1967; Irion et al., 1995). Sedimentation on slip-off slopes can reach 0.3–1 m every year (Junk, 1989; Campbell et al., 1992). On undercut slopes, erosion can wash out several hectares of forests during one high-water period (Wittmann, 2001). These unstable conditions result in the parallel existence of several forest types, forming a patchwork of microhabitats (Kalliola et al., 1991; Campbell et al., 1992).

The physiological responses of várzea tree species to the periodical inundations are well documented

(e.g. Schlüter et al., 1993; Parolin, 1997; Walhoff et al., 1998; Wittmann and Parolin, 1999; Müller and Junk, 2000; Piedade et al., 2000; Schöngart et al., 2002). However, information about the influence of flooding on richness and distribution of tree species in várzea forests is scarce. No information exists about the influence of sedimentation and the physical soil features on the establishment of different forest types. The present study provides a quantitative description of structure and floristic composition of trees ≥ 10 cm DBH in all registered forest types within two regions of the Amazonian várzea. Average inundation and sedimentation was recorded and the physical soil features were analysed in order to determine whether there is a tree species zonation along these environmental gradients, and how these gradients interact with natural forest succession.

2. Materials and methods

2.1. Study areas

The study was completed in two regions in the Brazilian Amazon, one located at the lower Solimões River ($3^{\circ}15'S$, $59^{\circ}58'W$) near the city of Manaus, the other located within the Mamirauá Sustainable Development Reserve (MSDR) ($2^{\circ}51'S$, $64^{\circ}55'W$), approximately 70 km NW of the city of Tefé. The study areas are influenced by annual inundations of the Solimões (Manaus) and the Japurá (MSDR) Rivers. Despite the distance of ± 500 km between both the regions, the study areas are comparable relating to forest structure and physiognomy, the location of forests along the flood-level gradient and the geomorphologic site conditions. However, due to the vicinity of the city of Manaus, the forests of the lower Solimões River are characterized by frequent timber exploitation, which results in general lower tree species diversity when compared with the Mamirauá forests.

Mean monthly temperature in the two regions vary little over the year and range between 25 and 28 °C. Between 1996 and 2000, mean annual rainfall was about 2300 mm near Manaus and about 3000 mm in Mamirauá (Max-Planck-Institute for Limnology, Manaus; Institute for Sustainable Development Research Mamirauá—ISDRM, Tefé). Mean amplitude of flooding was almost the same in both the

regions, and averaged to 10.8 m between 1995 and 2000.

2.2. Data collection

Floristic inventories were carried out in a total area of 5.24 ha, distributed on a total of nine sites. Plots with the size of 1 ha were installed when species richness exceeded 20 species, whereas plots with the sizes of 625 m² were installed when species richness was below that. The location of the studied plots was determined by forest structure (growth height, basal area) and the flood-level gradient, so that all recognised forest types within the surroundings of the regions (± 20 km²) were sampled (Table 1). In the region of the lower Solimões River, two plots with the size of 1 ha and two plots with the size of 625 m² were installed, within the MSDR, three plots (1 ha) and two plots (625 m²), respectively (Table 1).

According to the classification of Worbes et al. (1992), the plots were covered by forests of the early successional stage (plots I and II), early secondary stage (plot IV), secondary stage (plot V), late secondary stage (plot VI) and late successional stage of the low várzea (plot VII). In one plot, the 'chavascal' (Ayres, 1993), a type of swamp forest, localised at the margin of a still-water lake, is of an unknown successional stage. Two plots were installed in high-várzea forests (plots VIII and IX, Table 1).

All trees ≥ 10 cm DBH were identified to species and their diameters measured. Each individual tree was entered into a three-dimensional coordinate system (position: x , y , height: z) using a theodolite (Carl Zeiss Ni2, Jena, Germany). The vertical position of individual trees was derived comparing 1999 flood marks on trunks with water levels recorded in Manaus (Engenharia dos Portos) and in Tefé (ISDRM).

Sedimentation was recorded with the aid of measuring slats, put up at the end of the terrestrial phase in March 2000, and read at the end of the aquatic phase, in August/September 2000. The woody slats (3 cm \times 3 cm \times 200 cm) with a millimetre scale were dug right-angled into the ground to a depth of 60 cm. In each square plot (I–IV), one measuring slat was installed, while in each of the rectangular plots (IV–IX), two slats were installed.

Soil samples were obtained in a total of 14 sites, one in the centre of each square plot, and two in each

Table 1
Plot characteristics

Plot	Size (m ²)	Region*	Growth height (m)	Successional stage ^a	Age (year) ^a	Other designations
I	625	Ms	10–15	Early succession	0–10	<i>Salix</i> spp.-type ^a
II	625	Mm	10–15	Early succession	0–10	<i>Salix</i> spp.-type ^a
III	625	Mm	12–18	–	–	Chavascal ^b
IV	625	Ms	14–20	Early secondary	10–30	<i>Cecropia latiloba</i> -type ^a
V	10000	Mm	14–20	secondary	10–50	<i>Crataeva benthamii</i> -type ^a
VI	10000	Ms	20–25	Late secondary	20–60	<i>Pseudobombax munguba</i> -type ^a
VII	10000	Mm	30–35	Late succession	100–300	<i>Piranhea trifoliata</i> -type ^a
VIII	10000	Ms	35–40	Late succession	–	High restinga ^b High várzea ^c
IX	10000	Mm	35–40	Late succession	–	High restinga ^b High várzea ^c

* Ms: Manaus; Mm: Mamirauá.

^a Worbes et al. (1992).

^b Ayres (1993).

^c Wittmann et al. (2002).

rectangular plot, localised near the small sides of the plots. The samples were taken at the ground surface and depths of 40, 100 and 200 cm below the ground surface. The samples were dried, sieved and their particle size distribution was determined.

Phytosociological studies include calculations of the total importance value (TIV, Curtis and McIntosh, 1951), determinations of floristical equitability ('evenness', Shannon and Weaver, 1949), determinations of floristical similarity (Sørensen, 1948) and the β -diversity (' β -turnover', Shmida and Wilson, 1985). One-dimensional ordinations were performed to check the zonation of tree species along the environmental gradients.

3. Results

3.1. Inundation

In both the regions, the closed-forest border was established when the water column averaged 6.5–7 m, corresponding to a submersion period between 219 and 240 days per year. Below the forest border, single shrubs and trees were established in the marginal zone of lakes, but never developing closed-canopy forests.

Within the low várzea, average water column in the last 9 years reached to 7 m (231 days per year) at the slip-off slopes of the main-river channels (plots I and

II) and to 6.8 m (227 days per year) in the chavascal (plot III). Lowest inundation was recorded within the high várzea forests (plots VIII and IX, Table 1).

3.2. Sedimentation and soil texture

Sedimentation and soil texture was linked to the time of inundation, which the sites were subjected, and to the distance of the sites to the main-river channel. In general, sediment deposition decreased with increasing elevation of the sites. Simultaneously, the soil clay partition increased. Highest sedimentation was recorded at the slip-off slopes of the main-river channels (plots I and II), lowest rates within the high várzea (plots VIII and IX, Table 2). The soil clay partition reached low percentages near the riverbanks and higher percentages in the high várzea. In spite of the high inundations, sedimentation in the chavascal (plot III) was exceptional, and amounted to only 0.2 cm. The soil clay fraction was the highest recorded in this study (Table 2).

3.3. Stand structure and species composition

Field inventory yielded a total of 2609 individual trees ≥ 10 cm DBH on the entire research area of 5.24 ha, belonging to 222 species and 57 families. Species belonging to the Leguminosae dominated with a total of 11%, followed by species belonging

Table 2
Environmental site conditions

Plot	Distance to the river (km) ^a	Inundation height (m)	Inundation period (day per year)	Sedimentation (cm)	Soil clay partition (%)
I	0.1	7	232	19.8	53.2
II	0.2	6.9	230	14.7	54.6
III	4	6.8	227	0.2	83.2
IV	0.8	6	168	1.2	57.5
V	1.5	4.8	131	1.1	62.2
VI	2.8	5.5	155	0.5	67.6
VII	2.7	4.1	111	0.2	64.9
VIII	1.5	2.4	43	0.1	64.7
IX	7.2	1.9	36	0.1	65.4

^a Distance of the sites from the Solimões (Ms) and Japurá (Mm) Rivers.

to the Rubiaceae (8%), Euphorbiaceae and Annonaceae (both 7%, Fig. 1).

The stand densities were 32 and 27 individuals 625 m^{-2} (corresponding to 490 and 435 individuals ha^{-1}) in the early successional stages and 57 individuals 625 m^{-2} (corresponding to 912 individuals ha^{-1}) in the chavascal (Fig. 2). The highest stand density was within the early secondary stage, exceeding 1000 individuals ha^{-1} . Within the secondary and the late successional stages of the low and the high várzea, stand densities ranged between 370 and 466 individuals ha^{-1} (Fig. 2).

Tree species richness increased from 4 species ha^{-1} in the early successional stages to 172 species ha^{-1}

within the late successional stages of the high várzea (Fig. 2). The species/area curves for the nine plots indicate, that the plots covered by the early successional stages, the chavascal and the secondary stages were adequate samples for the plots I–VI. The slope of the late successional stages (plots VII–IX) were still steeply climbing after 1 ha ($m = 5.4$ species 0.05 ha^{-1} , 4.6 species 0.05 ha^{-1} and 9.4 species 0.05 ha^{-1} , respectively, Fig. 3).

In all forest types, the distribution of trees by DBH class showed reverse j-shaped curves. The basal areas per hectare averaged 5.3 m^2 in plot I and II, 13.9 m^2 in plot III, 17.3 m^2 in plot IV and 30 m^2 in plot V. The highest basal area of 48.2 m^2 was recorded in plot VI.

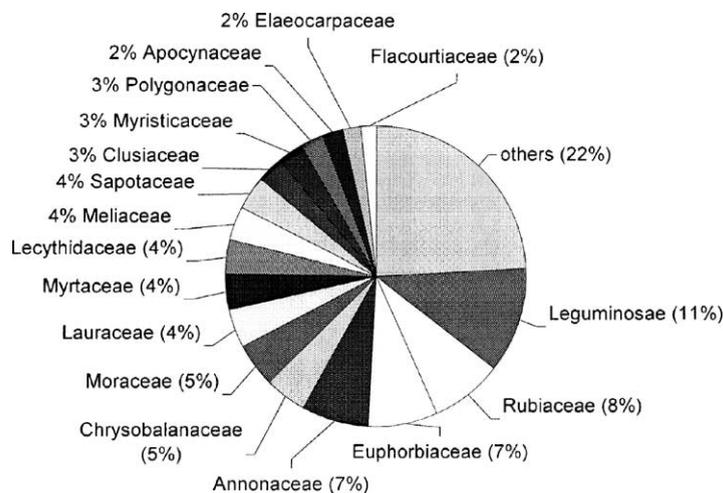


Fig. 1. Dominating tree families of the inventoried forests ($n = 2609$ individuals, 222 species).

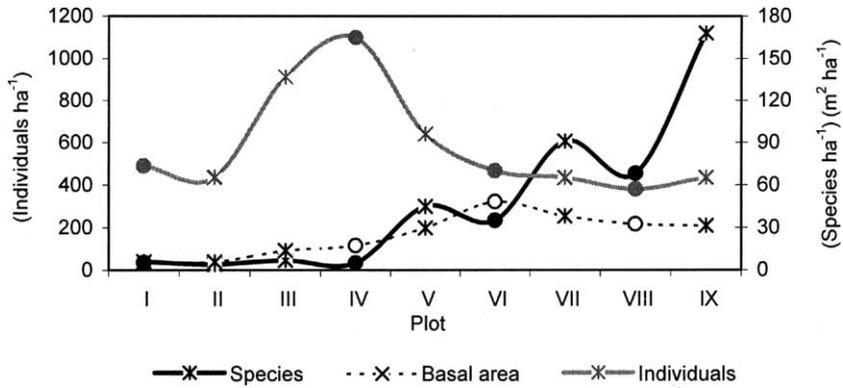


Fig. 2. Stand densities, species richness and basal area of the inventoried forests. Crosses: Mamirauá plots, circles: Manaus plots. With plots I and II: early successional stage, plot III: chavascal, plot IV: early secondary stage, plots V and VI: late secondary stages, plot VII: late successional stage, all low várzea; plots VIII and IX: late successional stages of the high várzea.

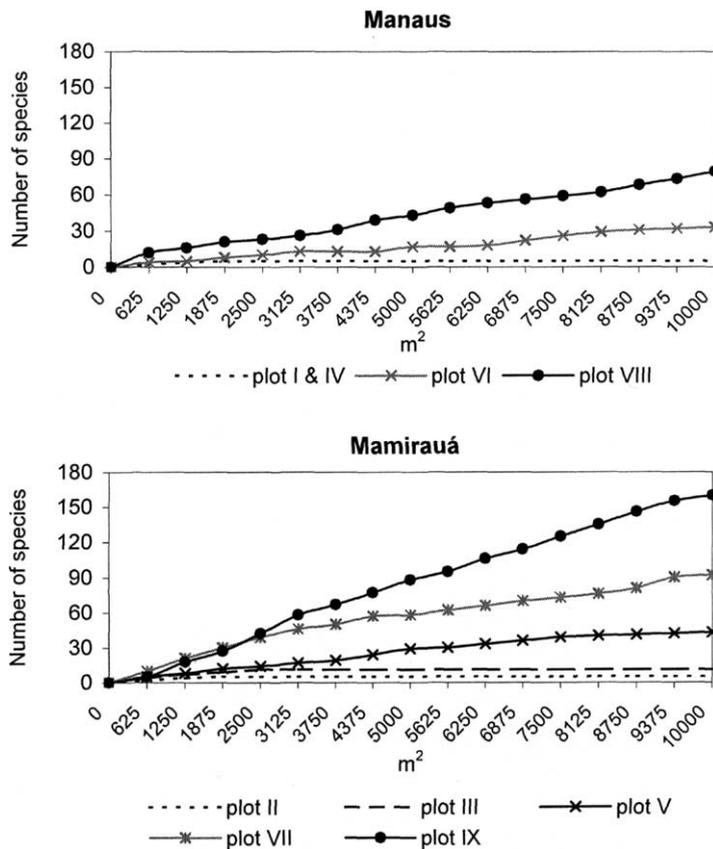


Fig. 3. : Species/area curves of the inventoried plots. For covering forest types see Table 1.

With proceeding succession, the basal areas in the plots VII–IX decreased to 38.1, 32.6 and 31.8 m² (Fig. 2).

The total importance values (TIV) between the forest types differed considerably. Within the low várzea, the plots I–IV were uniform stands, with one or two predominant species. At the slip-off slopes (plot I and II), both species, *Alchornea castaneifolia* and *Salix martiana* reached between 61 and 72% of the TIV, less important species, such as *Pseudobombax munguba* or *Ficus anthelminthica* reached at least 10% of the TIV. In the chavascal (plot III), *Buchenavia* sp. reached 43% of the TIV, followed by *Bactris maraja* (23.1%), *Pseudobombax munguba* (18.7%) and *Symmeria* sp. (12.3%). The most uniform stand was plot IV, covered by the early secondary stage. Among the five recorded species, *Cecropia latiloba* was predominant with 87% of the TIV, followed by *Nectandra amazonum* (8%) and *Crataeva benthamii* (3%). Within the subsequent stages of the low várzea, abundance and dominance values decreased continuously with proceeding succession. In plots V and VI (secondary stages), the 10 most important species account for 77–82% of the TIV, in plot VII (late successional stage) for 35%, respectively. Important species were *Crataeva benthamii*, *Vitex cymosa* and *Pseudobombax munguba* in the secondary stages and *Couepia* sp., *Tabebuia barbata* and *Piranhea trifoliata* in the late successional stage. In the high várzea, the 10 most important species account for 52% of the TIV in plot VIII and 26% in plot IX, important species were *Spondias monbim*, *Pouteria procera* and *Aspidos-*

perma riedelii. Species equitability was related to the successional sequence (Fig. 4). The highest degree of equitability was in the early successional stage (plot I), indicating the even distribution of the few tree species. With proceeding succession and increasing species richness, the equitability values decreased exponentially, reaching lowest degrees in the high várzea (plot IX, Fig. 4).

Sørensen's index of floristical similarity indicated that species composition among the plots differed both, along the flood-level gradient and the successional stage (Fig. 5). Highest similarity was 92% between plots covered by the early successional stage (plot I and II). Similarity amounted to 50% comparing the early secondary and the late successional stage of the low várzea (plots IV and VII), and decreased to 17–23% comparing the late successional stages between the low várzea and the high várzea (plots VII–IX). Similarity decreased below 5% when early successional stages of the low várzea were compared with the high-várzea forests (Fig. 5).

3.4. Species zonation along the environmental gradients

Species diversity was strongly linked to the flood-level gradient. Constructing a hypothetical β -diversity profile, the studied sites were compared in spatial order along the flood-level gradient with those of other, neighbouring plots. The β -turnover between highly inundated plots was low, and increased continuously with decreasing influence of flooding,

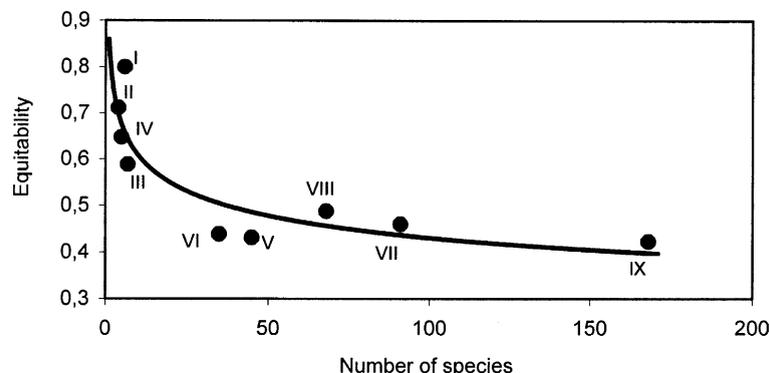


Fig. 4. Shannon and Weaver's equitability index of all inventoried plots. ($J = H(\ln S)^{-1}$, where H is the Shannon's diversity index ($H = -\sum P_i \ln P_i$, where P_i is the number of individuals of species A /total number of individuals of all species), S is the total number of species. For covering forest types see Table 1.

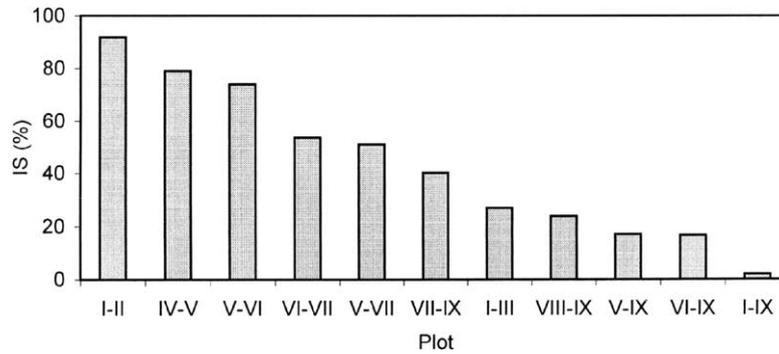


Fig. 5. Sørensen's index of similarity, $IS = 2a(2a + b + c)^{-1}$, where a is the number of species common to both plots, b and c are the number of species unique to plots 1 and 2. For covering forest types see Table 1.

reaching highest values between the low inundated high-várzea plots (Fig. 6).

The distribution of species along the flood-level gradient was well defined. Four species cluster showing a typical spatial-distribution range were distinguished (Table 3). Only eight species (2.6% of all species found) showed a wide spatial distribution along the whole inventoried area (e.g. *Laetia corymbulosa*, *Pseudobombax munguba* and *Calycophyllum spruceanum*), 84 species (27.4%) were restricted to an average water column of 7–3 m ('low-várzea association', e.g. *Vitex cymosa*, *Crataeva benthamii* and *Pouteria elegans*), 93 species (30.4%) were restricted to 6–1 m ('intermediate association', e.g. *Etaballia dubia*, *Gustavia poeppigiana* and *Mabea nitida*) and 121 species (39.5%) to 3–1 m ('high-várzea associa-

tion', e.g. *Spondias monbim*, *Acacia lorentensis* and *Hura crepitans*, Table 3).

Besides inundation, the zonation of tree species also showed relationships to the gradient of sediment deposition and to the soil texture. Sedimentation during the aquatic phase 2000 decreased with increasing topographic level of the sites and increasing distance of the sites to the main-river channels. In general, the late successional stages were located more distant to the river than earlier stages (Table 2). They were characterized by a higher amount of fine grain sizes in the soil samples. In spite of the high inundations, sedimentation and soil texture was exceptional in the chavascal. Therefore, it cannot rank with the successional sequence in forests directly influenced by the main-river systems (Table 2).

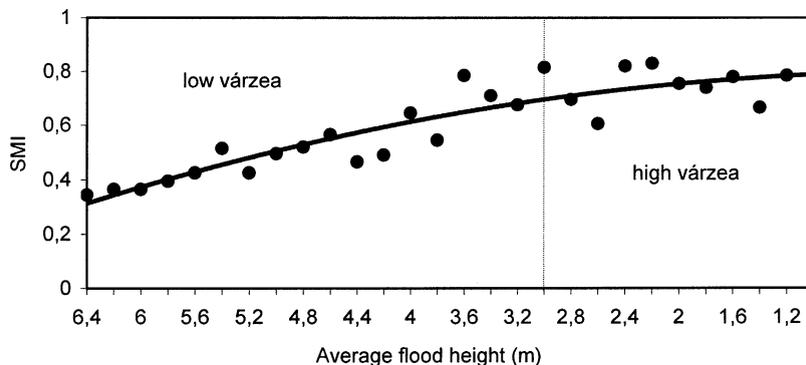


Fig. 6. Hypothetical β -diversity profile (Shmida and Wilson's index) between the plots (1 ha) along the flood-level gradient. $SMI = (g + l)/(a + b)$, where g and l are the gained and lost species from site 1 to site 2; a and b are the number of species in sites 1 and 2.

Table 3
Zonation of important tree species along the flood-level gradient

	Species	Average flood height (m)						Σ
		Low várzea				High várzea		
		7–6	6–5	5–4	4–3	3–2	2–1	
1	<i>Laetia corymbulosa</i> Spruce ex Benth	9	60	64	6	11		150
2	<i>Pseudobombax munguba</i> Dugand	8	43	32	3	9	1	96
3	<i>Calycophyllum spruceanum</i> K. Schum	6	12		1	5		24
4	<i>Tabebuia barbata</i> Sandwith	1	8	18	7		3	37
Σ5–8		19	228	170	44	15	8	484
Low-várzea association								
1	<i>Buchenavia</i> sp.	37						37
2	<i>Alchornea castaneifolia</i> A. Juss	16						16
3	<i>Vitex cymosa</i> Bert. Ex Spreng	65	80	9	1			155
4	<i>Crataeva benthamii</i> Eichl.	28	67	63				158
5	<i>Pouteria elegans</i> Baehni	2	19	23	7			51
6	<i>Nectandra amazonum</i> Nees		6	44	4			54
7	<i>Luehea cymulosa</i> Spruce ex Benth		18	17	1			36
8	<i>Maclura tinctora</i> (L.) Grisebach		8	34	14			56
9	<i>Piranhea trifoliata</i> Baill.		3	10	3			16
10	<i>Conceveiba</i> sp.		5	7				12
11	<i>Inga cinnamonea</i> Spruce ex Benth.			2	4			6
Σ12–84		83	91	148	59			381
Intermediate association								
1	<i>Triplaris</i> sp.		5	5	4	36	1	51
2	<i>Cecropia membranacea</i> Trec		5	3		1	5	14
3	<i>Paramachaerium ormosioides</i> Ducke		1	1	2	5	2	11
4	<i>Etaballia dubia</i> (H.B. & K.) Rudd.			8	3	3	1	15
5	<i>Gustavia augusta</i> L.			3		1	10	14
6	<i>Neea ovalifolia</i> Spruce ex J.A. Schmidt			3	4	1		8
7	<i>Mabea nitida</i> Spruce ex Benth.			4	14	1		19
8	<i>Vatairea guianensis</i> Aubl.			3	9	3		15
9	<i>Naucleopsis</i> sp.				5	20	1	26
10	<i>Virola calophylla</i> Warb.				3	12	5	20
11	<i>Pseudoxandra polyphleba</i> Diels (R.E. Fries)				2	7	3	12
Σ12–93			22	76	45	81	74	298
High-várzea association								
1	<i>Spondias monbim</i> L.					21		21
2	<i>Acacia lorentensis</i> Machr.					16	4	20
3	<i>Annona hypoglauca</i> Mart.					9	2	11
4	<i>Tapura juruana</i> (Ule) Rizzini					1	9	10
5	<i>Guatteria inundata</i> Mart.					1	6	7
6	<i>Pouteria procera</i> (Mart.) K. Hammer					5	22	27
7	<i>Aspidosperma riedelii</i> Muell. Arg.					2	11	13
8	<i>Hura crepitans</i> L.					2	6	8
9	<i>Aniba riparia</i> Mez.					2	5	7
10	<i>Rollinia cuspidata</i> Mart.					2	3	5
11	<i>Apeiba membranacea</i> Spruce ex Benth.					2	3	5
12	<i>Ocotea floribunda</i> Benth. & Hook						9	9
Σ12–121						75	116	191
Σ		274	681	747	245	348	314	2609

Values represent absolute abundances of trees ≥ 10 cm DBH 5.24 ha^{-1} .

4. Discussion

4.1. Species zonation along the environmental gradients

Floristic composition, tree species richness and structure of várzea forests is strongly linked to the location of forest types along the flood-level gradient (Junk, 1989; Ayres, 1993), and to the geomorphologic behaviour of forest covered sites as a result to their location to the highly dynamic river systems. The várzea is characterized by a patchwork of microhabitats (Campbell et al., 1992), including sites with unstable environmental conditions next to the rivers, and sites with relative longstanding stable conditions when located off the direct influence of the rivers. Early successional stages normally establish within the unstable, low várzea. These stages are characterized by low species richness, high tree density and poorly stratified canopies (Worbes et al., 1992; Wittmann et al., 2002). As response to the prolonged inundations, trees of early successional stages often show adaptations to the anoxic site conditions, such as a reduced metabolism during the aquatic phase and the formation of hypertrophic lenticells (Kozłowski, 1984; Parolin, 1997; Piedade et al., 2000; Parolin et al., 2002). They are light-demanding pioneers, and as such typical ‘r-strategists’ (Pianka, 1970), characterized by fast growth, relative short life cycles and a high potential of vegetative and sexual reproduction (Puhakka and Kalliola, 1993; Worbes, 1997; Parolin, 1998). Furthermore, tree species colonising highly inundated areas show specific adaptations to the geomorphologic site conditions at the root level: Wittmann and Parolin (in press) observed, that species establishing near riverbanks form deep primary roots, which probably offer good mechanical support against the relative high water velocity during the aquatic phases. Moreover, *Salix martiana* and *Alchornea castaneifolia* form new secondary root layer every year, which are installed above the fresh deposited sediment. Trees of the chavascal establish on fine-grained soils with a high content of organic matter. Therefore, they are subjected to extreme anoxic conditions at the root level, which persist during the most part of the year. Thus, tree species of the chavascal often develop stilt roots to get better aeration, whereas the below-ground roots hardly reach depths of up to 1 m

below the ground surface (Wittmann and Parolin, in press).

The well-defined zonation of tree species along the flood-level gradient becomes evident with regard to the floristical evolution of várzea forests since the tertiary. Kubitzki (1989) stated, that many várzea tree species are ecotypes originating from the surrounding terra firme. When they immigrated to the nutrient-rich várzea, they gradually developed adaptations to the periodic inundations. The high várzea maybe an important transitional zone for these immigrants. The ability of some species to develop adaptations to flooding favoured them to colonise the higher inundated low várzea.

With increasing water column and inundation period, natural selection led to only a few species, which tolerate the extreme inundations near the forest border, where inundation persists during the most part of the year.

Only a few tree species inventoried in this study were distributed along the whole flood-level gradient. Moreover, some of these species, like *Pseudobombax munguba* or *Duroia duckei*, are known to have a widespread distribution over the whole Neotropis, in particular in semi-deciduous forests and savannas (Prance, 1979). Junk (1989) and Worbes (1997) assume that those widespread species are not primarily adapted to flooding, but generally tolerant to seasonally poor growing conditions.

4.2. Allogenic versus autogenic succession

The results of this study indicate, that forest succession alters the geomorphologic site conditions in várzea forests. The establishment of early successional stages intensifies the deposition of coarse-grained sediment because high tree densities offer resistance against water energy. This leads to an increasing topographic level of the sites. With decreasing inundation, secondary stages be composed of trees with large basal areas-establish. So far, the causes of changes in vegetation are alterations triggered by the environmental site conditions, and succession can be defined as ‘allogenic’ (Tansley, 1929; Burrows, 1990). However, geomorphologic site dynamic is strongly reduced when subsequent stages establish. Water velocity is slowed down and the coarse grains were already deposited on riverbanks, dunes or tree

stems when inundation reaches the high-lying sites. Therefore, the causes of changes in vegetation in late successional stages are alterations mainly triggered by the vegetation itself ('autogenic succession', Tansley, 1929) and to a lesser extent by changes of the environmental conditions. Finally, succession results in high-várzea forests, where structure and species richness is almost similar to the non-flooded terra firme. Wittmann et al. (2002) documented the general small size and the isolated character of patches of high-várzea forests and assume, that they could also be regressive forest types, formed from previous forests of more elevated Pleistocene terraces, as a consequence of the constantly changing riverbeds of white-water rivers. Up to date, no dendro-chronological information exists about high-várzea trees. Therefore, it remains unclear if the high várzea develops in natural forest succession from low-várzea forests, or if it is a regressive forest type.

Due to the relative stable environmental site conditions, the chavascal represents a special vegetation unit within the low várzea. The chavascal establishes in the marginal zone of still-water lakes or in ancient, silted up river-arms that do not drain. In spite of the high inundations, sedimentation in the chavascal is low, because dunes and large stems building trees slow down water energy. Thus, the chavascal is not comparable to forests near the highly dynamic river systems. Rather its development shows similarities to long-term developing tropical fens, which are known as 'matupa' (Junk, 1983; Junk and Piedade, 1997) and which are characterized by the silting up of organic matter in self-contained still-water systems.

4.3. Species diversity in várzea forests

Worbes (1997) stated that the várzea is characterized by a trend of decreasing tree species diversity from western to eastern Amazonia. The results of the present study contradict such a gradient, because tree species diversity within the Mamirauá Reserve is higher than species diversity described in westerly located inventories, performed by Nebel et al. (2001) in Peruvian várzea forests adjacent to the Ucayali River (141 species ha⁻¹), Campbell et al. (1992) at the lower Juruá River, Brazil (106 species ha⁻¹) and Balslev et al. (1987) at the Napo River, Ecuador

(149 species ha⁻¹). Worbes (1997) and Parolin (2000) estimated overall tree species richness in the central Amazonian várzea to a number of 250–300 species in total. In this study, we recorded more than 200 species ≥ 10 cm DBH in an area of 5.24 ha, indicating that species richness of várzea forests may strongly underestimated. The parallel occurrence of several small-scaled habitats differing in hydrologic and geomorphologic conditions complicates the registration of all occurring tree species within a region. Besides, the dynamic of geomorphology may not identical along the Amazon River and its tributaries, but changes in response to the local inclination, the amount of regional precipitation and the local behaviour of the 'flood pulse' (Junk et al., 1989). In Peruvian várzea forests, the whole successional sequence from early to late successional stages succeeds in a few hundred of years (Terborgh and Petren, 1991). By comparison, inclination, sedimentation and erosion are lower in central Amazonian floodplains. However, species diversity of a region seems to depend on the local behaviour of the subsoil. Comparing both regions chosen for the floristic inventories in the present study, species diversity was significantly lower near Manaus than in the Mamirauá region. The low species diversity near Manaus becomes evident through the extension of area potentially available for the establishment of várzea forests. Due to the erosional resistance of the tertiary surroundings, the quarternary várzea is reduced to relatively small sectors on both banks of the Solimões River (Rosetti and De Toledo, 1999). For this reason, long-term developing late successional stages are scarce in the region of Manaus, and diversity consequently lower than in Mamirauá, where the confluence of two large rivers results in an extensive quarternary floodplain with the size of several millions of km². Finally, anthropogenic influence of várzea forests is common since the pre-Columbian era (Junk, 2000; Ohly, 2000). Since the forests near Manaus are located within easy reach to the river, long-term anthropogenic disturbance is probably.

4.4. Implications for biodiversity and the sustainable management of várzea forests

Floristic composition and tree species richness in várzea forests is strongly related to the height and the

duration of the annual inundations and to the related geomorphologic site conditions. This leads to a characteristic zonation of species groups along the flood-level gradient. This knowledge is fundamental to enable a sustainable forest management. According to Klenke and Ohly (1993) and Higuchi et al. (1994), 60–90% of timber exploited in central and western Amazonia originates from várzea forests. Many high-várzea trees are dense-wood species, such as *Virola calophylla*, *Calophyllum brasiliense* and *Ocotea cymbarum*, with a huge demand on the local, regional and even international timber market (Worbes et al., 2001). Other species, like *Ceiba pentandra* and *Hura crepitans* are characterized by low-density wood, which is used for plywood production and for the construction of floating houses by the local population. Besides, many várzea trees are used for the production of non-timber products, such as oil, palm heart and edible fruits, resins, textile fibres, aromas and tannins which are used in the treatment of hides, for colours and medicines (Parolin, 2000).

In comparison with non-flooded forests, costs of selective logging and of timber transport in várzea forests are low, because timber is removed by boats and shipped to the sawmills (Barros and Uhl, 1998). However, the selective logging endangers biodiversity of várzea forests, because wood in general is extracted without any forest management (Higuchi et al., 1994; Anderson et al., 1999). The selective logging of trees decreases species diversity in a regional scale, because especially the economical valuable dense-wood trees are species with natural low abundances. Therefore, many dense-wood species in frequently logged várzea forests near the centres of human concentration already disappeared. Moreover, large areas of forests are cleared to enable the agricultural use of the nutrient-rich várzea soils, especially in the lower inundated sites of the high várzea (Wittmann and Junk, 2003).

To maintain high biodiversity in Amazonian várzea forests, sustainable management plans must define the number of stems and the cutting cycles for every single species to be logged. As late successional stages, high-várzea forests need several hundred of years to develop. Since they are the most rich in species, they need preservation and particular attention in sustainable forest management plans.

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