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Forest structure and tree species composition of the understory of two central Amazonian várzea forests of contrasting flood heights

Rafael Leandro de Assis[a], Florian Wittmann[b,*]

[a] Instituto Nacional de Pesquisas da Amazônia, Av. André Araújo 2936, 69060-001 Manaus, Brazil
[b] Max Planck Institute for Chemistry, Biogeochemistry Department, Johann J. Becher-Weg 27, 55128 Mainz, Germany

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ABSTRACT

We investigated species composition, distribution, and forest structure of understory trees (≥1 m height, <10 cm diameter at breast height) in two late-successional várzea forests subject to contrasting levels of inundation within the Mamirauá Sustainable Development Reserve, western Brazilian Amazon, and compared it with the overstory flora at the same study sites. In total, 1486 individuals and 116 woody species were recorded on an area totaling 3140 m^2. Individual densities and tree species richness were considerably higher in the high várzea than in the low várzea, which suggests that the heights and durations of the annual inundations are the main factor limiting species regeneration. In addition, approximately one third of the recorded species with densities ≥8 individuals showed regular or random spatial distribution patterns, which suggests that floodwaters act on dispersal strategies and species establishment.

Independent of the forest type, floristic similarity between the understory and the overstory amounted to approximately 35%, and to approximately 10% when compared to other understory inventories in Amazonian várzea. Although the inventoried area of the understory amounted to only 16% of that of the overstory, species richness accounted for approximately 52–56% of that of the overstory. The results indicate that the understory flora of várzea forests is distinct and that it significantly increases local tree species richness. The understory flora of várzea forests therefore should be addressed in floristic inventories that provide the basis for regional and/or basin-wide estimations of tree diversity.

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Introduction

Amazonian várzea forests border the sediment-rich white-water rivers that originate from the Andes and the sub-Andean foothills, and they cover an area of approximately 150,000 km^2 (Junk, 1997). Due to the comparatively high cation exchange capacity of the alluvial substrate, várzea soils are rich in nutrients when compared to those of the adjacent uplands or those of floodplains that border the Amazonian black- and clear-water rivers (Furch and Junk, 1997; Prance, 1979). Forests are cleared to enable the agricultural use of the alluvial soils, whereas remaining forests undergo intense resource extraction by the local populations. Therefore, the várzea is the ecosystem most densely inhabited by humans within equatorial Amazonia (Junk et al., 2000).

Várzea trees are subjected to annual inundations that reach up to 7 m in height and last up to 230 days year^{-1} (Junk, 1989; Wittmann et al., 2002, 2004). The seasonal inundation of roots and/or parts of the aboveground tree reduces the oxygenation of submerged tissues and is widely considered as a potential stress factor (Armstrong and Drew, 2002; Jackson and Colmer, 2005). The heights and durations of the annual floods require specific adaptations of trees to cope with the seasonally anaerobic site conditions, which in Amazonian floodplain trees can be morpho-anatomical, eco-physiological, and biochemical (e.g., De Simone et al., 2002; Parolin, 2009; Schlüter et al., 1993; Schöngart et al., 2002; Waldhoff et al., 1998). Inundation influences processes such as reproductive biology, plant demography, and productivity of trees (e.g., Gottsberger, 1978; Kubitzki and Ziburski, 1994; Megonigal et al., 1997; Oliveira Wittmann et al., 2007; Schöngart et al., 2005; Worbes, 1986), and triggers tree species selection and distribution (Wittmann et al., 2004).

With up to 1000 flood-tolerant tree species, Amazonian várzea forests are the most species-rich floodplain forests worldwide (Wittmann et al., 2006a). They are the habitat of many, partially endemic plant and animal species and important as food source for the fish and mammal fauna. They offer a variety of timber species extracted by the local population, including timber for international export (Nebel et al., 2001a; Schöngart et al., 2007). In addition, várzea forests are an important landscape-scale component for carbon-sequestration, the regulation of water quality and the regional climate, and the protection of river banks against fluvial erosion (Junk et al., 2000).

* Corresponding author. Tel.: +55 92 36421503; fax: +55 92 36421503.
E-mail addresses: Rafael.assis@umb.no (R.L. de Assis), F-Wittmann@web.de (F. Wittmann).

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Due to the easy access by means of the rivers, the flora of Amazonian várzea forests is comparatively well-known (Junk, 1997). Several floristic inventories were performed all over the Amazon basin, i.e. in its eastern part (Carim et al., 2008; Cattanio et al., 2002; Gama et al., 2002, 2003), its central part (Ayres, 1993; Klinge et al., 1996; Prance, 1979; Wittmann et al., 2002, 2004; Worbes et al., 1992), and its western part (Balslev et al., 1987; Dallmeier et al., 1996; Duque et al., 2002; Nebel et al., 2001a). Most inventories, however, considered only trees ≥10 cm diameter at breast height – dbh, whereas smaller trees were rarely inventoried (but see Gama et al., 2002, 2003; Nebel et al., 2001b; Wittmann and Junk, 2003). Thus, information about species composition and structure of the forest understory including regeneration of overstory trees is scarce and mostly concentrated on experimental studies dealing with the seedling establishment of single tree species (e.g., Oliveira Wittmann et al., 2007; Parolin, 2000, 2001). The understory of a forest warrants special attention because it often contains distinct tree species which provide shelter and contribute to the food chains of many animals (Foster et al., 1986; Gentry and Emmons, 1987; Hubbell and Foster, 1992; Nebel et al., 2001b). Furthermore, they may substantially contribute to processes such as the recycling of nutrients and the regulation of the forests' micro-climate (Jordan, 1985).

Amazonian várzea forests are characterized by a well-defined zonation of tree species along the flood gradient and associated disturbance by fluvial sediment deposition and erosion (Ferreira, 2000; Junk, 1989; Kalliola et al., 1991; Salo et al., 1986; Wittmann et al., 2002, 2004). Several well-defined forest types are distributed along the flood gradient, which differ in both the composition and richness of tree species as well as in forest structure. According to the height and duration of the annual floods, Wittmann et al. (2002) classified Amazonian várzea forests in low-várzea forests and high-várzea forests based on phyto-sociological parameters. Low-várzea forests are subjected to inundations >3 m height, which corresponds to a waterlogged period of trees >50 days year^{-1}, while high-várzea forests are subjected to inundations <3 m (<50 days year^{-1}). Low-várzea forests consist of different forest types, which range from mono-specific forests at the highest flood-levels to late-successional forests at higher topographic levels with up to 90 species ha^{-1} (>10 cm dbh). High-várzea forests are late-successional stages where tree species richness can amount to >150 species ha^{-1} (>10 cm dbh) (Balslev et al., 1987; Nebel et al., 2001a; Wittmann et al., 2002).

The distribution of várzea tree species along the gradient of flooding and associated disturbance is relatively well-understood. Tree species and forest types establish in dependence of their flood-tolerance, and mostly occupy relatively small ecological niches. However, information on the composition and distribution of small arboreal and shrub species along the flooding gradient is scarce. In the present study, we investigated tree species composition, richness, distribution, and forest structure of the understory in two late-successional várzea forests of contrasting flood heights within the Mamirauá Sustainable Development Reserve, western Brazilian Amazon. Aim of this study is to test if species composition and structural parameters differ between the investigated forest types, and to what extent they differ from the overstory at the same sites. In addition, we compare our results with understory inventories of floodplain forests in other parts of the Amazon basin, and demonstrate that the understory of várzea forests contributes significantly to local species richness.

Material and methods

Study area

The study was performed in the focal area of the Mamirauá Sustainable Development Reserve (MSDR) (2°51′S, 64°55′W), approximately 70 km NW of the city of Tefé, western Brazilian Amazon. The focal area of the MSDR covers an area of approximately 260,000 ha and is located at the confluence of the Solimões and the Japurá Rivers (Fig. 1). Mean monthly temperatures in the MSDR vary little over the year and range between 25 and 28 °C (Wittmann et al., 2002). Mean annual rainfall is about 3000 mm, with a pronounced rainy season between November–April, and a dryer season between May–October. Annual water-level fluctuations of the Solimões and lower Japurá Rivers averaged 11.38 m for the period 1993–2000 (Schöngart et al., 2005). The alluvial soils are silt- and clay-rich hydromorphic gleys without stratification of the vertical profile.

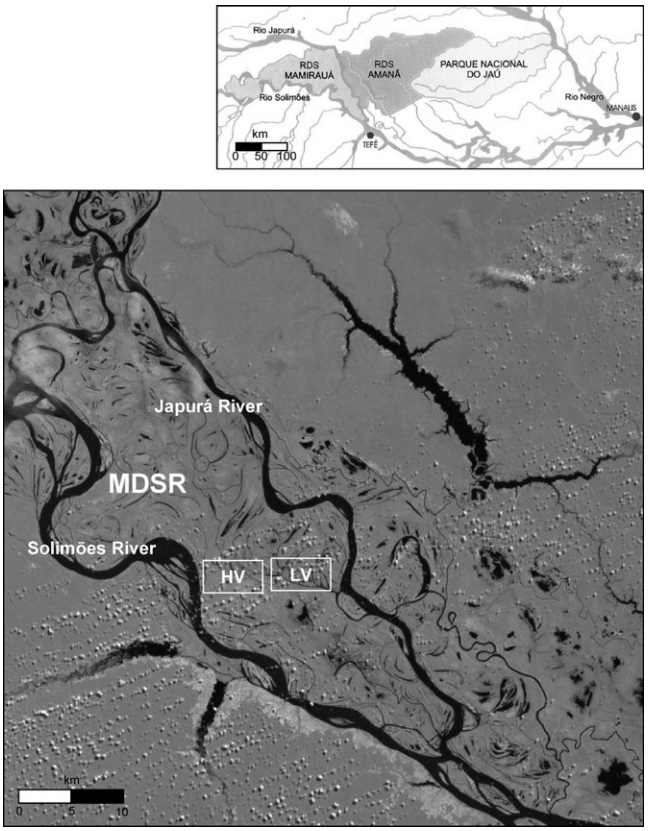

Fig. 1. Study plots within the focal area of the Mamirauá Sustainable Development Reserve (MSDR), located between the Japurá and Solimões Rivers. LV = Low-várzea forest, HV = High-várzea forest. Small map from the Institute for Sustainable Development Research Mamirauá, Tefé, large map derived from Landsat TM (001-062, 25.11.2000, Instituto Nacional de Pesquisas Espaciais – INPE).

The alluvial landscape is a small-scale mosaic of levees, depressions, lakes and river channels, periodically interconnected with each other and the main river system (Peixoto et al., 2009). The vegetation near the highly inundated river banks and lakes is dominated by aquatic and semi-aquatic herbaceous plants. About 90% of the focal area of MSDR is covered by closed-canopy forest. As a result of the small-scale irregular topography of the landscape, they form a patchwork of different forest types. About 92% of the closed-canopy forests in the focal area of MSDR are different successional stages of the low-várzea type, whereas approximately 8% of the forests are of the high-várzea type (Wittmann et al., 2002).

Within the focal area of the MSDR, Wittmann et al. (2002) investigated species composition and stand structure of trees ≥10 cm dbh in three different forest types, installing permanent rectangular plots each with the size of 1 ha (50 m × 200 m). We used two of these plots located in each a late-successional low-várzea forest (LV) and a late-successional high-várzea forest (HV), respectively, to install plots for the inventory of the understory. LV is annually

Table 1
Inventoried area, number of families, species and individuals, and basal area of trees ≥1 m height and <10 cm dbh (this study) in comparison to trees ≥10 cm dbh (Wittmann et al., 2002) in a low-várzea (LV) and a high-várzea forest (HV).

	Inventoried area (m^2)	Families (n)	Species (n)	Individuals ($n\ ha^{-1}$)	Basal area ($m^2\ ha^{-1}$)
LV trees ≥10 cm dbh	10,000	32	91	434	38.1
LV trees 1–10 cm dbh	1570	25	51	2752[a]	1.33[a]
HV trees ≥10 cm dbh	10,000	36	172	469	31.8
HV trees 1–10 cm dbh	1570	34	90	6713[a]	1.76[a]

[a] Values extrapolated to the area of 1 ha.

flooded by a mean water column of 4.1 m, corresponding to a period of 111 days $year^{-1}$, while HV is flooded by a mean water column of 2.2 m (36 days $year^{-1}$) (Wittmann et al., 2002). Structural and floristic parameters of the overstory flora of these plots are listed in Table 1.

Inventories

In each of the formerly investigated 1-ha plots, we installed 20 circular plots each with an area of 78.5 m^2 (r = 5 m), during the terrestrial phase in September–October 2007. All plots were established under the closed canopy, with a minimum distance of 20 m between them. Total inventoried area amounted to 1570 m^2 per forest type (3140 m^2 in total).

All woody individuals (trees and shrubs) ≥1 m height and ≤10 cm dbh present in the plots were labeled, numbered, and measured in dbh and height. Species were identified provisionally as morpho-species with voucher specimens collected for later identification at the herbarium of the National Institute for Amazon Research – INPA, Manaus.

All species were carefully checked in several herbaria (i.e., INPA, Missouri and New York Botanical Gardens, Royal Botanical Gardens Kew) in order to classify them as (1) shrubs or small arboreal trees of the understory, and (2) regeneration of overstory trees.

Data analysis

We calculated absolute and relative abundances, frequencies, dominances (basal areas), and the Total Importance Value (TIV, Curtis and McIntosh, 1951) of each species in each plot and forest type. The family importance value (FIV) for each family was derived according to Mori et al. (1983).

To test if the sampled area is representative, rarefaction curves were produced on the basis of 1000 random iterations using the computer program EcoSim (Gotelli and Entsminger, 2001). These curves used data pooled from all plots in the same forest type, and calculated the expected number of species added per 100 sampled individual trees.

A Mantel test was used to test if there is a relationship between geographic distance and species similarity between the plots of both investigated forest types (Sokal and Rohlf, 1995). Floristic similarity between plots and forest types was calculated using the Sørensen Index (SI, Sørensen, 1948). Non-metric multidimensional scaling (NMDS – Kruskal, 1964) was used to explore the variability in species composition between plots. We used the Bray-Curtis dissimilarity distance to compute the resemblance matrix between plots (Krebs, 1989). Mantel test, based on a Monte Carlo randomization of 1000 runs, and NMDS were calculated using a PC-ORD 4 System (McCune and Mefford, 1999).

Species distribution was investigated for all species with $n \geq 8$ individuals using the Morisita index $[Id = p\sum p_{i-1}n_i\ (n_i - 1)/N(N-1)]$ (Morisita, 1959), where p is the number of plots, n_i the number of stems of a given species in the ith plot, and N the total number of stems in all plots. According to Brower and Zar (1984) an $Id > 1.0$ describes a clumped dispersion, an $Id < 1.0$ a regular dispersion, and an $Id = 1.0$ a random dispersion. Each $Id > 1.0$ was tested with an F statistic to determine whether it varied significantly ($P < 0.05$) from a random distribution (Poole, 1974).

One-way ANOVAs with Tukey's post-hoc test were applied in the understory structure parameters using the Program Bioestat 2.0 (Ayres et al., 2000).

Results

The field inventory yielded a total of 1486 woody individuals ≥1 m height and <10 cm dbh on the entire research area of 3140 m^2, belonging to 116 species and 38 families (Tables 1 and 2, Appendix A). Sixty-six species were classified as overstory trees,

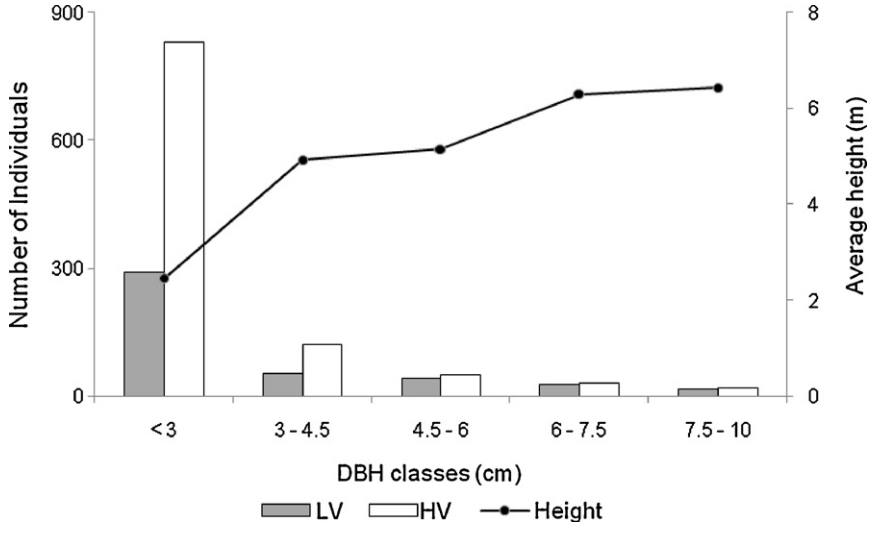

Fig. 2. Number of individuals, average tree heights and dbh-class distribution of all recorded understory trees in low váreza (LV) and high várzea (HV).

Table 2
Relative abundance (rA), relative dominance (rD), relative frequency (rF), and family importance values (FIV) of the 15 most important families in the understory of the inventoried low-várzea and high-várzea forest. Family classification is according to the Angiosperm Phylogeny Group (3).

		Low várzea				High várzea				
		rA	rD	rF	FIV	FIV	rF	rD	rA	
1	Clusiaceae	19.21	40.23	3.92	63.36	92.92	9.9	57.32	25.71	Rubiaceae
2	Sapotaceae	21.76	25.04	7.84	54.64	37.53	4.4	20.13	13	Myristicaceae
3	Rubiaceae	9.5	5.83	11.76	27.08	16.53	8.8	2.81	4.93	Fabaceae
4	Euphorbiaceae	4.63	5.74	11.76	22.13	16.2	3.3	5.88	7.02	Moraceae
5	Urticaceae	9.03	6.98	1.96	17.97	14.36	7.7	1.73	4.93	Euphorbiaceae
6	Apocynaceae	4.40	2.17	7.84	14.41	13.85	7.7	2.64	3.51	Annonaceae
7	Violaceae	6.71	4.09	1.96	12.76	12.4	6.6	2.67	3.13	Sapotaceae
8	Fabaceae	2.55	1.9	7.84	12.37	9.32	4.4	0.46	4.46	Clusiaceae
9	Chrysobalanaceae	3	1.55	5.88	10.44	9.17	1.1	1.81	6.26	Melastomataceae
10	Moraceae	3.24	1.1	3.92	8.26	8.38	5.5	0.42	2.47	Malvaceae
11	Myrtaceae	1.85	1.2	3.92	6.96	7.79	4.4	0.55	2.85	Apocynaceae
12	Malvaceae	2.08	0.65	3.92	6.65	6.96	4.4	0.67	1.9	Myrtaceae
13	Nyctaginaceae	2.78	1.34	1.96	6.07	6.73	1.1	0.51	5.12	Solanaceae
14	Solanaceae	1.62	0.1	3.92	5.64	6.6	4.4	0.3	1.9	Lauraceae
15	Annonaceae	2.08	1.28	1.96	5.33	4.6	2.2	0.31	2.1	Violaceae
16–25	5.56	0.76	19.61	25.92	36.68	24.18	1.79	10.72	16–34	
$\sum$	100	100	100	300	300	100	100	100	$\sum$	

each 14 species to understory trees and shrubs, and 22 species could not be identified to the species-level, thus remaining as morpho-species. Most important families (FIV) in LV were Clusiaceae, Sapotaceae, Rubiaceae, and Euphorbiaceae, whereas most important families in HV were Rubiaceae, Myristicaceae, Fabaceae, and Moraceae (Table 2).

The stand densities totaled 432 individuals in LV and 1054 individuals in HV (corresponding to 2752 and 6713 individual's ha^{-1}, respectively: Table 1). Total basal area in LV amounted to 0.23 m^2, and in HV to 0.31 m^2 (1.33 and 1.76 m^2 ha^{-1}, respectively), indicating larger individual average basal area in LV (9.65 ± 10.33 cm^2) than in HV (5.26 ± 6.21 cm^2): Table 1. Tree heights averaged 2.83 ± 1.94 m in LV, and 3.29 ± 2.25 m in HV. In both forest types, the distribution of trees by dbh-classes showed negative exponential curves (Fig. 2), which are characteristic for mature tropical forests (e.g., Pragasan and Parthasarathy, 2010; Zent and Zent, 2004). Tree

Table 3
Relative Abundance (rA), relative Dominance (rD), relative Frequency (rF), Species Importance values (IV), and Total Importance Values (TIV) of the 15 most important understory species in both investigated forest types.

Species	rA	rD	rF	IV	$\sum$TIV (1-15)	
						Lowvárzea
1	*Elaeoluma glabrescens*	20	8.48	7.93	36.4	198.7 (66.3%)
2	*Tovomita schomburgkii*	9.65	3.76	7.92	21.35	
3	*Cecropia latiloba*	8.96	7.35	3.96	20.27	
4	*Leonia glycycarpa*	6.67	6.31	4.87	17.86	
5	*Duroia genipoides*	5.05	4.74	4.88	14.68	
6	*Neea madeirana*	2.76	4.74	4.88	12.37	
7	*Oxandra riedeliana*	2.07	5.1	4.27	11.44	
8	*Mabea nitida* Spruce	1.15	7.03	3.05	11.23	
9	*Rheedia brasiliensis*	9.42	0.76	0.61	10.8	
10	*Pterocarpus amazonum*	1.61	4.58	1.83	8.02	
11	*Calyptranthes crebra*	1.61	4.04	1.83	7.48	
12	*Couepia paraensis*	1.84	2.42	3.05	7.31	
13	*Drypetes* cf. *variabilis*	1.15	4.78	1.22	7.15	
14	*Sorocea duckei*	1.15	3	2.44	6.59	
15	*Maclura tinctoria*	2.07	0.71	3.66	6.43	
16–51	24.82	32.54	43.9	101.3		
$\sum$	100	100	100	300		
						Highvárzea
1	*Coussarea ampla*	17.94	13.34	3.65	34.94	162 (54%)
2	*Virola calophylla*	7.69	5.96	4.62	18.28	
3	*Tococa capitata*	6.26	3.42	2.92	12.61	
4	*Naucleopsis ternstroemiiflora*	3.79	4.57	3.4	11.78	
5	*Inga* sp.1	3.51	3.57	2.91	10	
6	*Solanum leucocarpon*	5.12	1.16	2.67	8.96	
7	*Virola elongata*	2.94	3.54	2.19	8.67	
8	*Alchorneopsis floribunda*	3.13	2.07	3.16	8.36	
9	*Iryanthera juruensis*	1.99	4.54	1.46	8	
10	*Clarisia racemosa*	3.03	2.27	2.19	7.5	
11	*Micropholis egensis*	1.32	3.87	2.19	7.38	
12	*Heisteria acuminata*	1.61	3.3	2.43	7.34	
13	*Neea madeirana*	1.99	2.33	2.18	6.52	
14	*Tovomita schomburgkii*	2.66	0.47	2.67	5.8	
15	*Unonopsis guatterioides*	0.66	3.6	1.46	5.72	
16–92	36.27	41.96	59.8	138.1		
$\sum$	100	100	100	300		

Table 4
Inventoried area, number of species, and the Sørensen's similarity coefficient (SI) of understory inventories in Amazonian low-várzea (LV) and high-várzea forests (HV) from three different regions. WA = western Amazonian várzea near the city of Iquitos, Peru (Nebel et al., 2001b); CA = central Amazonian várzea, this study; EA = eastern Amazonian várzea near the Amazon estuary (Gama et al., 2002, 2003).

Region				SI (%)		
Inventoried area (m^2)	WA	CA	EA	WA × CA	WA × EA	EA × CA
LV	3200	1570	2500			
HV	3200	1570	2900			
No of species						
LV	166	51	63	4.7	3.5	10.5
HV	160	90	70	4.8	3.5	7.5
LV + HV	204	116	83	8.1	2.7	6.0

heights were significantly related to dbh in both forest types (LV: $R^2 = 0.71$, $P < 0.001$; HV: $R^2 = 0.75$, $P < 0.001$), independent if analyses considered only understory species or all species.

The 15 most important LV species accounted for 66.3% of the TIV, whereas they accounted for 54% in HV (Table 3). Tree species richness was considerably higher in HV (90 species) than in LV (51 species). However, the rarefaction curve did not reach an asymptote in LV, whereas it indicated that sample size in HV was sufficient (Fig. 3).

Out of all recorded species, 66 (56.9%) showed restricted occurrence in HV, and 27 (23.3%) in LV whereas 24 species (20.7%) occurred in both habitats. Floristic similarity (SI) between both forest-types amounted to 35.4%, with highest similarities between plots located in the same forest type, as also indicated by the NMDS (Fig. 4). Despite lower species richness in LV, the NMDS indicated closer floristic relationship within HV plots than within LV plots. The Mantel test also indicated no significant correlation between species similarity and spatial distance between LV plots ($r = 0.02$; $P = 0.82$), whereas it was significant between HV plots ($r = 0.296$; $P < 0.05$).

The Morisita's index of dispersion was calculated for 12 species in LV and 31 species in HV ($n \geq 8$ individuals, Appendix A). Four species, *Neea madeirana*, *Cecropia latiloba, Garcinia brasiliensis* and *Tovomita schomburgkii,* occurred in both forest types. Three LV species and 12 HV species had random or regular dispersion, while the remaining species showed trends of spatial aggregation (clumping). *N. madeirana* was regularly dispersed in LV, but aggregated in HV, while dispersion was opposite in *Garcinia brasiliensis* (Appendix A).

The comparison of the species composition and richness of the forests' understory with that of the overstory (trees ≥10 cm dbh) nearby our studied plots (Wittmann et al., 2002) indicated considerable differences. Although the inventoried area of the understory amounted to only 16% of that of the overstory, tree species richness in the understory accounted for 56% (LV) and 52% (HV) of that of the forest's overstory. In LV, 18 species (35.3%) also were inventoried in the overstory, with floristic similarity (SI) between both strata accounting for 33.9%. Thus, approximately 80% of all species present in the LV overstory were absent in the understory. Conversely, approximately 65% of all understory species were absent in the overstory.

In HV, 34 species (38.2%) also were recorded in the overstory, and the IS between understory and overstory amounted to 35.2%. Again, approximately 80% of all HV overstory species were absent in the understory, while 62% of the understory species were absent in the overstory.

Discussion

Although it is well-known that the flora of the understory of many tropical forests differs considerably from that of the overstory (e.g., Bazzaz, 1991; Bongers et al., 1988; Budowski, 1965; Lieberman and Lieberman, 1987; Oliveira and Amaral, 2005), information about species composition and richness of the forest's understory in Amazonian floodplain forests is scarce. The few available studies that compared floristic composition of the várzea's understory with that of the overstory reported floristic similarities between both strata to range from approximately 30% (late-successional stages; Wittmann and Junk, 2003) to 45–56% (younger successional stages; Nebel et al., 2001b; Wittmann and Junk, 2003). Together with the floristic similarity between both strata found in the present study (35%), and assuming that the

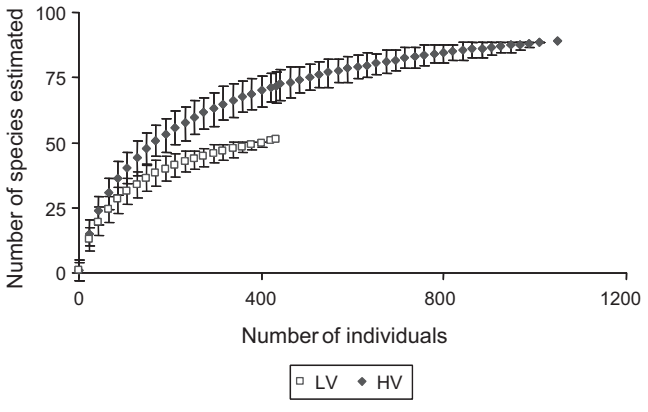

Fig. 3. Number of species accumulated per 100 individuals in low várzea (LV) and high várzea (HV).

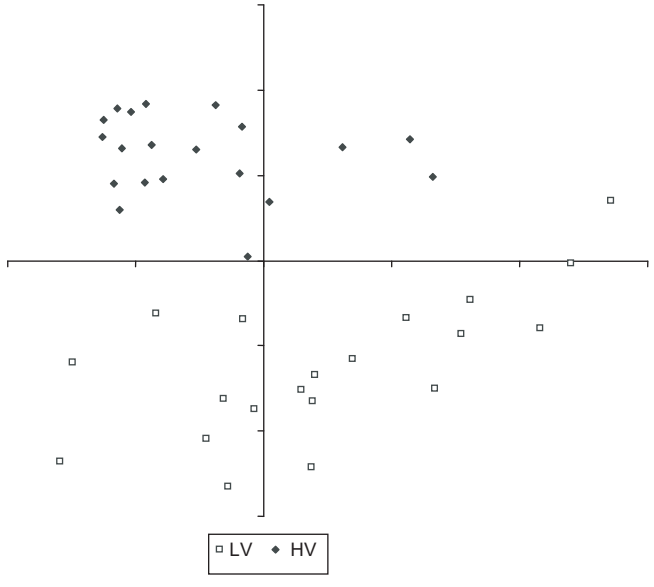

Fig. 4. Ordination analysis (Non-metric multidimensional scaling – NMDS, Kruskal, 1964) of low-várzea (LV) and high-várzea plots (HV).

várzea understory harbors approximately half of the numbers of species of the overstory (present study: 56% in LV, 60.8% in HV), the inclusion of species with restricted occurrence in the understory increases total species richness (all strata) by at least 16% (LV) and 18% (HV). These numbers demonstrate that small trees substantially contribute to total species richness, and that they should be addressed in local floristic inventories that provide the basis for regional and/or basin-wide estimations of tree diversity.

The periodical floods are considered the most important environmental factor influencing growth, species distribution and richness in Amazonian floodplain forests (e.g., Ayres, 1993; Ferreira, 2000; Junk, 1989; Wittmann et al., 2002, 2004). In Amazonian várzea, most tree species are well-zoned along the flooding gradient, thus reflecting the degree of adaptations that were developed to tolerate the seasonally hypoxic or anoxic site conditions. The results of our study demonstrate that the overwhelming part of overstory trees are absent within the understory, in both low-várzea and high-várzea forests. This can be traced to the occurrence of many rare tree species with highly specialized establishment strategies in late-successional floodplain forests (Wittmann and Junk, 2003). Many várzea tree species do not establish consecutively as a response to the periodic inundations, because they may be flooded for several weeks or months. Besides oxygen deficiency, flooding by up to 4 m in height implies that seedlings remain in complete darkness, as light penetration in Amazonian white-waters occurs only to water depths of approximately 50 cm (Furch and Junk, 1997). Successful establishment in many tree species is thus likely to be linked to years with exceptional low inundations, as they occur, e.g., during El Niño years (Schöngart et al., 2005).

Understory trees may be better suitable as bio-indicators for flood-induced growth limitations than larger trees, which maintain parts of stems and crowns above the highest flood-levels. This is especially valid in late-successional stages of the várzea where other biotic and abiotic variables acting on species establishment and distribution are relatively constant. Incoming relative photosynthetically active radiation (rPAR) at the forest floor is reduced by 97–99% in both, low-várzea and high-várzea late-successional forests (Wittmann and Junk, 2003). Although tree species richness is much higher in the high várzea than in the low várzea, structural parameters such as mean maximum tree ages, mean wood specific gravities, stem densities, and basal areas of the overstory are nearly constant in both forest types (Schöngart, 2003; Wittmann et al., 2004, 2006b). Small-scale variations in soil texture, which lead to different degrees of soil aeration in earlier successional stages, are very similar in low-várzea and high-várzea old-growth forests (Wittmann et al., 2004), and small-scaled variability in soil nutrients can be neglected due to the alluvial origin of the substrate (Furch and Junk, 1997). The structural and floristic differences of the understory found in the present study therefore should be primarily linked to the height and duration of the periodical inundations.

Besides increasing tree species richness with decreasing impact of flooding, our results indicate that stem densities are much higher in the high-várzea than in the low-várzea understory. These findings are in accordance with Wittmann and Junk (2003), who reported on stem densities of approximately 2300 and 5000 individuals ha^{-1} in the understory of a low-várzea and a high-várzea forest nearby our study site, respectively, and they are close to densities reported for understory trees in a tropical floodplain forest in Mexico (2250–5000 individuals ha^{-1}, Bongers et al., 1988). In várzea forests, contrasting stem densities in the understory may be directly related to seedling mortality caused by the inundations. Many várzea tree species synchronize fruit production with the highest flood-levels and disperse diaspores by flood waters (Gottsberger, 1978; Goulding, 1983; Kubitzki and Ziburski, 1994; Oliveira Wittmann et al., 2007). The overall dispersed seeds germinate as soon water levels decline and seeds land on substrates. Establishment occurs during the terrestrial phase, and the subsequent inundation selects species able to survive at the respective elevations. Comparatively low stand densities in low-várzea forests therefore suggest high disturbance especially during tree establishment. However, in a floristic inventory of the understory of Peruvian várzea forests, Nebel et al. (2001b) found no differences in stem densities between two forests of contrasting flood heights (4400 individuals ha^{-1}). This possibly reflects the diverging hydrologic conditions between central Amazonian and western Amazonian floodplains: Slopes are higher in the western part of Amazonia than in the central part, and river catchments are smaller. Flood amplitudes are reduced, and flood durations shorter than in central Amazonia. In the western Amazonian várzea, flooded forests are located next to the main river channels, where erosion and sedimentation processes are extreme (e.g. Kalliola et al., 1991; Peixoto et al., 2009; Salo et al., 1986). Low-várzea old-growth forests that are subjected to flood heights >3 m and flood durations >100 days $year^{-1}$ thus are scarce in the western Amazonian várzea, whereas they cover huge areas in the extended floodplains of the central part of the basin.

Tendency of random dispersion is rare in tree populations, and many studies conducted in non-flooded Amazonian forests stated that most species have some degree of spatial aggregation (e.g., Horvitz and Le Corff, 1993; Legendre and Fortin, 1989; Oliveira and Amaral, 2005). However, we found that approximately 25% (LV) and 39% (HV) of the understory species with abundance $\geq$8 individuals had regular or random distribution patterns. Similar values were reported by Gama et al. (2002, 2003) in eastern Amazonian várzea forests (36% in LV, and 32% in HV). Regular or random dispersion in approximately one third of understory trees in the várzea can possibly be traced to seed dispersal by flood-waters. Although most studies describing hydrochoric and ichthyochoric seed dispersal prevailing in low-várzea tree species (e.g., Kubitzki and Ziburski, 1994; Oliveira Wittmann et al., 2007), it is thought that some high-várzea tree species disperse their seeds also by flood-waters even when not primarily being hydrochoric (Marinho, 2008; Oliveira Wittmann et al., 2010). As such, seeds mainly originate from locations outside the studied plots, whereas inventoried trees may disperse to long distances (Wittmann and Junk, 2003), This might explain why many tree species of the overstory lack individuals within the understory, and it contributes to elevated numbers of randomly distributed tree species in várzea forests. On the other hand, the NMDS in the present study indicated higher floristic resemblance between plots of the high-várzea than between plots of the low várzea. This indicates that most high-várzea trees disperse their seeds during the terrestrial phase, which increases the probability of regeneration nearby the mother tree. In fact, most high-várzea tree species are widely distributed across Neotropical forests and not restricted to flooded habitats, whereas low-várzea forests contain a considerable amount of highly specialized and endemic species (Wittmann et al., 2006a). The terrestrial seed dispersal in many high-várzea species could explain why the NMDS indicated higher floristic resemblance between high-várzea plots than between low-várzea plots: In the latter forest type, most seeds are dispersed by water.

A comparison of the floristic composition of the understory in the present inventory with those performed in other parts of the Amazon basin (Gama et al., 2002, 2003; Nebel et al., 2001b) indicated exceptional low floristic similarities in both low-várzea and high-várzea forests (Table 4). The understory species composition among regions differs already at the family level: The overall most important family in the eastern Amazonian várzea forest are the Arecaceae (Carim et al., 2008; Gama et al., 2002, 2003). In western Amazonia, low-várzea forests are dominated by Euphorbiaceae, Myrtaceae, and Olacaceae, whereas high-várzea forests are dominated by Violaceae and Arecaceae (Nebel et al., 2001a,b).

That Arecaceae had especially low importance in central Amazonian floodplains was formerly reported for the overstory of várzea forests (Wittmann et al., 2006a). This fact can be attributed to the exceptional high flood amplitudes in this part of the basin. Many Amazonian palm species are well-adapted to swamps, and have specialized roots such as aerial roots, adventitious roots, and pneumatophores to avoid oxygen deficiency in permanently flooded environments (e.g., *Astrocaryum*, *Socratea*, *Oenocarpus*, *Mauritia*). In environments where flood oscillations are high these specialized roots lose functionality, as they become completely submerged. Therefore, palm species with specialized roots are more likely to establish in the eastern and western Amazonian várzea regions, where flood amplitudes are reduced.

In a basin-wide comparison of floristic inventories in várzea forests (mainly trees ≥10 cm dbh), Wittmann et al. (2006a) found mean floristic similarities of approximately 33% between low-várzea forest inventories, and approximately 12% between high-várzea forest inventories across the Amazon basin. Based on these findings, the authors concluded that low-várzea forests are characterized by pronounced hydrologic connectivity, with many dominant tree species being common over huge geographic distances, from western to eastern Amazonia. By contrast, high-várzea forests share many tree species from the adjacent uplands, which makes them floristically distinct (Wittmann et al., 2004, 2006a). Although our comparison is based on only three understory inventories, we also detected slightly higher floristic similarity in the understories of low-várzea forests than in those of high-várzea forests. However, our values are much lower than those reported by Wittmann et al. (2006a), reinforcing that the understory is an important component of várzea forests with a partially distinct flora. Wittmann and Parolin (2005).

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Appendix A.

Families, species, individual numbers and Importance Values (IV) of all recorded understory species; and spatial distribution of species with n ≥ 8 individuals calculated by the Index of species dispersion (*Id*; Morisita, 1959) in the investigated low-várzea (LV) and high-várzea forest (HV). In *Id*, the *F*-test in brackets indicates the degree of confidence in spatial distribution patterns (Dist), which can be regular (reg), random (ran), or aggregated (agg)

Family	Species	LV	HV	IV	*Id* (*F*)	Dist
Anacardiaceae	*Spondias lutea* L.		2	0.52		
Annonaceae	*Anaxagorea brevipes* Benth.		2	0.79		
	Duguetia quitarensis Benth.		5	2.3		
	Guatteria inundata Mart.		15	3.69	2.47 (2.08)	agg
	Oxandra riedeliana R.E. Fr.	9	1	3.92	1.11 (1.04)	reg
	Rollinia sp.1		4	1.56		
	Unonopsis guatterioides (A. DC.) R.E. Fr.		7	3.9		
	Xylopia calophylla R.E. Fr.		3	1.61		
Apocynaceae	*Aspidosperma rigidum* Rusby		4	1.46		
	Himatanthus sucuuba K. Schum. ex Markgr.	6	8	3.31	5 (2.47)	agg
	Malouetia tamaquarina (Aubl.) A. DC.	4	9	4.03	0.55 (-)	ran
	Rauvolfia sprucei Müll. Arg.	2		0.49		
	Tabernaemontana juruana Markgr.	7		1.3		
	Tabernaemontana sananho Ruiz & Pav.		9	2.36	5 (2.68)	agg
Bignoniaceae	*Tabebuia barbata* (E. Mey.) Sandwith	1		0.53		
Boraginaceae	*Cordia goeldiana* Huber		7	2.08		
Capparaceae	*Capparis* sp.1		1	1.04		
Chrysobalanaceae	*Couepia paraensis* (Mart. & Zucc.) Benth. ex Hook.	8		2.9	3.57 (1.94)	reg
	Licania heteromorpha (Mart. ex Hook. f.) Prance	1		0.51		
	Licania mollis Benth	4	5	3.68		
	Parinari montana Aubl.		1	0.24		
	Tapura juruana (Ule) Rizzini		3	0.85		
Clusiaceae	*Calophyllum brasiliense* Cambess.		3	0.86		
	Garcinia brasiliensis (Mart.) Planch. & Triana	41	13	5.56	LV:20 (41) HV:2.05 (1.66)	LV:agg HV:reg
	Tovomita schomburgkii Planch. & Triana	42	28	10.46	LV:1.72 (2.55) HV:2.78 (3.11)	LV:agg HV:agg
	Vismia guianensis (Aubl.) Pers.		3	0.79		
Connaraceae	*Connarus* sp.1		4	1.02		
Ebenaceae	*Diospyros guianensis* (Aubl.) Gürke	2	3	1.17		
Elaeocarpaceae	*Sloanea* sp.1		4	0.99		
Euphorbiaceae	*Acalypha macrostachya* Jacq.	3		0.66		
	Alchornea discolor Poepp. & Endl.	1	2	0.87		
	Alchorneopsis floribunda (Benth.) Muell. Arg.		33	5.87	1.85 (2.43)	agg
	Aparisthmium cordatum (A. Juss.) Baill	4		0.73		
	Drypetes cf. *variabilis* Uittien	5	2	3.59		
	Hevea spruceana (Benth.) Müll. Arg.	2	2	1.41		
	Hura crepitans L.		8	2.29	3.57 (1.94)	reg
	Mabea nitida Spruce ex Benth.	5	3	4.26		
	Sapium sp.1		2	0.51		

Appendix A (*Continued*)

Family	Species	LV	HV	IV	*Id* (*F*)	Dist
Lauraceae	*Endlicheria* cff. *formosa* A.C. Sm.	2	10	3.85	1.13 (1.15)	reg
	Nectandra amazonum Nees	1		0.45		
	Ocotea cymbarum Kunth		7	1.26		
	Ocotea sp.1		2	0.5		
	Ocotea sp.2		1	0.24		
Lecythidaceae	*Gustavia augusta* L.		4	0.58		
Fabaceae	*Abarema jupunba* (Willd.) Britton & Killip		1	0.27		
	Clitoria amazonum Mart. ex Benth.		2	0.88		
	Clitoria leptostachya Benth.	2		0.78		
	Inga disticha Benth.		2	0.36		
	Inga sp.1	1	37	7.24	5.04 (8.66)	agg
	Inga sp.2	1		0.92		
	Lecointea amazonica Ducke		1	0.49		
	Pterocarpus amazonum (Mart. ex Benth.) Amshoff	7	5	4.47		
	Vatairea guianensis Aubl.		1	0.41		
	Zygia cataractae (Kunth) L. Rico		4	0.66		
Malvaceae	*Pachira aquática* Aubl.		1	0.26		
	Pseudobombax munguba (Mart. & Zucc.) Dugand	7	1	2.89		
	Quararibaea sp.1	2		1.41		
	Herrania mariae (Mart.) Decne. ex Goudot		2	0.49		
	Apeiba echinata Gaertn.		17	3.3	7.2 (6.2)	agg
	Luehea cymulosa Spruce ex Benth.		5	0.77		
Melastomataceae	*Tococa capitata* Trail ex Cogn.		66	8.83	2.78 (7.11)	agg
	Mouriri acutiflora Naudin		1	0.24		
Meliaceae	*Guarea* sp.1		2	0.79		
	Trichilia sp.1		7	2.7		
Moraceae	*Clarisia racemosa* Ruiz & Pav.		32	5.25	2.54 (3.51)	agg
	Maclura tinctoria (L.) D. Don ex Steud.	9		1.88	3.33 (1.98)	agg
	Naucleopsis ternstroemiiflora (Mildbr.) C.C. Berg		40	8.23	1.41 (1.84)	reg
	Pseudolmedia laevis (Ruiz & Pav.) J.F. Macbr.		2	0.52		
	Sorocea duckei W.C. Burger	5		2.13		
Myristicaceae	*Iryanthera juruensis* Warb.		21	5.55	8 (8.36)	agg
	Virola calophylla (Spruce) Warb.		81	12.7	1.5 (3.1)	agg
	Virola elongata (Spruce ex Benth.) Warb		31	6.05	2.58 (3.49)	agg
	Virola surinamensis (Rol. ex Rottb.) Warb.		4	1.56		
Myrsinaceae	*Cybianthus* sp.1	1	2	1.21		
Myrtaceae	*Calyptranthes crebra* Mc Vaugh	7	4	2.83		
	Eugenia sp.1		3	0.84		
	Myrcia fallax (Rich.) DC.		3	0.84		
	Myrciaria dubia (Kunth) McVaugh		10	2.06	1.77 (1.36)	reg
	Psidium acutangulum DC.	1		0.56		
	Triplaris surinamensis Cham.		2	0.55		
Nyctaginaceae	*Neea madeirana* Standl.	21	12	3.19	LV:1.51 (1.29) HV: 2.09 (2.14)	LV: reg HV: agg
Olacaceae	*Heisteria acuminata* (Humb. & Bonpl.) Engl.		17	7.34	2.5 (2.26)	agg
Piperaceae	*Piper* sp.1		2	0.31		
Polygonaceae	*Symmeria paniculata* Benth.	8	1	1.83	4.28 (2.2)	agg
Quiinaceae	*Quiina rhytidopus* Tul.	5		1.26		
Rhamnaceae	*Cormonema spinosum* (Vell.) Reiss.	1		0.57		
Rubiaceae	*Alibertia edulis* (Rich.) A. Rich. ex DC.		16	3.13	2 (1.78)	reg
	Borojoa verticillata (Ducke) Cuatrec.		3	0.68		
	Coussarea ampla Müll. Arg.		189	24.3	2.15 (12.4)	agg
	Duroia duckei Hook. f. ex K. Schum.	22		4.45	7.96 (8.69)	agg
	Faramea sp.1	1	7	1.42		
	Genipa americana L.	1		0.27		
	Palicourea crocea (Sw.) Roem. & Schult.	5		0.71		
	Psychotria sp.1		21	3.06	10 (10.4)	agg
	Psychotria sp.2		15	2.63	1.62 (1.45)	reg
	Psychotria sp.3		11	2.29	1.1 (1.04)	reg
	Psychotria sp.4	4		0.93		
	Psychotria sp.5	8		1.27	15 (6.15)	agg
	Randia sp.1		1	0.24		
	Rubiaceae indet. sp.1		8	3.2		
Salicaceae	*Laetia corymbulosa* Spruce ex Benth.	1		0.25		

Appendix A (*Continued*)

Sapindaceae	*Talisia cupularis* Radlk.		1	0.35		
Sapotaceae	*Chrysophyllum argenteum* Jacq.	1		0.64		
	Elaeoluma glabrescens (Mart. & Eichler) Aubrév.	87		10.6	4.8 (8.69)	agg
	Micropholis egensis (A. DC.) Pierre		14	5.14	1.32 (1.11)	reg
	Pouteria sp. 1		3	1.34		
	Pouteria sp. 2		10	2.64	3.55 (2.2)	agg
	Pouteria elegans (A. DC.) Baehni	4	5	3.51		
	Pouteria gomphiifolia (Mart. ex Miq.) Radlk.	2		0.61		
	Sapotaceae indet. sp. 1		1	0.28		
Solanaceae	*Solanum leucocarpon* Dun.	5	54	7.13	3.62 (8.3)	agg
	Solanum sessile Ruiz & Pav.	2		0.5		
Theophrastaceae	*Clavija lancifolia* Desf.	2	15	4.29	0.57 (-)	ran
Urticaceae	*Cecropia latiloba* Miq.	39	8	6.83	LV:6.82 (12.64) HV:6.43 (3)	LV:agg HV:agg
Violaceae	*Leonia glycycarpa* Ruiz & Pav.	29	5	7.74	5.07 (7)	agg
	Leonia racemosa Mart.		17	2.99	1.76 (1.64)	reg

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