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AMAZONIAN WHITE- AND BLACKWATER FLOODPLAIN FORESTS IN BRAZIL: LARGE DIFFERENCES ON A SMALL SCALE

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Abstract. The floodplains of the Amazon can be differentiated according to the type of flooding water and soil qualities, which reflect their geological origins. In Brazilian Amazonia, the most representative types are those flooded periodically by both whitewater rivers (locally called várzea) and blackwater rivers (called igapó). In these environments, vegetation structure and species composition are clearly different, related to the differences in nutrient availability and sedimentation rate. The objective of the present study was to test the differences in richness, species richness, structure (density and basal area), and composition of tree species in a forest of adjacent igapó and várzea in the Parque Ecológico de Gunma, in Pará state, Brazil. Climate and river hydrology are identical, water and soil quality differ. The sampled sites are only 2 km distant from each other and are connected at high water. The cumulative curve of new species per area reached an asymptote in the várzea forest, but only a tendency towards an asymptote in the igapó forest. The total number of species identified in the igapó floodplain forest was higher (153 species) than in várzea floodplain forest (82 species). Species richness and diversity were not significantly different; density and basal area were significantly lower in the igapó forest than in the várzea forest. It was possible to group the sampled quadrats, and the results show a clear separation of the two types of floodplain forest indicating different species compositions, with both forest types having only 24 species (out of a total number of 208) in common. *Accepted 17 November 2009*.

Resumo. As áreas alagadas da Amazônia se diferenciam em relação ao tipo de inundação, cor da água, tipo de solo, que dependem da origem geológica. Os tipos mais representativos na Amazônia brasileira são as áreas periodicamente inundadas por rios de água branca, localmente denominada de várzeas e rios de água preta ou clara denominados de igapós. Nestes ambientes a estrutura e composição de espécies arbóreas são claramente diferentes, relacionado às diferenças na disponibilidade de nutrientes e da taxa de sedimentação. O objetivo deste trabalho é testar as diferenças de riqueza, diversidade, estrutura e composição de espécies arbóreas em uma floresta de igapó e de várzea no Parque Ecológico de Gunma, Município de Santa Bárbara no estado Pará. O clima e a hidrologia do rio são idênticos, enquanto a qualidade da água e do solo diferem. Eles distam só 2 km uma da outra e são conectados na fase de água alta. A curva acumulativa de novas espécies atingiu a assíntota na floresta de várzea e uma tendência de assintota na floresta de igapó. Foram identificadas 153 e 82 espécies nas florestas de igapó e várzea, respectivamente, mas somente 24 espécies foram comuns em ambas as florestas amostradas (de um total de 208 espécies enocontradas). A riqueza e diversidade de espécies não foram significativamente diferentes entre as florestas amostradas. A densidade e área basal foram significativamente menores na floresta de igapó em comparação a floresta de várzea. Os dois tipos de floresta alagada amostradas foram separados em relação à distribuição dos indivíduos das espécies amostradas.

Key words: *igapó*, *richness*, *species composition*, *structure*, *Várzea*, *vegetation structure*.

INTRODUCTION

Amazonian floodplains occupy about 8% of the Amazonian biome, which lies in several South American countries. These forests have been described by several authors, especially their different structural and floristic characteristics (Ducke & Black 1950, Rodrigues 1961, Takeuchi 1962, Prance 1979, Keel & Prance 1979, Ayres 1986, 1993, Ferreira 1991, 1997a,b, 2000, Worbes 1986, Wittmann *et al.* 2002, Wittmann & Junk 2003, Schöngart *et al.* 2002, Schöngart 2003). Pires and Prance (1985) differentiated seven main types of floodplain based on the type of flooding, water colour, soil type, geological origin, structure, and species composition. Among these, the most representative in Brazilian Amazonia are the floodplains periodically inundated by whitewater rivers (locally called várzea) and by blackwater rivers (locally called igapó). Both floodplain types present cyclic water level fluctuations between the high and low water periods, which reach 12 meters,

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and flooding periods of between 50 and 210 days per year in the plain colonized by trees in Central Amazonia (Junk 1989). This results in a synchronization of most ecological processes, e.g. plant reproduction cycles, animal migrations or human fishing activities. Especially the timing of phenological events (flowering, fruiting) in many species occurs within a short period during high water (Goulding 1980, Worbes 1986, Parolin *et al*. 2002, Schöngart *et al*. 2002). On the other hand, flooding tolerance and the responses to the variation of these inundation cycles vary greatly between species, depending on genetic constitution and plant age (Kozlowski 1984, Junk 1989, Worbes *et al*. 1992, Parolin 2001), which results in a mosaic of habitats within and between floodplain ecosystems.

Tree species richness and distribution in the floodplains are influenced mainly by flooding duration, soil type, plant tolerance to inundation, sedimentation, and erosion (Junk 1989, Worbes *et al*. 1992, Ayres 1993, Ferreira & Stohlgren 1999, Ferreira 2000, Wittmann *et al*. 2002, Parolin *et al*. 2004b, Parolin 2009). Tree species composition is clearly different between várzeas and igapós, probably as a result of the different geological origin of the two ecosystems (Keel and Prance 1979). Várzeas dominate the Amazonian lowlands along the river courses, and are concentrated where sediments have been deposited since the Holocene over the past 10 000 years, whereas igapós are normally associated with soils originating in the Precambrian and the Tertiary period. The differences in nutrient availability in the two systems are reflected by higher primary productivity in várzea and a clear lack of nutrients in igapó (Irmler 1977, Klinge *et al*. 1983, Sioli 1984, Furch 1997). Some authors affirmed that nutrient-rich várzeas are also richer in species than igapós (Kubitzki 1989, Worbes 1997), whereas Ferreira (1997b) observed that species richness and diversity are higher in igapó.

The goal of the present study is to test for differences on a small spatial scale in richness, diversity, structure, and composition of tree species in adjacent floodplain forests of igapó and of várzea in the Parque Ecológico de Gunma, Pará, Brazil (Figure 1). The findings of this study are also a contribution to finding potential areas for protection *in situ* within the park.

METHODS

Study area. The Ecological Park Gunma (PEG), with 580 hectares, is located in the municipality of Santa Bárbara, in the northeast of the state of Pará (1°13'86"S, 48°17'41.18"W), about 48 km from Belém, near the road PA-391 (Figure 2).

Data collection. Twenty-five plots of 20 x 20 m, totalling 1 hectare, were installed in both the igapó and várzea forests, spread over the area in a random design. In each plot, all trees with diameter at breast height DBH ≥ 10 cm were numbered, mapped, measured, and identified to the most specific level possible. The areas are 2 kilometers apart but are connected to each other in the high water period, when water levels are high in the river system of the Igarapé-Tracuateua. Flood level and duration was the same in the plots, documented by the high water marks on the trees inside the plots.

Data analysis. We used analysis of variance to test differences in density (number of individuals) and basal area (calculated from diameter at breast height, dbh) of the trees, as well as species richness and diversity (dependent variables) in the two sampled floodplain forest types (factor) (Systat 10).

We used ordination analysis to test the different distribution of species in the sampled plots in the two floodplain types, using Sørensen's similarity index to compare nearest neighbors (PC-ORD 4).

RESULTS

Cumulative species numbers. In both várzea and igapó a considerable number of new species was found in the first sampled plots, which then decreased with increasing plot number. The cumulative curve of new species presented an asymptote in várzea forest, and a tendency towards an asymptote in the igapó forest (Figure 3), with a minimum sampled area of about 4800 m^2 in várzea and twice as much in igapó.

Diameter distribution. At the community level, both floodplain types presented diameter distribution curves with an inverse j-shaped pattern (Figure 4), with a high concentration of trees in the first diameter class (10-20 cm) and less trees with greater diameters.

Species richness and diversity. Species richness was not significantly different in the two analyzed forests when means were compared, with X = 18.3 species (SD = 3.59) in igapó and X = 16.7 species (SD = 4.71) in várzea (ANOVA, $F_{[1,48]} = 1.734$; $p = 0.194$) (Table 1). Species diversity also was not significantly different between the igapó and várzea analyzed here:

FIG. 1. Floodplain forest of igapó (A) and várzea (B) in the Parque Ecológico de Gunma, Pará, Brazil.

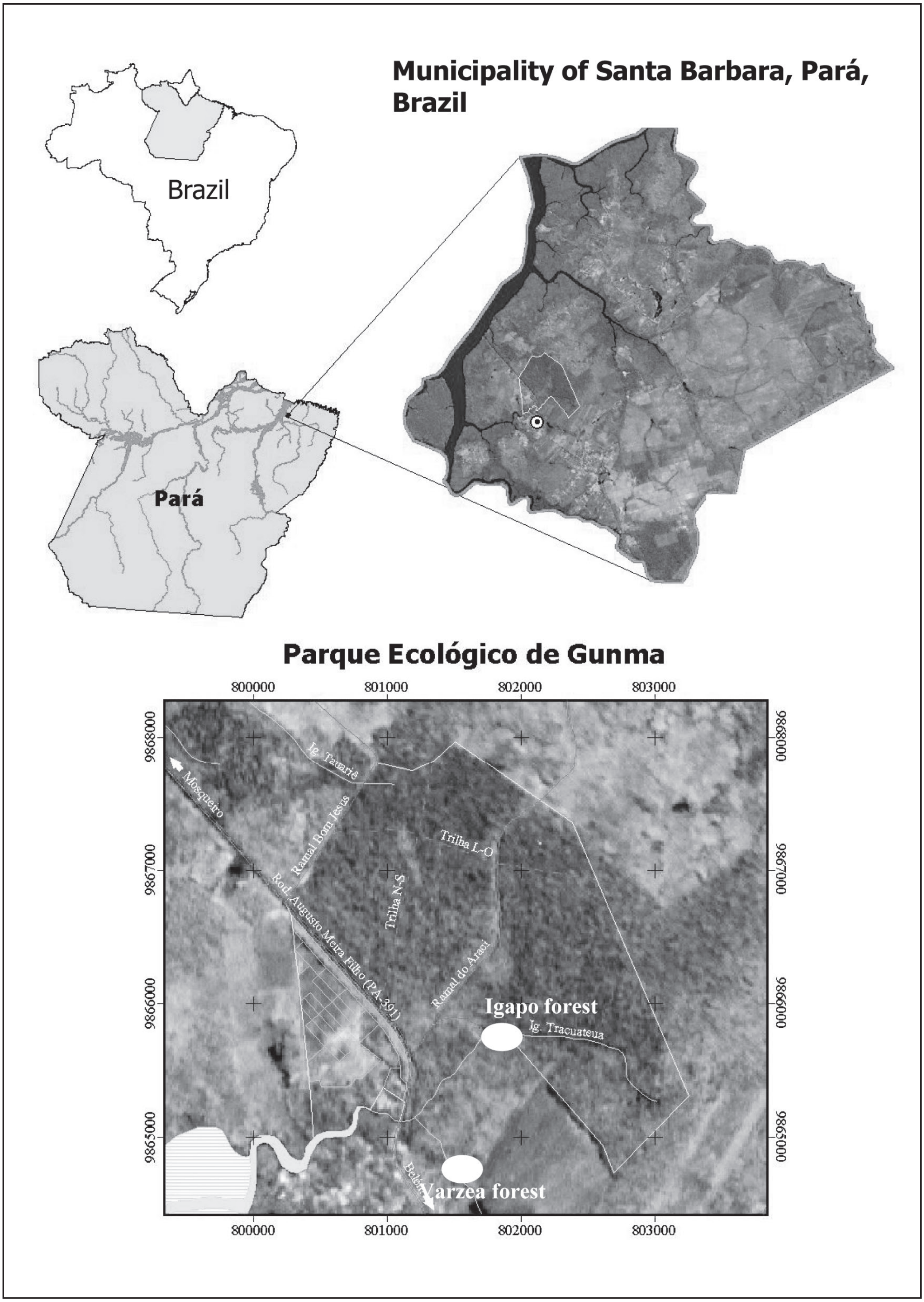

FIG. 2. Location of the Parque Ecológico de Gunma, in the municipality of Santa Bárbara, Pará, Brazil.

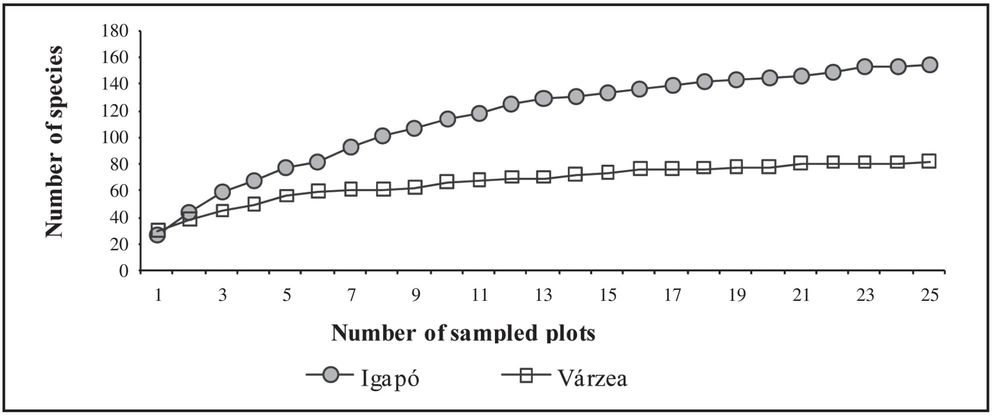

FIG. 3. Cumulative curve of new species in relation to sampled plots in the igapó and várzea forests in this study.

X = 2.78 (SD = 0.28) and X = 2.50 (SD = 0.315) respectively (r^2 = 0.028; $F_{[1,48]}$ = 1.784; P = 0.177) (Table 1).

However, the total number of sampled species was 153 in igapó and 82 in várzea forest, so the igapó forest is clearly more species rich at this study site than the várzea.

Basal area and tree density. Mean basal area was significantly different between the studied forests of igapó (X = 10.402 m^2 ha^{-1}; SD = 3.035) and várzea (X = 11.877 m^2 ha^{-1}; SD = 2.126) (ANOVA, $F_{[1,48]}$ = 3.959; P = 0.05) (Tables 1, 3).

Mean tree density was also significantly different between igapó (X = 23.96 individuals ha^{-1}; SD = 4.31) and várzea (X = 42.00 individuals ha^{-1}; SD = 9.62) in this study (ANOVA, $F_{[1,48]}$ = 73.271; P = 0.0001) (Tables 1, 3).

Species dominance. The five most abundant species in várzea were *Pterocarpus officinalis*, *Euterpe oleracea*, *Macrolobium angustifolium*, *Pentaclethra macroloba*,

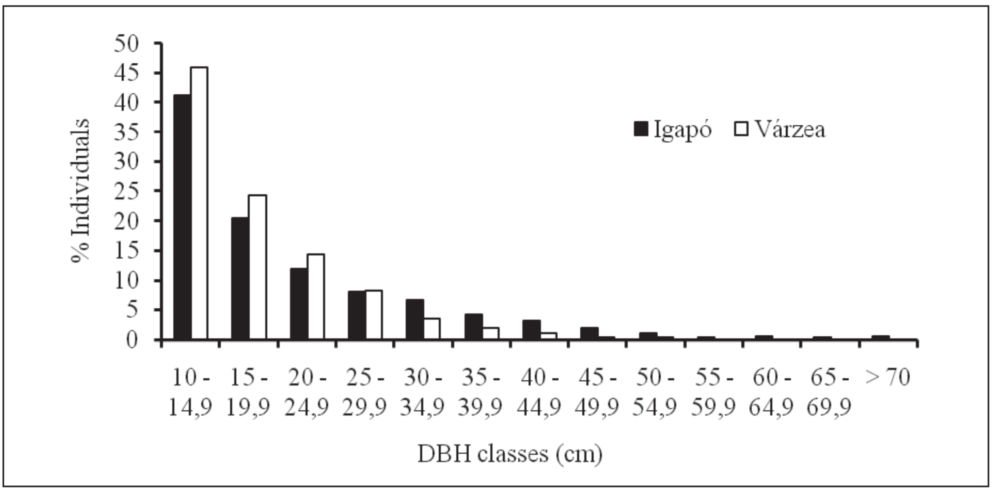

FIG. 4. Proportion of trees according to diameter at breast height (dbh) class in the igapó and várzea forests in this study.

TABLE 1. Species richness and diversity, density and basal area of the trees in the floodplain forests of igapó and várzea sampled in this study.

		Richness	Diversity	Density	Basal area
Igapó	X	18,28	2,778	23,96	10,402
	SD	3,59	0,28	4,31	3,035
Várzea	X	16,72	2,500	42,00	11,877
	SD	4,71	0,315	9,62	2,126

and *Virola surinamensis*, totaling 55% of the total number of individuals in the study area (Table 2). In the igapó forest, the five most abundant species were *Lecythis idatimon*, *Ormosia coutinhoi*, *Symphonia globulifera*, *Caraipa grandiflora*, and *Vochysia inundata*, totaling only 26% of the total number of individuals in the study area (Table 2).

Species distribution. Out of a total of 153 species in igapó and 82 in várzea, only 24 species were common to both forest types (Table 3). The two types of floodplain forest sampled here can be separated from each other by the distribution of individuals of the different species forming two groups in the ordination analysis (Figure 5).

DISCUSSION

The main findings of this study are that a) species richness and diversity were not significantly different in the two forests studied, but b) basal area and tree density were (both higher in várzea than in igapó), and c) species composition shows clearly distinct patterns in the two environments.

The non-significant difference of richness and diversity between the two floodplain forest types support the studies of Ferreira (1997b), who did not find significant species diversity differences in forest

TABLE 2. Phytosociological parameters of the principal tree species of várzea and igapó forest in the Parque Ecológico de Gunma.

	Name	Family	N° of indiv.	Rel. density	Rel. frequency	Rel. dominance	Importance value (%)
Várzea floodplain forest							
1	*Pterocarpus officinalis* Jacq.	Fabaceae	147	14	5,98	15,81	11,93
2	*Macrolobium angustifolium* (Benth.) R.S. Cowan	Fabaceae	116	11,05	5,98	9,24	8,76
3	*Virola surinamensis* (Rol. ex Rottb.) Warb.	Myristicaceae	85	8,1	5,5	10,57	8,06
4	*Pentaclethra macroloba* (Willd.) Kuntze	Fabaceae	101	9,62	5,98	5,74	7,11
5	*Symphonia globulifera* L. f.	Clusiaceae	59	5,62	5,02	10,06	6,9
6	*Euterpe oleracea* Mart.	Arecaceae	123	11,71	4,78	4,12	6,87
7	*Pachira aquatica* Aubl.	Bombacaceae	59	5,62	5,5	7,03	6,05
8	*Caraipa grandiflora* Mart.	Clusiaceae	36	3,43	4,55	2,39	3,46
9	*Swartzia polyphylla* DC.	Fabaceae	25	2,38	3,59	2,96	2,98
10	*Campsiandra laurifolia* Benth.	Fabaceae	27	2,57	3,11	2,52	2,73
Igapó floodplain forest							
1	*Lecythis idatimon* Aubl.	Lecythidaceae	56	9,35	4,86	6,67	6,96
2	*Symphonia globulifera* L. f.	Clusiaceae	25	4,17	3,31	9,36	5,61
3	*Vochysia inundata* Ducke	Vochysiaceae	23	3,84	2,21	4,75	3,6
4	*Ormosia coutinhoi* Ducke	Fabaceae	27	4,51	3,09	2,88	3,49
5	*Licania membranacea* Sagot ex Laness.	Chrysobalanaceae	15	2,5	2,43	4,45	3,13
6	*Caraipa grandiflora* Mart.	Clusiaceae	25	4,17	2,43	2,7	3,1
7	*Dendrobangia boliviana* Rusby	Icacinaceae	20	3,34	2,21	3,56	3,04
8	*Dimorphandra macrostachya* Benth.	Fabaceae	13	2,17	2,65	3,64	2,82
9	*Sterculia pruriens* (Aubl.) K. Schum.	Sterculiaceae	17	2,84	2,65	1,99	2,49
10	*Tovomita choisyana* Planch. & Triana	Clusiaceae	16	2,67	2,65	1,15	2,16

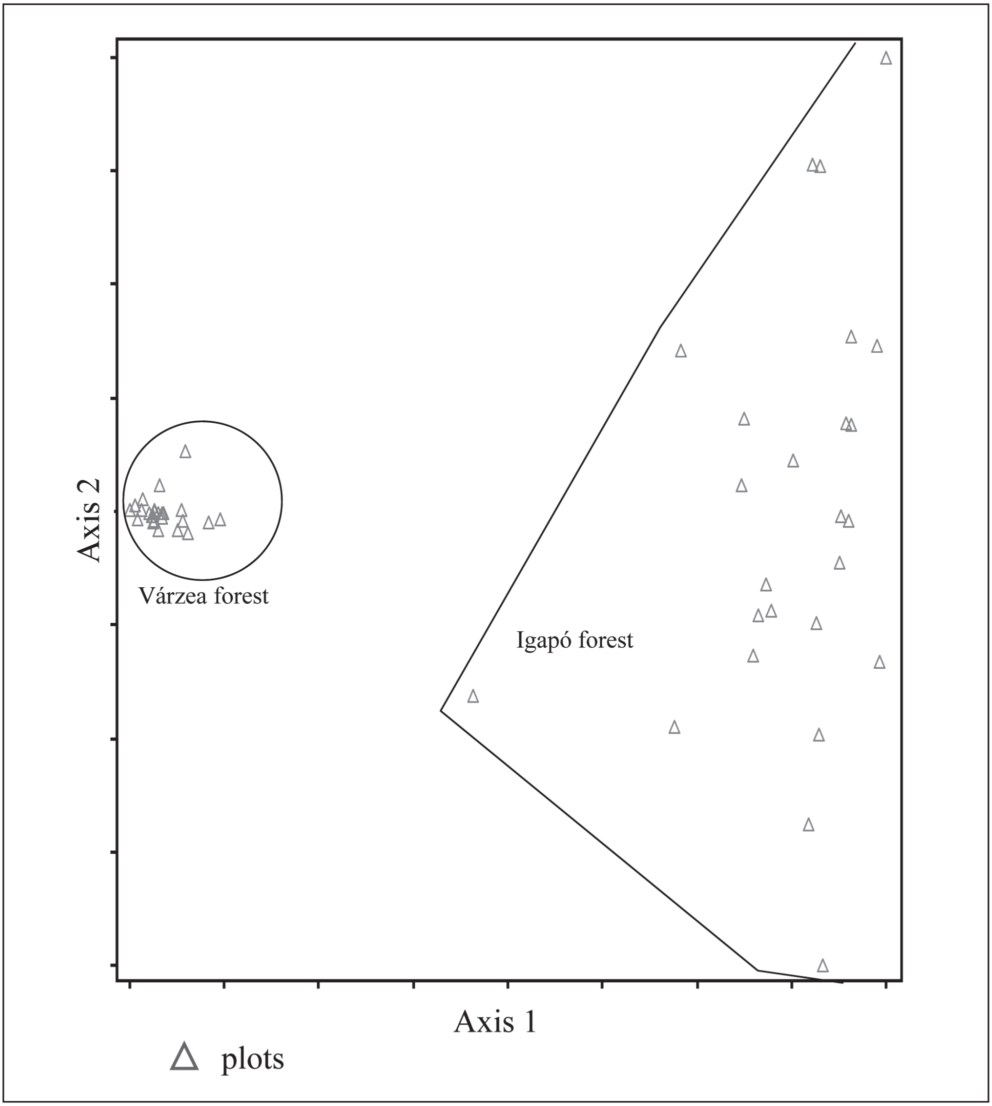

FIG. 5. Ordination analysis of the sampled plots in the igapó and várzea (circle) forests in this study using Sørensen's similarity index and as measure of linking the nearest neighbor (PC-ORD 4).

inventories performed in igapó and várzea forests in Brazilian Amazonia. These findings contradict most other studies, which have concluded that várzea forests are more species rich than igapó forests (Kubitzki 1989, Worbes 1997, Wittmann *et al*. 2002). The focal misunderstanding in this discussion may be that the inventoried plots were not initially related to their topographic positions in the flooding gradient and to the annual flooding duration. Later studies (e.g. Ferreira 1997a, Ferreira & Stohlgren 1999, Wittmann *et al*. 2002) did consider this aspect in their data analyses, and when sites at the same height in the flooding gradient were compared they did not find any differences, just as in the present study. The distinct separation between low-várzea forests and high-várzea forests is also highlighted in the study by

TABLE 3. Species common to both floodplain types, igapó and várzea, in the study area, with number of individuals in the sampled area (1 ha) and mean dbh and standard deviation (sd).

	N° individuals (density)		Mean dbh (cm) ± sd	
	Igapó	Várzea	Igapó	Várzea
Amanoa guianensis Aubl.	2	15	37,80 ± 2,4	14,42 ± 3,2
Caraipa grandiflora Mart.	25	36	17,81 ± 6,9	15,47 ± 4
Carapa guianensis Aubl.	6	22	30,93 ± 11,9	15,98 ± 4,9
Caryocar microcarpum Aubl.	1	8	17,00	14,30 ± 5,2
Cassipourea guianensis Aubl.	1	2	13,10	11,76 ± 1,1
Dimorphandra macrostachya Benth.	13	3	25,20 ± 18,2	42,38 ± 13,9
Diospyros guianensis (Aubl.) Gürke	3	2	25,84 ± 14,9	17,98 ± 8,2
Diplotropis purpurea (Rich.) Amshoff	1	9	41,10	19,20 ± 5,2
Eschweilera collina Eyma	1	1	21,20	24,00
Eschweilera decolarans (Rich.) S.A. Mori	1	2	13,60	13,43 ± 1,4
Eschweilera pedicellata (Rich.) S.A. Mori	6	2	24,15 ± 11,9	16,9 ± 4,0
Euterpe oleracea Mart.	1	123	10,70	11,27 ± 1,2
Guatteria williamsii R.E. Fr.	1	1	18,80	11,00
Iryanthera laevis Markgr.	9	1	13,77 ± 2,3	11,30
Laetia procera (Poepp.) Eichler	4	3	22,19 ± 12,6	18,44 ± 5,2
Licania heteromorpha Benth.	3	3	27,77 ± 6,1	22,05 ± 7,5
Licania membranacea Sagot ex Laness.	15	14	28,80 ± 13,3	15,68 ± 4,8
Licania sclerophylla (Hook. f.) Fritsch	2	1	41,92 ± 12,9	13,80
Ormosia coutinhoi Ducke	27	1	17,19 ± 8,1	9,80
Protium decandrum (Aubl.) Marchand	2	1	18,02 ± 10,6	21,20
Symphonia globulifera L. f.	25	59	32,53 ± 14,4	23,72 ± 9,6
Tapirira cf. *peckoltiana* Engl	2	1	26,07 ± 1,8	11,30
Tovomita choisyana Planch. & Triana	16	2	14,92 ± 4,6	17,25 ± 7,6
Virola surinamensis (Rol. ex Rottb.) Warb.	1	85	15,10	20,77 ± 6,8

Wittmann *et al*. (2006). In this recent study, where only whitewater floodplains are analyzed, Amazonian várzea forests are classified as the most species-rich floodplain forests worldwide (Wittmann *et al*. 2006). Although the study of Wittmann *et al*. includes 44 plots throughout Amazonia covering an area of 62 ha, the lack of data on species occurrence and distribution is still dramatic, even more so in igapó forest. More inventories are urgently needed to at least get an idea of how many species there are and how they are distributed.

The later stabilization of the species-area curve in igapó than in várzea (Figure 3) shows an expected pattern. The várzea species-area curve indicates that sampling was sufficient to cover local species richness, but not so in the igapó where there is only a tendency towards an asymptote. A clear limitation of the present study is the fact that there is no replication of other igapó and várzea forests within the Parque Ecológico de Gunma. This fact may be critical in the igapó forest, which is characterized by high heterogeneity at beta and gamma diversity level (Ferreira & Stohlgren 1999). Whether effects of human impact differ between the two systems cannot be stated in the present study.

Ferreira (2000) showed this phenomenon when studying the variation in species composition along the flooding gradient in two floodplain forests, in the Rio Jaú and Rio Tarumã-Mirim. In both forests, species compositions were grouped according to the period of inundation to which each environment was subjected over the year (beta diversity). The study also showed that species composition between the two rivers – at sites subjected to the same flooding durations – was different, indicating a high gamma diversity.

The higher basal area in várzea is most likely related to the higher productivity of this ecosystem, where high nutrient availability enhances plant growth (Klinge *et al*. 1983, Furch 1997, Junk 1997). Annual increment rings are broader in trees growing in the várzea than in igapó, as was found in *Macro-*

lobium acaciifolium growing in várzea and igapó (Schöngart *et al.* 2005), as well as in other species (Parolin & Ferreira 1998, Fonseca Júnior *et al.* 2008).

The higher tree density found in várzea may also be related to differing nutrient availability in the two ecosystems (Désilets & Houle 2005). This difference is reflected also in species dominance, with the five most abundant species accounting for 55% of the tree individuals in the várzea plots (compared to only 26% in the igapó plots). It is a common pattern in nutrient-rich environments, where high nutrient availability allows single species to dominate and form large homogeneous stands. *Euterpe oleracea*, a species with high tolerance of flooding and sedimentation, typically forms high-density stands in the várzea floodplains.

In the igapó forest, by contrast, under conditions of low nutrient availability species have to compete more strongly for specific niches, which allows more species to become established instead of monospecific stands being formed. The higher number of rare species in the igapó forest accounts for the lower dispersion of plots in the ordination analysis found in the várzea as compared with the igapó. How characteristic these species are of the respective environments is evident when their populations are compared. *Euterpe oleracea* and *Virola surinamensis* are abundant in várzea forest, with 123 and 85 individuals respectively (Table 3). Other species occur with populations reaching 59, 36, or 22 individuals. In igapó, the highest number of individuals per species is reached by *Ormosia coutinhoi* with 27, which occurred in várzea with only one individual and is a clear blackwater specialist. Most other species with high numbers of individuals also occur in high numbers in várzea: *Caraipa grandiflora* (36 individuals in várzea, 25 in igapó), *Symphonia globulifera* (59 and 25) *Licania membranacea* (14 and 15) and thus appear to be generalists. This is a common feature in várzea, and as Wittmann *et al.* (2006) point out, 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.

The higher tree density in várzea was related mainly to a higher number of trees. Tree regeneration is in a good state in all forest plots. The diameter distribution curves of both várzea and igapó (Figure 4) show high concentrations of trees in the lower diameter classes and less trees with greater diameters. This indicates a positive balance between recruitment and mortality, as is typical for the auto-regenerating system of tropical forests.

The clear difference in species composition between várzea and igapó forest in the present study in the Parque Ecológico de Gunma is typical for these environments (Keel & Prance 1979, Ferreira *et al.* 2005) and may be related to the geological origin of the two floodplain systems and the resulting water and soil conditions. Flooding regime and impact are identical in the forest plots, but the hydromorphic soils with high contents of alluvial clay in várzea are responsible for a different set of species than in the igapó, where the hydromorphic soils are of Tertiary origin and very acid, and with low nutrient content (Sioli 1984, Furch 1997). Plant responses to flooding and lack of nutrients are very diversified and depend on the sets of adaptations and growth strategies, and on plant age (Junk 1989, Worbes *et al.* 1992, Parolin *et al.* 2004a, Parolin 2009). The different adaptive strategies of plant species are shown by the distribution of different species with different levels of flooding tolerance along the flooding gradient (Ferreira 1997a, Ferreira & Stohlgren 1999, Wittmann *et al.* 2002) and also by the differing occurrence in the two ecosystems varying in nutrient availability, which is also common among trees in Amazonian uplands (ter Steege *et al.* 2006).

In conclusion, our results show that although species diversity and richness are similar, species composition is distinct in the adjacent floodplain forests of várzea and igapó at study sites in the Parque Ecológico de Gunma. Thus we recommend that whenever management plans and conservation areas are defined for floodplains forests, both várzea and igapó should be included. Furthermore, the clear differences found between the inventoried plots, despite the small distances between them, show the necessity of protecting large areas which cover the whole range of small-scale habitats and different environments along gradients. With the emerging threats to floodplain forests in particular and tropical forests in general (Laurance *et al.* 2001, Laurance & Peres 2006), this is the only way to maximize the conservation of biodiversity.

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