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Floristic composition and topographic variation in a tidal floodplain forest in the Amazon Estuary

JOSÉ H. CATTANIO[1,4], ANTHONY B. ANDERSON[2] and MANOEL S. CARVALHO[1,3]

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ABSTRACT – (Floristic composition and topographic variation in a tidal floodplain forest in the Amazon Estuary). Slight topographic variations appear to exert dramatic effects on the structure of forests subject to inundation. In a late successional tidal floodplain forest near the Amazon port of Belém, Brazil, we examined these effects by studying floristic composition along a topographic gradient. We predicted that, relative to high sites, low sites would be characterized by high representation of life forms and taxa characteristic of inundated sites. We found striking variations in floristic composition along a slight topographic gradient. In comparison with topographically high sites, low sites were characterized by a high representation of Palm trees (Arecaceae), low diversity of trees and lianas, and high plant density. These variations appear to reflect edaphic limitations imposed by periodic flooding. The high spatial variation in floristic composition found in this ecosystem suggest caution in implementing intensive forms of agriculture.

RESUMO – (Composição florística e variação topográfica em uma floresta de várzea no Estuário Amazônico). Pequena variação topográfica aparentemente exerce um dramático efeito na estrutura florestal sujeita à inundação. Em uma floresta de várzea em avançado estágio sucessional de perto do porto amazônico de Belém, Brasil, examinamos este efeito estudando a composição florística ao longo de um gradiente de topografia. Prevíamos que, relativo a locais altos, locais baixos seriam caracterizados por alta representação de formas de vida e táxons característicos de locais inundados. Encontramos impressionantes variações ao longo de um ligeiro gradiente de topografia. Em comparação com locais de topografia alta, locais baixos foram caracterizados por uma alta representação de palmeiras arbóreas (Arecaceae), baixa diversidade de árvores e cipós, e alta densidade de plantas. Esta variação reflete, aparentemente, limitações edáficas impostas pelo alagamento periódico. A alta variação espacial na composição florística encontrada neste ecossistema sugere precaução na implementação de formas intensivas de agricultura.

Key words - Floodplain, floristic, forest, topography, várzea

Introduction

Debate on development options for the Amazon basin has frequently focused on floodplain areas, where relatively high levels of soil fertility hold the promise of supporting sustainable forms of agriculture, thus diminishing land-use pressures on the less fertile uplands (Lima 1956, Sioli & Klinge 1962, Falesi 1974, Alvim 1978). Yet the duration and predictability of the flooding period influences many ecological processes such as productivity, plant distribution, plant demography and reproductive and reproductive biology (Junk 1997)

This study focuses on such a tidal floodplain, which covers a total area of 25,000 - 30,000 km^2 in the Amazon estuary (Lima 1956). Most of this area is covered by secondary forests that - together with floodplain forests elsewhere in the Amazon basin - provided the region's principal source of timber for nearly three centuries (Rankin 1985). Even today, the estuarine floodplain is a critical source of non-timber forest products such as palm heart, rubber, fruit, and game for local populations (Anderson 1990).

The economic importance of floodplain forests in the Amazon estuary indicates the need for sustained management of this ecosystem. Yet little ecological information has been published on these forests that could serve as a basis for their management. This study aims to fill that gap by providing a detailed analysis of the structure of a late successional floodplain forest on Combu Island, located at the mouth of the Guamá River, 1.5 km south of the major port city of Belém (figure 1). These forests are often submitted twice daily to freshwater flooding backed up from tides. High tides temporarily block the flow of the rivers in the estuarine region and cause them to flood the adjacent forest.

Preliminary observations on Combu indicated that slight variations in topography (< 1 m) are associated

1. Museu Paraense Emilio Goeldi, Departamento de Ecologia; currently: Institute of Agriculture in the Tropics (IAT), Grisebachstr. 6, D-37077 Goettingen, Germany.
2. Museu Paraense Emilio Goeldi, Departamento de Ecologia, Av. Perimetral s.n., 66040-170 Belém, PA, Brazil.
3. Museu Paraense Emilio Goeldi, Departamento de Ecologia; currently: Faculdade de Ciências Agrárias do Pará, Departamento de Ciências Florestais.
4. Corresponding author: jcattan1@gwdg.de

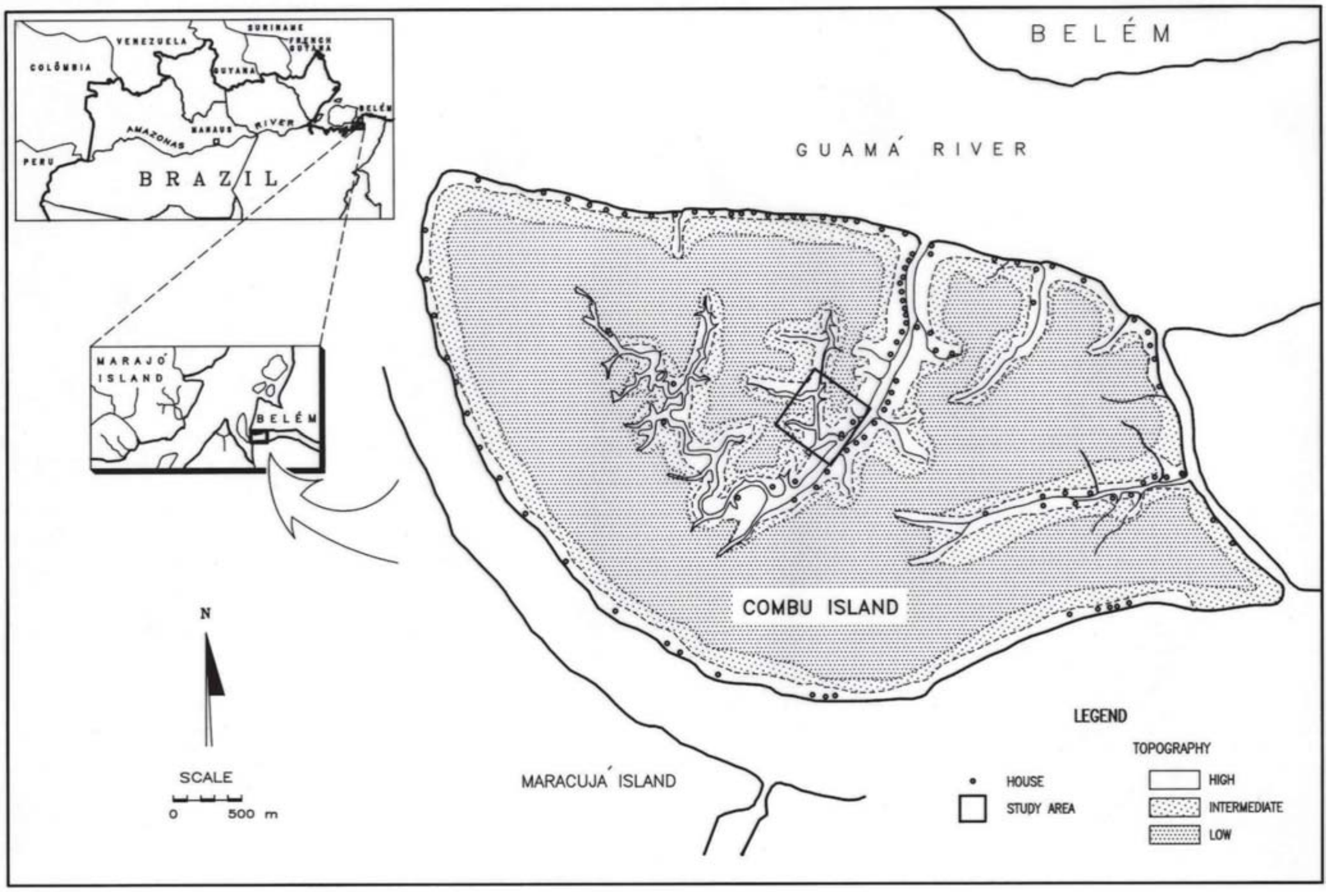

Figure 1. Location of study site in the Amazon estuary and distribution of topographic zones and households on Combu Island, Belém, PA, Brazil.

with dramatic changes in the structure and floristic composition of the floodplain forest (A. Anderson, unpublished data). Such changes appear to reflect the effects of varying degrees of flooding on the vegetation. We examined the vegetation located along a topographic gradient and, consequently, subject to differing frequencies of flooding. Since flooding is associated with anaerobic soil conditions that are stressful to many plants, we predicted that, relative to high sites, low sites would be characterized by i) low diversity of plants, ii) high degree of dominance in a few flood adapted species, and iii) high representation of life forms and characteristic taxa of inundated sites. To test these predictions, we examined forest floristic composition in relation to topography on Combu Island.

Material and methods

The study took place on Combu Island (figure 1). In the nearby city of Belém, monthly temperatures vary from 26 °C to 27 °C, and annual rainfall totals 3,174 mm (mean for 1982-1989, Superintendência do Desenvolvimento da Amazônia – SUDAM, unpublished data). Topographic relief on the island is generally low (< 4 m above mean sea level), and the predominant soil type is a low humic gley (Vieira 1979), characterized by a high percentage of kaolinite clay and silt and a low percentage of sand (Falesi 1986). Due to the low relief and fine texture of the soil, drainage is poor and oxygen levels are low for long periods (S. Subler, unpublished data).

Tide-driven floods exert a powerful effect on soils and topography in the estuarine floodplain (Falesi 1986). For example, oscillations in the water table result in alternating oxidation and reduction in the soil, which are associated with gleying (Sioli 1951, Falesi 1974). Likewise, although low, topographic relief is accentuated by differential sedimentation during floods, in which coarse sediments are deposited on levees adjacent to rivers or streams and fine sediments are deposited behind the levees (Pires 1974, Prance 1979). The effects of these processes are evident in the topography of Combu Island (figure 1). Here, high sites are restricted to areas adjacent to waterways and represent the preferred locations for settlement, while the more extensive low sites occupy most of the central portions of the island and are generally uninhabited.

To characterize the forest structure of the floodplain forest on Combu Island, we selected sampling sites covered by late successional forest that, according to local informants, had undergone little or no disturbance over the past 40 years. Such sites were scarce due to the high population density and intensive forest use on the island. As a result, we were obliged to use small (20 × 25 m, plus a 10 m wide border) sampling plots widely scattered in the central part of island (figure 1). In each plot, we measured the diameter at breast height (dbh) and identified 89, 94% and 98% of the total number de plant with dbh ≥ 5 cm for high, intermediate and low topography, respectively. Voucher specimens were deposited in the herbarium of the Museu Paraense Emilio Goeldi in Belém.

To detect structural variations in relation to topography, the vegetation was sampled along a topographic gradient. With the assistance of local inhabitants, we distinguished three types of forest according to topography (table 1) and location in relation to streams and rivers (figure 1). Four plots (totaling 0.2 ha in area) were located not continuous on topographically high sites, at a mean altitude of 366 ± 5.0 cm (average ± SE) above sea level. Altitudes were derived from a topographic reference point on Combu Island, with the lowest tide as zero (sea level)., and using standard topographic surveying techniques whit theodolite. An additional four plots (totaling 0.2 ha in area) were located not continuous on topographically low sites, at a mean altitude of 312 ± 2.5 cm.

Table 1. Number of plots and altitude (cm) above sea level of vegetation sampling plots on topographically high, intermediate, and low sites on Combu Island, Belém, PA, Brazil. The topographical survey was making with theodolite and using the lowest tide as zero (sea level).

Topography	Number of plots	Total (ha)	Altitude (above sea level) Min. (cm)	Max. (cm)	Average (cm)
High	4	0.2	359.3	383.4	366.5
Intermediate	20	1.0	328.0	343.7	335.7
Low	4	0.2	305.9	317.2	311.8

Finally, we sampled not continuous 20 plots (totaling 1 ha in area) on topographically intermediate sites, at a mean altitude of 336 ± 1.3 cm. Because of small size and discontinuity of the areas this work use small parcels for floristic survey (figure 1).

For each species, we calculated absolute and relative values of abundance, frequency, and dominance (Brower & Zar 1977, Matteucci *et al.* 1982). Importance values were calculated as the mean of relative abundance, frequency, and dominance.

Results

Although the topographically high, intermediate, and low sites were defined by small altitudinal differences (approximately 77 cm), the corresponding forest communities varied considerably in floristic composition.

Along the slight topographic gradient on Combu Island, the largest variations involved the floristic composition of the vegetation. The distribution of palms along this gradient was especially noteworthy. On topographically high and intermediate sites, this family represented 9% and 10% of the total basal area, respectively; in contrast, on topographically low sites palms constituted 40% of the total basal area. All references to parameters of vegetation refer to plants with dbh ≥ 5.0 cm. The varying importance of palms was due largely to a single species, *Euterpe oleracea* Mart., which ranged from 1% of total basal area on high sites to 32% on low sites (tables 2, 3, 4). *E. oleracea* was by far the most dominant, frequent, and abundant species on the low sites, representing more than half (56%) of the individuals present.

The relative dominance of life forms other than palms also varied inversely of dicotyledonous along the topographic gradient (figure 2). The percentage of basal area in lianas (woody vines) was 2% on high sites, 2% on intermediate sites, and < 1% on low sites. The low relative dominance of lianas on topographically low sites could be due to the abundance of palms, which prevent liana establishment by shedding relatively large leaves (Putz 1984).

In addition to Arecaceae, families that exhibited greater relative dominance on topographically low sites included Bombacaceae (22% ± 6.2%), Euphorbiaceae (6% ± 3.8%), Moraceae (7% ± 6.1%), and Myristicaceae (5% ± 2.4%) (figure 3). These families were represented by species characteristic of bottomland sites in Amazon, such as *Quararibea guianensis* Aubl. and, especially, *Pseudobombax munguba* (Mart. & Zucc.) Dugand (Bombacaceae), *Hura crepitans* L. and, to a lesser degree, *Hevea brasiliensis* (Willd. ex A. Juss.) Müll. Arg. (Euphorbiaceae), *Brosimum lactescens* (S. Moore) C.C. Berg (Moraceae), and *Virola surinamensis* (Rol.) Warb. (Myristicaceae) (tables 2, 3, 4). *H. brasiliensis* had a relative dominance of 1.3% and 1.9% on topographically low and intermediate sites, respectively; it was not found on high sites (tables 2-4).

By contrast, the following families showed greater relative dominance on topographically high sites: Anacardiaceae (28% ± 8.3%), Lecythidaceae

Table 2. Composition of plants with dbh ≥ 5 cm in 0.2 ha (4 × 0.05 ha) of topographically high floodplain forest on Combu Island, Pará, Brazil.

Scientific Name	Family	Abundance		Frequency		Dominance		Importance
		ABS	REL	ABS	REL	ABS	REL	
Spondias mombin L.	Anacardiaceae	3	1.26	3	1.42	17,341.5	28.60	10.43
Astrocaryum murumuru Mart.	Arecaceae	21	8.82	17	8.06	3,689.5	6.08	7.65
Euterpe oleracea Mart.	Arecaceae	19	7.98	14	6.64	784.6	1.29	5.30
Sarcaulus brasiliensis (A. DC.) Eyma	Sapotaceae	15	6.30	14	6.64	1,434.8	2.37	5.10
Terminalia dichotoma G. Mey.	Combretaceae	3	1.26	3	1.42	5,568.6	9.18	3.96
Quaribea guianensis Aubl.	Bombacaceae	11	4.62	10	4.74	1,309.2	2.16	3.84
Protium cf. *krukoffii* Swart	Burseraceae	10	4.20	10	4.74	1,389.3	2.29	3.74
Trichilia quadrijuga Kunth	Meliaceae	7	2.94	7	3.32	1,527.1	2.52	2.93
Rheedia macrophylla (Mart.) Pl. & Tr.	Guttiferae	6	2.52	5	2.37	2,143.5	3.53	2.81
Pouteria macrocarpa (Mart.) Dietrich	Sapotaceae	8	3.36	8	3.79	616.9	1.02	2.79
Pithecellobium cauliflorum (Willd.) Benth.	Leguminosae	3	1.26	2	0.95	2,984.3	4.92	2.38
Machaerium cf. *macrophyllum* var. *brevialatum* Rudd	Leguminosae	9	3.78	6	2.84	191.9	0.32	2.31
Lecythis pisonis Camb.	Lecythidaceae	3	1.26	3	1.42	2,487.8	4.10	2.26
Eschweilera coriacea (DC.) S.A. Mori	Lecythidaceae	3	1.26	3	1.42	2,164.7	3.57	2.08
Carapa guianensis Aubl.	Meliaceae	4	1.68	4	1.90	1,508.2	2.49	2.02
Gustavia augusta L.	Lecythidaceae	5	2.10	5	2.37	870.5	1.44	1.97
Rinorea pubiflora (Benth.) Sprague & Sandw.	Violaceae	6	2.52	6	2.84	144.1	0.24	1.87
Couratari sp.	Lecythidaceae	1	0.42	1	0.47	2,732.6	4.51	1.80
Licania heteromorpha Benth.	Chrysobalanaceae	5	2.10	5	2.37	489.2	0.81	1.76
Guarea kunthiana A. Juss.	Meliaceae	5	2.10	5	2.37	375.4	0.62	1.70
Machaerium leiophyllum (DC.) Benth.	Leguminosae	5	2.10	5	2.37	105.4	0.17	1.55
Crudia oblonga Benth.	Leguminosae	1	0.42	1	0.47	2,221.7	3.66	1.52
Unidentified 1	Malpighiaceae	5	2.10	4	1.90	106.2	0.18	1.39
Pentaclethra macroloba (Willd.) Kuntze	Leguminosae	3	1.26	3	1.42	781.3	1.29	1.32
Zygia cf. *juruana* (Harms) L. Rico	Leguminosae	5	2.10	2	0.95	445.5	0.73	1.26
Unidentified 2	Malpighiaceae	4	1.68	4	1.90	89.5	0.15	1.24
Dialium guianense Aubl.	Leguminosae	1	0.42	1	0.47	1,589.6	2.62	1.17
Bauhinia guianensis Aubl.	Leguminosae	4	1.68	3	1.42	85.1	0.14	1.08
Pithecellobium cf. *inundabile* Ducke	Leguminosae	4	1.68	2	0.95	214.6	0.35	0.99
Maximiliana maripa (Aubl.) Drude	Arecaceae	2	0.84	2	0.95	647.1	1.07	0.95
Omphalea diandra L.	Euphorbiaceae	3	1.26	3	1.42	61.3	0.10	0.93
Pachyptera kerere (Aubl.) Sandw.	Bignoniaceae	3	1.26	3	1.42	64.5	0.11	0.93
Combretum cf. *cacoucia* (Aubl.) Excell	Combretaceae	3	1.26	3	1.42	66.2	0.11	0.93
Unidentified 3	Bignoniaceae	3	1.26	3	1.42	61.3	0.10	0.93
Inga nobilis Willd.	Leguminosae	3	1.26	2	0.95	186.4	0.31	0.84
Swartzia racemosa Benth.	Leguminosae	2	0.84	2	0.95	178.2	0.29	0.69
Ampelocera edentula Kuhlm.	Ulmaceae	1	0.42	1	0.47	660.2	1.09	0.66
Couratari guianensis Aubl.	Lecythidaceae	1	0.42	1	0.47	669.3	1.10	0.67
Theobroma speciosum Willd.	Sterculiaceae	2	0.84	2	0.95	91.9	0.15	0.65
Eugenia cf. *muricata* DC.	Myrtaceae	2	0.84	2	0.95	60.4	0.10	0.63
Unidentified 4	Malpighiaceae	2	0.84	2	0.95	59.7	0.10	0.63
Mucuna altissima DC.	Leguminosae	2	0.84	2	0.95	44.1	0.07	0.62
Lophostoma calophylloides (Meisn.) Meisn.	Thymelaeaceae	2	0.84	2	0.95	40.8	0.07	0.62
Caraipa richardiana Camb.	Guttiferae	2	0.84	2	0.95	46.8	0.08	0.62
Lecythis idatimon Aubl.	Lecythidaceae	1	0.42	1	0.47	506.5	0.84	0.58

(cont.)

Scientific Name	Family	Abundance		Frequency		Dominance		Importance
		ABS	REL	ABS	REL	ABS	REL	
Maytenus sp.	Celastraceae	1	0.42	1	0.47	329.9	0.54	0.48
Unidentified 5	Menispermaceae	2	0.84	1	0.47	43.3	0.07	0.46
Doliocarpus dentatus (Aubl.) Stand.	Dilleniaceae	2	0.84	1	0.47	43.3	0.07	0.46
Davilla rugosa Poir.	Dilleniaceae	2	0.84	1	0.47	40.0	0.07	0.46
Oenocarpus distichus Mart.	Arecaceae	1	0.42	1	0.47	280.4	0.46	0.45
Theobroma grandiflorum (Willd. ex Spreng.) K. Schum.	Sterculiaceae	1	0.42	1	0.47	218.9	0.36	0.42
Protium tenuifolium (Engl.) Engl.	Burseraceae	1	0.42	1	0.47	145.2	0.24	0.38
Chaunochiton cf. *loranthoides* Benth.	Olacaceae	1	0.42	1	0.47	151.7	0.25	0.38
Iriartea exorrhiza Mart.	Arecaceae	1	0.42	1	0.47	103.8	0.17	0.36
Licania macrophylla Benth.	Chrysobalanaceae	1	0.42	1	0.47	91.6	0.15	0.35
Parinari cf. *excelsa* Sabine	Chrysobalanaceae	1	0.42	1	0.47	40.7	0.07	0.32
Eugenia cf. *coffeifolia* DC.	Myrtaceae	1	0.42	1	0.47	40.7	0.07	0.32
Unonopsis guatterioides (A. DC.) Fries	Annonaceae	1	0.42	1	0.47	39.6	0.07	0.32
Zygia latifolia (L.) Fawc. & Rendle	Leguminosae	1	0.42	1	0.47	40.7	0.07	0.32
Sterculia speciosa Schum.	Sterculiaceae	1	0.42	1	0.47	28.3	0.05	0.31
Swartzia arborescens (Aubl.) Pittier	Leguminosae	1	0.42	1	0.47	23.6	0.04	0.31
Heisteria cf. *acuminata* (H. et B.) Engl.	Olacaceae	1	0.42	1	0.47	31.2	0.05	0.32
Erythroxylum kapplerianum Peyr.	Erythroxylaceae	1	0.42	1	0.47	23.8	0.04	0.31
Unidentified 6	Bignoniaceae	1	0.42	1	0.47	22.9	0.04	0.31
Casimirella ampla (Miers) R.A. Howard	Icacinaceae	1	0.42	1	0.47	20.4	0.03	0.31
Elvasia sp.	Ochnaceae	1	0.42	1	0.47	19.6	0.03	0.31
Unidentified 7	Bignoniaceae	1	0.42	1	0.47	22.1	0.04	0.31
		238	100	211	100	60,639	100	100

(13% ± 6.1%), and Burseraceae (2% ± 0.9%) (figure 3). Based on their topographic distribution on Combu Island, species that appear to be better adapted to relatively elevated sites include *Spondias mombin* L. (Anacardiaceae); *Lecythis pisonis* Camb., *Eschweilera coriacea* (DC.) S.A. Mori, *Couratari* sp. (Lecythidaceae) and *Protium* cf. *krukoffii* Swart (Burseraceae) (table 2).

In comparison with topographically low sites, on high sites the diversity of tree and lianas was greater, while species dominance was less pronounced (table 2 and 4). In the 0.2 ha areas sampled in each community, we found a total of 45 species on the low sites and 67 species on the high sites. At the same time, the five species with greatest basal area had a combined relative dominance of 68% on the low sites and 48% on the high sites.

Plant density was also found to vary along the topographic gradient on Combu Island (tables 2-4). We found 2,520 individuals.ha^{-1} on the low sites, 1,425 individuals.ha^{-1} on the intermediate sites, and 1,190 individuals.ha^{-1} on the high sites. In addition to high density, the topographically low sites were characterized by a relatively high representation of small-girth individuals. For example, the relative abundance of plants with dbh < 15 cm was 87% on the low sites, compared with 76% and 67% on the intermediate and high sites, respectively (figure 4A). In terms of relative dominance, the differences were even more pronounced: 45%, 20%, and 12%, respectively (figure 4B).

In contrast, the topographically high sites exhibited a relatively high presence of large-girthed individuals. For example, the relative abundance of plants with dbh > 20 cm was 5% on the low sites, compared with 14% and 18% on the intermediate and high sites, respectively (figure 4A). In terms of relative dominance, the figures were 43%, 72%, and 78%, respectively (figure 4B).

Discussion

Pires & Koury (1958) provided descriptive observations concerning the effects of small topographic changes on floodplain forests of the Amazon estuary. The variations in forest structure between the sites

Table 3. Composition of plants with dbh ≥ 5 cm in 1 ha (20 × 0.05 ha) of topographically intermediate floodplain forest on Combu Island, Pará, Brazil.

Scientific Name	Family	Abundance		Frequency		Dominance		Importance
		ABS	REL	ABS	REL	ABS	REL	
Euterpe oleracea Mart.	Arecaceae	244	17.12	118	10.38	13,677.8	4.21	10.57
Quararibea guianensis Aubl.	Bombacaceae	114	8.00	84	7.39	12,160.4	3.74	6.38
Sarcaulus brasiliensis (A. DC.) Eyma	Sapotaceae	81	5.68	74	6.51	14,958.2	4.60	5.60
Spondias mombin L.	Anacardiaceae	11	0.77	11	0.97	47,285.9	14.55	5.43
Astrocaryum murumuru Mart.	Arecaceae	73	5.12	61	5.36	13,747.6	4.23	4.90
Terminalia dichotoma G. Mey.	Combretaceae	17	1.19	17	1.50	38,448.1	11.83	4.84
Theobroma cacao L.	Sterculiaceae	76	5.33	44	3.87	3,191.5	0.98	3.39
Carapa guianensis Aubl.	Meliaceae	30	2.11	28	2.46	13,552.7	4.17	2.91
Protium cf. *krukoffii* Swart.	Burseraceae	42	2.95	40	3.52	6,829.8	2.10	2.86
Iriartea exorrhiza Mart.	Arecaceae	45	3.16	39	3.43	3,345.9	1.03	2.54
Gustavia augusta L.	Lecythidaceae	36	2.53	30	2.64	5,914.3	1.82	2.33
Inga splendens Willd.	Leguminosae	20	1.40	20	1.76	10,400.2	3.20	2.12
Pentaclethra macroloba (Willd.) Kuntze	Leguminosae	30	2.11	27	2.37	5,982.2	1.84	2.11
Crudia oblonga Benth.	Leguminosae	8	0.56	8	0.70	16,386.4	5.04	2.10
Inga sp.	Leguminosae	26	1.82	23	2.02	4,705.6	1.45	1.76
Pouteria macrocarpa (Mart.) Dietrich	Sapotaceae	24	1.68	22	1.93	4,833.3	1.49	1.70
Rinorea pubiflora (Benth.) Sprague & Sandw.	Violaceae	31	2.18	28	2.46	1,238.8	0.38	1.67
Hura crepitans L.	Euphorbiaceae	11	0.77	11	0.97	6,975.9	2.15	1.30
Guazuma ulmifolia Lam.	Sterculiaceae	7	0.49	4	0.35	9,369.7	2.88	1.24
Hevea brasiliensis (Willd. ex A. Juss.) Müll. Arg.	Euphorbiaceae	11	0.77	11	0.97	6,136.4	1.89	1.21
Machaerium leiophyllum (DC.) Benth.	Leguminosae	25	1.75	19	1.67	609.3	0.19	1.20
Zygia cf. *juruana* (Harms) L. Rico	Leguminosae	20	1.40	17	1.50	2,096.3	0.64	1.18
Swartzia racemosa Benth.	Leguminosae	17	1.19	17	1.50	2,191.0	0.67	1.12
Guarea kunthiana A. Juss.	Meliaceae	18	1.26	16	1.41	1,422.5	0.44	1.04
Hernandia guianensis Aubl.	Hernandiaceae	8	0.56	8	0.70	5,469.7	1.68	0.98
Bauhinia guianensis Aubl.	Leguminosae	15	1.05	15	1.32	1,594.5	0.49	0.95
Inga nobilis Willd.	Leguminosae	13	0.91	13	1.14	2,264.7	0.70	0.92
Inga edulis Mart.	Leguminosae	13	0.91	13	1.14	2,107.9	0.65	0.90
Unidentified 3	Bignoniaceae	17	1.19	15	1.32	617.3	0.19	0.90
Hymenaea oblongifolia Huber	Leguminosae	5	0.35	5	0.44	6,060.1	1.86	0.88
Guarea guidona (L.) Sleumer	Meliaceae	12	0.84	11	0.97	2,576.4	0.79	0.87
Trichilia quadrijuga Kunth	Meliaceae	12	0.84	12	1.06	2,225.6	0.68	0.86
Sterculia elata Ducke	Sterculiaceae	4	0.28	4	0.35	6,290.1	1.94	0.86
Mora paraensis Ducke	Leguminosae	2	0.14	2	0.18	7,061.8	2.17	0.83
Omphalea diandra L.	Euphorbiaceae	15	1.05	13	1.14	720.0	0.22	0.80
Virola surinamensis (Rol.) Warb.	Myristicaceae	12	0.84	12	1.06	783.9	0.24	0.71
Sterculia speciosa Schum.	Sterculiaceae	9	0.63	9	0.79	1,720.3	0.53	0.65
Cecropia concolor Willd.	Moraceae	7	0.49	7	0.62	2,751.5	0.85	0.65
Licania guianensis (Aubl.) Griseb.	Chrysobalanaceae	11	0.77	11	0.97	530.7	0.16	0.63
Bactris sp.	Arecaceae	17	1.19	5	0.44	461.7	0.14	0.59
Pithecellobium cauliflorum (Willd.) Benth.	Leguminosae	5	0.35	5	0.44	2,600. 5	0.80	0.53
Davilla rugosa Poir.	Dilleniaceae	10	0.70	7	0.62	528.4	0.16	0.49

(cont.)

Scientific Name	Family	Abundance		Frequency		Dominance		Importance
		ABS	REL	ABS	REL	ABS	REL	
Trichilia micrantha Benth.	Meliaceae	8	0.56	8	0.70	609.1	0.19	0.48
Zygia latifolia (L.) Fawc. & Rendle	Leguminosae	8	0.56	6	0.53	652.2	0.20	0.43
Rheedia macrophylla (Mart.) Pl. & Tr.	Gutifereae	5	0.35	5	0.44	1,450.3	0.45	0.41
Uncaria guianensis (Aubl.) Gmel.	Rubiaceae	8	0.56	6	0.53	294.7	0.09	0.39
Mucuna altissima DC.	Leguminosae	7	0.49	7	0.62	153.0	0.05	0.39
Unidentified 1	Malphighiaceae	6	0.42	6	0.53	580.8	0.18	0.38
Cordia tetrandra Aubl.	Boraginaceae	3	0.21	3	0.26	2,032.8	0.63	0.37
Licania heteromorpha Benth.	Chrysobalanaceae	5	0.35	5	0.44	1,012.4	0.31	0.37
Ocotea cf. *caudata* Mez	Lauraceae	4	0.28	4	0.35	1,428.4	0.44	0.36
Hymenaea cf. *palustris* Ducke	Leguminosae	2	0.14	2	0.18	2,495.7	0.77	0.36
Toulicia guianensis Aubl.	Sapindaceae	5	0.35	5	0.44	623.8	0.19	0.33
Heisteria cf. *acuminata* (H. & B.) Engl.	Olacaceae	6	0.42	6	0.53	148.9	0.05	0.33
Pterocarpus officinalis Jacq.	Leguminosae	2	0.14	2	0.18	2,185.1	0.67	0.33
Unidentified 6	Bignoniaceae	7	0.49	5	0.44	139.0	0.04	0.32
Licaria mahuba (Samp.) Kosterm.	Lauraceae	5	0.35	5	0.44	561.7	0.17	0.32
Macrolobium pendulum Willd.	Leguminosae	3	0.21	2	0.18	1,821.3	0.56	0.32
Machaerium cf. *macrophyllum* var. *brevialatum* Rudd	Leguminosae	6	0.42	5	0.44	220.5	0.07	0.31
Ceiba pentandra Gaertn.	Bombacaceae	5	0.35	4	0.35	673.2	0.21	0.30
Lecythis idatimon Aubl.	Lecythidaceae	5	0.35	5	0.44	342.2	0.11	0.30
Mouriri grandiflora DC.	Melastomataceae	5	0.35	5	0.44	164.9	0.05	0.28
Maytenus sp.	Celastraceae	2	0.14	2	0.18	1,657.0	0.51	0.28
Parinari cf. *excelsa* Sabine	Chrysobalanaceae	4	0.28	4	0.35	606.2	0.19	0.27
Ficus sp.1	Moraceae	3	0.21	3	0.26	1,109.4	0.34	0.27
Cedrela odorata L.	Meliaceae	4	0.28	4	0.35	469.1	0.14	0.26
Unidentified 1	Malphighiaceae	5	0.35	4	0.35	204.1	0.06	0.25
Theobroma speciosum Willd.	Sterculiaceae	5	0.35	3	0.26	409.6	0.13	0.25
Matisia paraensis Huber	Bombacaceae	3	0.21	2	0.18	1,103.8	0.34	0.24
Unidentified 3	Bignoniaceae	4	0.28	4	0.35	208.5	0.06	0.23
Combretum cf. *cacoucia* (Aubl.) Excell	Combretaceae	4	0.28	4	0.35	92.0	0.03	0.22
Symphonia globulifera L. f.	Gutifereae	3	0.21	3	0.26	474.7	0.15	0.21
Tapirira guianensis Aubl.	Anacardiaceae	4	0.28	3	0.26	255.1	0.08	0.21
Coccoloba latifolia Lam.	Polygonaceae	4	0.28	2	0.18	546.0	0.17	0.21
Campsiandra laurifolia Benth.	Leguminosae	2	0.14	2	0.18	924.5	0.28	0.20
Maximiliana maripa (Aubl.) Drude	Arecaceae	2	0.14	2	0.18	922.5	0.28	0.20
Unidentified 2	Malphighiaceae	4	0.28	3	0.26	88.3	0.03	0.19
Lecythis pisonis Camb.	Lecythidaceae	1	0.07	1	0.09	1,293.9	0.40	0.19
Caraipa richardiana Camb.	Guttiferae	3	0.21	3	0.26	231.6	0.07	0.18
Ampelocera edentula Kuhlm.	Ulmaceae	3	0.21	3	0.26	149.3	0.05	0.17
Pachyptera kerere (Aubl.) Sandw.	Bignoniaceae	3	0.21	3	0.26	70.4	0.02	0.16
Entada cf. *palystachya* (L.) DC.	Leguminosae	2	0.14	2	0.18	377.2	0.12	0.15
Genipa americana L.	Rubiaceae	1	0.07	1	0.09	849.7	0.26	0.14
Oenocarpus distichus Mart.	Arecaceae	2	0.14	2	0.18	281.7	0.09	0.14
Phenakospermum guianense Endl.	Musaceae	3	0.21	2	0.18	132.5	0.04	0.14
Dalbergia monetaria L. f.	Leguminosae	3	0.21	2	0.18	69.6	0.02	0.14
Annona montana Macf.	Annonaceae	2	0.14	2	0.18	98.3	0.03	0.12

(cont.)

Scientific Name	Family	Abundance		Frequency		Dominance		Importance
		ABS	REL	ABS	REL	ABS	REL	
Licania macrophylla Benth.	Chrysobalanaceae	2	0.14	2	0.18	95.0	0.03	0.12
Swartzia polyphylla A. DC.	Leguminosae	2	0.14	2	0.18	112.8	0.03	0.12
Casimirella ampla (Miers) R.A. Howard	Icacinaceae	2	0.14	2	0.18	100.9	0.03	0.12
Pithecellobium cf. *inundabile* Ducke	Leguminosae	2	0.14	2	0.18	61.6	0.02	0.11
Derris sp. 1	Leguminosae	2	0.14	2	0.18	72.9	0.02	0.11
Ardisia sp.	Myrsinaceae	2	0.14	2	0.18	70.7	0.02	0.11
Crudia bracteata Benth.	Leguminosae	2	0.14	2	0.18	58.9	0.02	0.11
Unidentified 6	Bignoniaceae	2	0.14	2	0.18	44.1	0.01	0.11
Terminalia guianensis Eichl.	Compositae	1	0.07	1	0.09	490.6	0.15	0.10
Parkia multijuga Benth.	Leguminosae	1	0.07	1	0.09	320.3	0.10	0.09
Chaunochiton cf. *loranthoides* Benth.	Olacaceae	1	0.07	1	0.09	268.7	0.08	0.08
Ficus trigona L. f.	Moraceae	2	0.14	1	0.09	44.2	0.01	0.08
Eugenia cf. *coffeifolia* DC.	Myrtaceae	1	0.07	1	0.09	128.6	0.04	0.07
Derris sp. 2	Leguminosae	1	0.07	1	0.09	136.8	0.04	0.07
Alibertia sp.	Rubiaceae	1	0.07	1	0.09	211.1	0.06	0.07
Simarouba amara Aubl.	Simaroubaceae	1	0.07	1	0.09	186.2	0.06	0.07
Eschweilera coriacea (DC.) S.A. Mori	Lecythidaceae	1	0.07	1	0.09	56.7	0.02	0.06
Pouteria cf. *glomerata* (Miq.) Radlk.	Sapotaceae	1	0.07	1	0.09	36.3	0.01	0.06
Theobroma grandiflorum (Willd. ex Spreng.) K. Schum.	Sterculiaceae	1	0.07	1	0.09	95.0	0.03	0.06
Sophonandra sp.	Solanaceae	1	0.07	1	0.09	33.2	0.01	0.06
Chamaecrista sp.	Leguminosae	1	0.07	1	0.09	43.0	0.01	0.06
Doliocarpus dentatus (Aubl.) Standl.	Dilleniaceae	1	0.07	1	0.09	22.1	0.01	0.05
Sacoglottis amazonica Mart.	Humiriaceae	1	0.07	1	0.09	49.0	0.02	0.06
Couepia sp.	Chrysobalanaceae	1	0.07	1	0.09	49.0	0.02	0.06
Eugenia cf. *lambertiana* DC.	Myrtaceae	1	0.07	1	0.09	31.2	0.01	0.06
Inga velutina Willd.	Leguminosae	1	0.07	1	0.09	26.4	0.01	0.06
Unidentified 8	Leguminosae	1	0.07	1	0.09	22.1	0.01	0.05
Salacia sp.	Celastraceae	1	0.07	1	0.09	50.2	0.02	0.06
Paullinia pinnata L.	Sapindaceae	1	0.07	1	0.09	21.2	0.01	0.05
Hippocratea sp.	Hippocrateaceae	1	0.07	1	0.09	45.3	0.01	0.06
Dioclea sp.	Leguminosae	1	0.07	1	0.09	21.2	0.01	0.05
		1425	100	1137	100	325,045.3	100	100

studied in Combu Island appear to be caused by edaphic factors associated with topography. Specifically, reduced diversity and high representation of palms on topographically low sites may reflect lack of oxygen in the waterlogged soils of such sites, which limits the establishment and survival of seedlings of many plant species (Esau 1967, Lunt *et al.* 1973, Crawford 1989). The vegetation on excessively humid sites frequently exhibits a high abundance of aerial roots and lenticels, which are believed to assist in absorption of oxygen (Winter 1976, Frangi & Lugo 1985). Aerial roots are especially characteristic of palm species such as *Euterpe oleracea*, *Mauritia flexuosa* L. f., and *Iriartea exorrhiza* Mart., which proliferate on topographically low sites on Combu Island. However, Scarano *et al.* (1993), studying root carbohydrate storage in these forests, concluded that plant survival in these floodplain forests seems to be the result of more than only one adaptive mechanism.

The comparison between the two studies in tidal

Table 4. Composition of plants with dbh ≥ 5 cm in 0.2 ha (4 × 0.05 ha) of topographically low floodplain forest on Combu Island, Pará, Brazil.

Scientific Name	Family	Abundance		Frequency		Dominance		Importance
		ABS	REL	ABS	REL	ABS	REL	
Euterpe oleracea Mart.	Arecaceae	284	56.35	55	24.55	23,946.0	32.46	37.79
Quararibea guianensis Aubl.	Bombacaceae	50	9.92	28	12.50	3,972.1	5.38	9.27
Pseudobombax munguba (Mart. & Zucc.) Dugand	Bombacaceae	6	1.19	5	2.23	12,578.6	17.05	6.82
Astrocaryum murumuru Mart.	Arecaceae	21	4.17	15	6.70	4,033.4	5.47	5.45
Hura crepitans L.	Euphorbiaceae	8	1.59	8	3.57	4,752.2	6.44	3.87
Carapa guianensis Aubl.	Meliaceae	13	2.58	12	5.36	1,408.6	1.91	3.28
Virola surinamensis (Rol.) Warb.	Myristicaceae	6	1.19	5	2.23	4,079.4	5.53	2.98
Brosimum lactescens (S. Moore) C.C. Berg	Moraceae	1	0.20	1	0.45	5,087.0	6.90	2.52
Symphonia globulifera L. f.	Guttiferae	7	1.39	5	2.23	2,703.7	3.67	2.43
Bactris sp.	Arecaceae	13	2.58	5	2.23	365.9	0.50	1.77
Inga edulis Mart.	Leguminosae	6	1.19	6	2.68	1,042.2	1.41	1.76
Inga sp.	Leguminosae	6	1.19	5	2.23	1,198.2	1.62	1.68
Gustavia augusta L.	Lecythidaceae	7	1.39	7	3.12	272.3	0.37	1.63
Cordia tetranda Aubl.	Boraginaceae	6	1.19	5	2.23	641.3	0.87	1.43
Theobroma cacao L.	Sterculiaceae	8	1.59	5	2.23	327.5	0.44	1.42
Sarcaulus brasiliensis (A. DC.) Eyma	Sapotaceae	6	1.19	6	2.68	286.6	0.39	1.42
Matisia paraensis Huber	Bombacaceae	4	0.79	4	1.79	474.8	0.64	1.07
Zygia latifolia (L.) Fawc. & Rendle	Leguminosae	7	1.39	3	1.34	278.1	0.38	1.04
Inga nobilis Willd.	Leguminosae	4	0.79	4	1.79	326.8	0.44	1.01
Hevea brasiliensis (Willd. ex A. Juss.) Müll. Arg.	Euphorbiaceae	2	0.40	2	0.89	946.9	1.28	0.86
Sterculia speciosa Schum.	Sterculiaceae	3	0.60	2	0.89	749.9	1.02	0.84
Parinari cf. *excelsa* Sabine	Chrysobalanaceae	2	0.40	2	0.89	749.9	1.02	0.77
Inga splendens Willd.	Leguminosae	3	0.60	3	1.34	236.0	0.32	0.75
Scheelea huebneri Burret	Arecaceae	1	0.20	1	0.45	967.1	1.31	0.65
Pentaclethra macroloba (Willd.) Kuntze	Leguminosae	2	0.40	2	0.89	290.6	0.39	0.56
Ficus sp.1	Moraceae	2	0.40	2	0.89	279.7	0.38	0.56
Bauhinia guianensis Aubl.	Leguminosae	2	0.40	2	0.89	226.1	0.31	0.53
Crudia bracteata Benth.	Leguminosae	2	0.40	2	0.89	228.1	0.31	0.53
Zygia cf. *juruana* (Harms) L. Rico	Leguminosae	2	0.40	2	0.89	106.1	0.14	0.48
Toulicia guianensis Aubl.	Sapotaceae	2	0.40	2	0.89	96.7	0.13	0.47
Mouriri grandiflora DC.	Melastomataceae	2	0.40	2	0.89	83.7	0.11	0.47
Omphalea diandra L.	Euphorbiaceae	2	0.40	2	0.89	56.5	0.08	0.46
Swartzia racemosa Benth.	Leguminosae	2	0.40	2	0.89	65.6	0.09	0.46
Sterculia elata Ducke	Sterculiaceae	1	0.20	1	0.45	411.7	0.56	0.40
Guarea guidona (L.) Sleumer	Meliaceae	1	0.20	1	0.45	132.7	0.18	0.28
Cecropia concolor Willd.	Moraceae	1	0.20	1	0.45	88.2	0.12	0.26
Ampelocera edentula Kuhlm.	Ulmaceae	1	0.20	1	0.45	43.0	0.06	0.24
Combretum cf. *laxum* Jacq.	Combretaceae	1	0.20	1	0.45	36.3	0.05	0.23
Dalbergia monetaria L. f.	Leguminosae	1	0.20	1	0.45	30.2	0.04	0.23
Ficus trigona L. f.	Moraceae	1	0.20	1	0.45	25.50	0.03	0.23
Pterocarpus amazonicus Huber	Leguminosae	1	0.20	1	0.45	27.33	0.04	0.23
Hernandia guianensis Aubl.	Hernadiaceae	1	0.20	1	0.45	25.5	0.03	0.23
Licania guianensis (Aubl.) Griseb.	Chrysobalanaceae	1	0.20	1	0.45	30.2	0.04	0.23
Uncaria guianensis (Aubl.) Gmel.	Rubiaceae	1	0.20	1	0.45	37.4	0.05	0.23
Unidentified 1	Malpighiaceae	1	0.20	1	0.45	21.2	0.03	0.23
		504	100	224	100	73,766	100	100

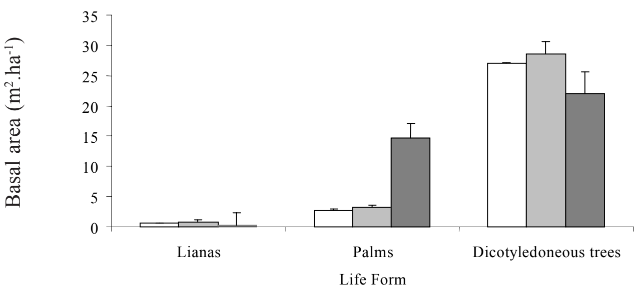

Figure 2. Total basal area of life forms on topographically high, intermediate and low sites on Combu Island, Belém, PA, Brazil. □ High sites, ■ Intermediate sites, ■ Low sites.

floodplain showed different diversity (table 5). Pires & Koury (1958) showed approximately the same number of plants in comparison with this study, but they found a lesser number of species, genera and families. The studied area in Combu Island was, according to local inhabitants, over the past 40 years with little or no disturbance. The different species diversity in this two areas maybe due to differences in soil chemistry and/or topography level, or recuperation of anthropogenic disturbance.

The few detailed studies focusing on floodplain forests in the Amazon basin emphasize their distinctiveness in relation to other forests. Compared with upland or "terra firme" forests, for example, floodplain forests in the Amazon are characterized by low diversity and high dominance of few flooded adapted species, many of which are economically important (Lima 1956, Pires & Koury 1958, Salo *et al.* 1986, Gentry & Dodson 1987, Peters *et al.* 1989, Anderson 1990, Kahn & Mejia 1990).

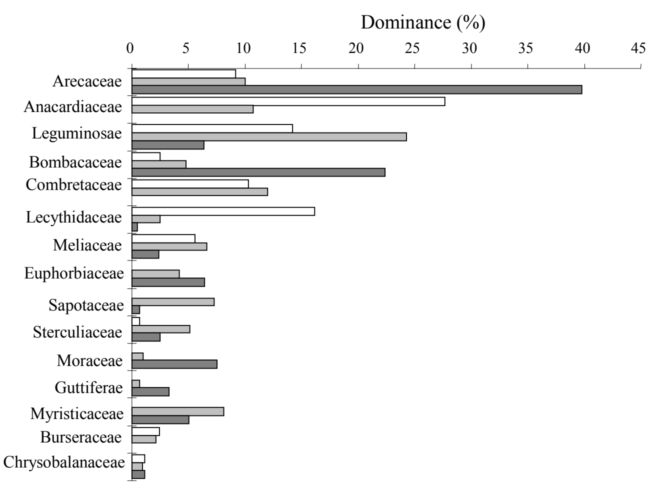

Figure 3. Dominance of selected 15 more important plant families on topography high, intermediate, and low sites on Combu Island, Belém, PA, Brazil. □ High sites, ■ Intermediate sites, ■ Low sites.

In comparison with other primary neotropical forests, the secondary tidal floodplain forest on Combu Island exhibits intermediate diversity (table 5). In contrast, the density of individuals with dbh > 10 cm is relatively high in this forest, as well as the sum of their basal areas (table 5). Intermediate low diversity may be the result of excessive soil moisture, which impedes the establishment of numerous forest species typical of upland sites; it may also be due to previous disturbance of the vegetation. High plant density, in turn, appears to reflect the dynamic nature of the floodplain ecosystem. In short, as well as floodplain forests elsewhere in the Amazon (Salo *et al.* 1986, Kahn & Mejia 1990), the floristic composition and structure of the floodplain forest on Combu seem to be determined by the frequency and intensity of an array of natural and anthropogenic disturbances, such as flooding and extraction of economic products.

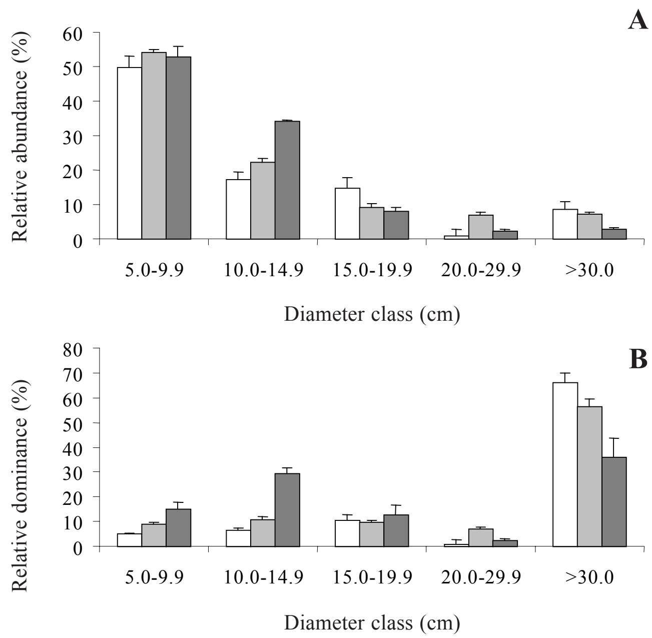

Figure 4. Diameter class and relative abundance (A) and dominance (B) of plants on topographically high, intermediate, and low sites on Combu Island, Belém, PA, Brazil. □ High sites, ■ Intermediate sites, ■ Low sites.

The findings of this study have implications for the management of tidal floodplain forests such as those found on Combu Island. As noted in the introduction, these and other forested ecosystems in the Amazon

Table 5. Comparison of floristic composition and basal area of neotropical forests (area = 1 ha and dbh > 10 cm). Data obtained from topographically intermediate sites (mean altitude = 3.36 m above sea level).

Location	Forest type	Families	Genera	Species	Plants (n.)	Basal Area (m^2ha^{-1})	Source
São Carlos, Venezuela	Upland			83	744	27.8	Uhl & Murphy 1981
Alto Ivon, Bolivia	Upland	28	61	94	649	21.5	Boom 1986
Carajás, Brazil	Upland	53	146	210	456	17.6	Silva *et al.* 1987
Carajás, Brazil	Upland	30	86	122	484	21.6	Salomão *et al.* 1988
Belém, Brazil	Floodplain	21	44	53	539		Pires & Koury 1958
Puerto Rico	Floodplain			27		42.4	Frangi & Lugo 1985
Belém, Brazil	Tidal floodplain	31	74	84	588	29.5	This study

floodplain are frequently cited as promising sites for conversion to intensive agriculture. High topographic variation in floristic composition in the Combu Island suggests caution in implementing such land use in floodplain forests of the Amazon estuary.

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