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CLASSIFICATION OF WATER BODIES BASED ON BIOTIC AND ABIOTIC PARAMETERS AT THE VÁRZEAS OF MAMIRAUÁ RESERVE, CENTRAL AMAZON.

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RESUMO

Visando descrever e melhor compreender os ambientes aquáticos dos lagos de várzea da Reserva Mamirauá ao longo do ciclo hidrológico da Amazônia, uma amostra de 11 lagos foi escolhida por sua acessibilidade e diversidade de ambientes. Estes foram visitados a cada estação do ciclo por dois anos consecutivos, e nestas visitas foram coletados dados morfológicos e limnológicos do lago, além de dados sobre a sua diversidade biológica. As macrófitas aquáticas e os invertebrados encontrados na sua zona radicular (especialmente moluscos, crustáceos, aracnídeos e insetos) foram os grupos taxonômicos focalizados. Toda a informação coletada foi utilizada para ordenar e agrupar as amostras, e gerar categorias amplas para os lagos da Reserva Mamirauá. Todos os lagos amostrados apresentaram alta similaridade entre eles, com a exceção de um, que se mostrou mais similar ao rio principal mais próximo. Entretanto, dois grupamentos distintos foram identificados, principalmente devido a diferenças na condutividade da água, sua temperatura, e presença ou abundância relativa de alguns grupos de alguns grupos de invertebrados. Estes grupos foram consistentes com a morfologia dos lagos, a existência de barrancos ou praias nas suas beiras, o tipo de vegetação marginal, e a origem geomorfológica dos lagos. Estas conclusões são úteis para a avaliação dos níveis de significância dos ambientes aquáticos nas zonas de proteção permanente da reserva e para o desenho de estudos posteriores da ecologia aquática na região.

PALAVRAS-CHAVE: Lagos de várzea, limnologia amazônica, classificação ambiental, ecologia aquática, Mamirauá.

ABSTRACT

In order to describe and better understand the aquatic environment of the várzea lakes at Mamirauá Reserve throughout the Amazonian hydrologic cycle, a sample of 11 of those lakes were chosen mainly for their accessibility and diversity. They were visited every season, for 2 consecutive years and morphological, limnological and biodiversity data was recorded. The aquatic macrophytes and the invertebrates (specially molluscs, crustaceans, arachnids, and the insect orders) found in its root zone were the taxonomic groups aimed. All information was used to group and ordinate the samples, to generate broad categories of lakes for Mamirauá Reserve. All sampled lakes proved to present high similarity with others, with the exception of one, more similar with the closest main river. However, two distinct groups were identified, mainly due to differences in conductivity of the water, its temperature and the presence or relative abundance of particular groups of invertebrates. These groups were consistent with the morphology of the lakes, the types of banks and levees, the type of riparian forest and the geomorphologic origin of the lake. This conclusion is useful for the evaluation of significance levels of aquatic environment at protected zones for the management of the reserve, and for the design of further ecologic research on the aquatic environment at the area.

KEYWORDS: Várzea lakes, Amazonian limnology, environment classification, aquatic ecology, Mamirauá.

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INTRODUÇÃO

The Amazon is the biggest bloc of tropical forest remaining in the world today (W.R.I., 1988). The Amazon River is the major factor defining this forest (SIOLI, 1984). The Amazon Basin is larger than Europe (Russia excluded), with 6,300,000 km^2, and covers an immense area with tributaries, small creeks, channels, swamps, and many other aquatic environments.

About 60% of the Amazon lies in Brazilian territory, and the rest of it extends to parts of Bolivia, Peru, Colombia, Ecuador, Venezuela, the Guyana and Suriname. The northern limit for the Amazon is the Mountain Complex of Parima-Paracaíma; the western limit is made by the Andes and the eastern limit is the Atlantic Ocean; the Cerrado,a savannah-like vegetation domain that covers the Central Brazilian Plateau sets the southern limit (AYRES, 1993).

The geological history of the Amazon is quite recent, and started about 20 million years ago. Due to changes on the sea level, heavy tropical rain and sedimentation processes, the Amazon region has a central part with a very flat relief, covered in sedimentary detritus. The altitudinal gradient from the foothills of the Andes towards the coast is less than 200m. There also is not much variation in the annual temperature, around 31 to 35ºC in average, but there is a strong variation in rainfall for different parts of the basin. While the average annual rainfall is 2,200mm, it can vary from 1,600 up to 6,000mm every year at different sites (AYRES, 1993).

This much rain, especially in the heads of the main river and its tributaries, combined with the partial melt of Andean glaciers during the summer, affect tremendously the level of the water in almost all Amazonian rivers. Close to the Atlantic coast, annual variation on the water level is usually around 4 to 7m, only. In the opposite part of the Amazon, closer to the Andes, this variation can reach up to 15 or even 20m every year (AYRES, 1993). As a consequence, most of the forests in the central part of the Amazon, laying in a low relief, is annually flooded by an enormous mass of water that runs west to east like a wave that lasts almost 7 months, from Peru to reach the Atlantic (BARTHEM; GOULDING, 1997). This was appropriately described as a flooding pulse (JUNK et al., 1989), with a strong impact on the vegetation and other components of the Biota (PIEDADE et al., 2000).

It is the variation of the water level, along with the precipitation of rain, the main aspects to define the Amazonian seasonality. Atypically, seasons at the Amazon are not the usual temperate cycle of spring-summer, autumn-winter. Floods, or "High Water" (cheia), and droughts, or "Low Water" (seca), are the extreme points of a cycle, and the intermediate steps are the "Raising of Water Level" (enchente) and the"Dropping of Water Level" (vazante). These seasons vary in duration and in timming among different sites in the Amazon and in between years, but always have a strong ecological meaning wherever and whenever it is considered. Big changes in the patterns of primary production in the forests are observed (QUEIROZ, 1994; PIEDADE et al., 2000; SCHÖNGART; JUNK; 2007), but equally strong impacts are also observed in the fish fauna and the fish resource (QUEIROZ; CRAMPTON, 1999).

The Amazon River, from its head to its mouth, travels about 6.600km to discharge into the ocean 175.000m^3 of water each second (AYRES, 1993), and its silt can be transported through the sea until the end of Suriname's cost line (AMATALI, 1993), in the northern end of the continent. Total annual Amazon water discharge means one fifth of all river discharges into the oceans of the planet (BARTHEM; GOULDIN, 1997). It runs almost parallel to the Equator Line, and maximum divergence is reached in Peru, with only 4ºS. In the Brazilian Amazon alone, the big river has about one thousand known affluent rivers, and some of them, like the Madeira, Purus, Juruá, Tapajós and Xingu rivers, are more than 1,500 km long. It can be consequently understood that the Amazon Region is mainly defined and sustained by its water bodies, forming the Amazon Basin.

General morphology, hydrology, and ecology of Amazonian rivers are mainly defined by the chemical and physical properties of their waters (FURCH, 1984), which are consequence of their geological substrates (AYRES, 1993). This is the basis for the more comprehensive system of classification of Amazonian rivers used to date (SIOLI, 1975). Named after the colours of the waters, Amazonian rivers are grouped in three categories.

Black-water rivers, like Negro, Tefé and Jutaí rivers are originated at the archean lowlands, at south and north of the Amazon. The general dark coloration is due to a high level of humic acid dissolved, and to low levels of sediment in the water. Nutrients solved in the water are equally low, as it is the pH (as low as 2.4 or 3.8 in some sites of Negro River). Forests flooded by this type of river are known as "igapós". Clear-water rivers, as Xingu, Tapajós and Araguaia rivers are originated far north or south, at the Central Brazilian Shield or at the Guyana Shield. With high transparency, these rivers have higher levels of sediments, though. The amount of dissolved nutrients varies, as the water pH. Forests flooded by clear-water rivers are also denominated "igapós". White-water rivers, as the Amazon itself, Purus and Madeira rivers, are originated at the Andes or at the Andean slopes, and carry a large amount of sediments since their origins. The great amount of sediments gives the beige colour to the water. There is also a high level of nutrients dissolved along with the sediments, and water pH ranges from 6.0 to 7.2. The sedimentation that takes place at the lowlands of the Central Amazon creates all different sorts of intricate systems of channels, river islands and archipelagos, lakes and other water bodies. This water-related morphology varies from one year to another, due to the dynamics of the water level, destroying land during floods and creating lands due to the sedimentation processes during the droughts. The forests flooded by white-water rivers are called "várzea".

The várzea environment

Várzea accounts for only 2-3% of the whole Amazon Basin area, but play a major role in Amazonian life. Most of the human population is located in várzea, due to its high productivity. Apparently várzea forests were also important during the colonisation period (LA CONDAMINE, 1778; BATES, 1892), when most of the economic activities were developed in this environment, and even before that (Carvajal, in Medina, 1894), when native Amazonians lived in large settlements along the white-water rivers. The high biological productivity and the high bio and social diversity in várzea are due to the diversity of environments and the high nutrient levels of its waters (GOULDING, 1999). So, these are a direct consequence of the sedimentation process. As such, várzea has been heavily exploited for centuries, especially as a source of natural resources (for hunting, fishing and logging) or as very fertile agricultural grounds.

Várzea is a very recent geological event. As a result of erosion and sedimentation, the older parts of várzea were formed during the inter-glacial periods of the Pleistocene, in areas where erosion was not complete, while the more recent parts of várzea were formed during the Holocene, in lower areas, and it is still in progress. The degree of erosion and deposition of sediments, and the size of particles deposited, seems to be determined by a large number of variables, among which are water speed and the profile of the annual flooding. There is a tendency of larger sediments be deposited close to or on the banks of channels and lakes, forming levees. Behind the banks it is usually observed the deposition of thinner sediments. This contributes to the maintenance of relief differences between these two parts, and is a consequence of their distances to the closer water body. So, in general, major relief features in várzea are the sand beaches or mud beaches, banks and levees, and also the low areas in the back, result of the deposition of thinner sediments. As the sediment deposition and the annual flooding are part of a strong dynamic process, channels can be pushed away along time, new islands can be formed or destroyed in a matter of a few years, and new lakes can be isolated in old and abandoned channels in one single year. This continual reworking of the floodplain is described (HENDERSON et al., 1998) and detailed (PUHAKKA et al., 1992), where the scaling of lake sizes in várzea, and the time scale of their formation are discussed.

The major relief features present define the types of vegetation they can support, since the relief determines the length and depth of the flooding in each of the habitats (AYRES, 1993). The forests of várzea at the study site are described in more detail in Ayres (1993) and Queiroz (1994), in terms of their composition, structure and phenology. Várzea forests are generally lower and less diverse when compared with forests growing in dry high areas of the amazon, outside the floodplain. The water level during floods determines the structure and composition of várzea forests in its different habitats, as determines major anatomical and physiological adaptations in tree species living there. As such, tree communities tend to be endemic to várzea, and a few endemic species can be found. On the other hand, there is an endemic vegetation community made of aquatic macrophytes that encompass almost 60 different species and harbour part of the invertebrate biodiversity that can be found in várzea (JUNK, 1970; 1973).

Endemic animal species are also present in várzea, among vertebrates and invertebrates (AYRES, 1993). Also, a large number of vertebrate endangered or threatened species can still be found in this environment. Again, as among trees, biodiversity of vertebrates is lower than in dry higher surrounding areas, but adaptations for living in a place under an annual flooding regime are responsible for the presence of unique communities (PROJETO MAMIRAUÁ, 1996). There are an estimated 2,800 to 3,000 fish species in the Amazon Basin (VAL; ALMEIDA-VAL, 1995). Várzea sites seem to hold around 10-15% of this diversity, and hold a great diversity of forms and lifestyles (HENDERSON; ROBERTSON, 1999). The high productivity of várzea makes it an important site for fisheries development and exploitation at the Amazon (GOULDING, 1999).

The objective of this study was to describe and better understand the aquatic environment of the várzea environment at Mamirauá Reserve throughout the seasonal cycle, with especial attention to what is locally called "lakes".

METHODS

The study site was the várzea forest of Mamirauá Sustainable Development Reserve (MSDR), at the heart of Central Brazilian Amazon. This is a protected area created by the government of Amazonas State, in Brazil, and its objectives include the promotion the sustainable development of local rural human communities and biodiversity conservation. Mamirauá Reserve, with 1,124,000ha, is the only official area in Brazil protecting várzea (PROJETO MAMIRAUÁ, 1996). Mamirauá Reserve is contiguous with Amana Sustainable Development Reserve and Jau National Park. These three conservation units together form the biggest bloc of officially protected rainforest in the world, with circa 6,000,000ha.

The Reserve is located in the floodplains of Solimões-Amazonas and Japurá rivers, and presents the characteristic várzea mosaic of water bodies and forest types. Local fish fauna and its most important aspects have been studied in the area in the last 15 years (QUEIROZ; CRAMPTON, 1999). After a number of fish surveys in the area, it was recorded about 300 species at Mamirauá Reserve, and estimates point to a total figure between 295 to 320 species (CRAMPTON, 1999; CHAVES, 2006).

Henderson (1999) recognised at Mamirauá Reserve 3 main kinds of lakes, due to their morphology and geological origin. Oxbow lakes are those made from the natural interruption of river or channel meanders. Sometimes the migration of these meanders along the time results in a ridge-and-swale topography. Ria lakes are formed by the isolation of old abandoned channels, and tend to appear along the main rivers. Central or swampy lakes, formed by the accumulation of water, are located between meanders and marginal areas, and tend to be turned into swamps and lowland forests due to the slow succession of deposition of sediments. All these lakes are part of tree-like systems of bifurcated channels that links them to the main rivers or to the bigger channels. These are known as "systems of lakes", and eight of them can be found inside Mamirauá focal area. With approximately 260,000 hectares, the focal area is a part of the reserve where most of the activities for the reserve implementation were focused.

At Mamirauá Reserve, the seasonality is defined by the variation on the water level. This results in strong variation on the general physical condition of the whole environment and in aquatic habitat availability as well. Annual variation of the water level is 10.5m in average, but in a period of five consecutive years (1995-2000) this variation was higher than 14m, stressing the importance of inter-annual differences. Usually the "low water" period (the droughts) is short (October and November), followed by a long period of "rinsing of the water" level, from December until April. "High water" (the floods) goes from May until July, followed by a short "dropping of the water" level period in August and September. No significant seasonal variation on temperature is observed. There is a rainy season from December to March, but during the other months there is always a rainfall bigger than 150mm. Total annual rainfall is circa 2,100mm of rain (QUEIROZ, 1984).

Water quality and its chemical and physical characteristics are very much influenced by the main rivers present (Solimões-Amazonas and Japurá), both white-water rivers, with some input from black-water tributaries in the case of Japurá River. However, in some lakes at Mamirauá Reserve, water looks rather "black" (in the sense they look similarly to black water rivers or lakes) during most of the year, because almost all the big sediments are filtered and retained in the root zone of aquatic macrophytes and/or deposited on the bottom of the water bodies. Water conductivity varies from lake to lake, and is related to the conductivity of the river providing water for that particular lake. There is also some seasonal variation. In general, conductivity ranges from 80 to 160 S/cm, but in special places it can be as high as 400 S/cm during drought. Water temperature ranges from 27 to 31 C, but stratified water bodies have surface temperatures of 34 or even 40 C. Into the flooded forest, water temperatures are always between 27 and 28 C. There are always low levels of dissolved oxygen in Mamirauá waters. Close to the surface, 10-15% of saturated oxygen (0,1-0,15mgO2/ml) is the usual readings, but below the surface level very low oxygen can be recorded. Shallow water bodies can be often anoxic (HENDERSON, 1999).

The local "lakes", as in all várzea sites, are not real lakes, since there is some degree of connection among them and other lakes, channels or even the main rivers themselves, at least during the high water period (the floods). Actually, during that time, all lakes in this floodplain can be seen as one single big water body, and one can simply find empty open spaces in the middle of the flooded forest where it used to be located a "lake". The white-water várzea lakes present one of the highest primary production recorded for the Amazon. Phytoplankton production is usually higher than in rivers, even those running white waters (FISHER, 1979).

A small sample of 12 of those lakes, located in two systems of lakes at the focal area of Mamirauá, was set with the purpose to represent the large amount and variety of lakes at the Reserve. These 12 lakes were chosen from interviews with local fishermen, aiming to embrace all diversity of lakes present at the Reserve, but located in only two systems of lakes present, the Jarauá and the Mamirauá systems, for their accessibility. From these twelve lakes, only one was removed from the sample due exactly to difficulties in accessibility in particular seasons.

The remaining selected lakes were visited once each season, for 2 consecutive years (from 1994 to 1995). During these visits, some morphological data was recorded (size of the lake or area, slope of banks and borders, type of surrounding vegetation, size and location of floating vegetation). The identification of floating macrophytes was made possible by a field handbook put together by Dr. W. Hamilton (unpublished).

Limnological information was also gathered, such as water temperature, water pH, conductivity, amount of dissolved oxygen (with the help of digital sensors), and transparency (a Secchi-disc was employed). Each parameter was measured five times, to provide a safe average measurement. The measurements were taken between 11 a.m. and 1 p.m., in sunny warm days. If rain started during measurement of parameters, procedures stopped and would be re-started only after the water column was stable again.

Finally, one square meter of floating vegetation was collected with large hand-nets in five randomly chosen places in the lake for accounts of the invertebrate fauna living in the root zone. Hand nets mesh size was 2mm, and only invertebrates bigger than that were collected. Samples were taken to the laboratory and fauna collected was accommodated in large taxonomic categories (molluscs, crustaceans, arachnids, and the insect orders) and preserved.

All information collected throughout the eight consecutive seasons was stored in a database, and used afterwards to describe the aquatic environment of lakes in Mamirauá Reserve and to group these lakes in possible comprehensive ecological categories using multivariate analysis.

RESULTS

Lake structure and morphology

The 12 chosen lakes revelled to be quite difficult to be measured in loco, since the shape of their margins is very irregular. Because of that, all estimates of area (in terms of hectares) were reviewed with the help of a GIS package IDRISI, using satellite imagery (Landsat TM, all bands combined). Lake areas varied from almost 2 to almost 80 hectares, as shown in Table 1. The average size, however, was only 17.7 hectares.

Ayres (1993) described two types of forests at Mamirauá várzea. In areas flooded for about 4 months each year and where waters would rise as high as 4 or 5m (QUEIROZ, 1994), a tall and diverse forest could be established. The under-canopy is dark and empty, trees are sparse, and tree biodiversity is almost as high as in Amazonian dry land tall forests. The tall várzea forests are locally called "restingas", and are divided in higher or lower restingas accordingly with the water level during floods (2.5m is the divisor point) (AYRES, 1993). In areas flooded for up to 6 months each year, under 6 or more meters of water, another type of forest can be found, called "chavascal". In this formation, forests are low, with great amount of lianas and thorns, has a closed under-canopy, and high tree densities. Diversity, however, is very low (QUEIROZ, 1994). In Table 1 can also be observed the percentage of restingas or chavascais found in the shores around each of the studied lakes.

In the same way, Table 1 also presents the percentage of the lake bank covered by beaches or by levees. In the case of beaches, formed either by sand or by mud, there is a gentle slope leading to the edge of the surrounding forests. Levee banks, on the other hand, are steep and almost vertical. They can be sometimes as high as 3m.

Table 1. Morphological aspects of 11 lakes at Mamirauá Reserve, collected from 1994 to 1995.

Lake Name	Area (ha)	Frequency *Restinga* (%)	Frequency *Chavascal* (%)	Frequency Beaches (%)	Frequency Levees (%)
Maciel	22.5	40	60	60	40
Sumaumeirinha	6.0	75	25	10	90
Serapião	4.0	90	10	5	95
Buá-buá	78.5	5	95	90	10
Queimado	1.8	30	70	90	10
Pirarara	19.6	0	100	85	15
Teiu	24.0	95	5	5	95
Antônio	3.1	0	100	95	5
Araué-grande	20.0	80	20	20	80
Curuçá-redondo	3.1	80	20	45	55
Moura	12.4	40	60	70	30

Floating meadow coverage

The floating meadow coverage over water surface at the selected lakes during the seasonal cycle is shown in Table 2, along with the number of species of macrophytes found in the lakes in each one of the seasons sampled. Generally speaking, the amount of floating meadow coverage increases with the water level. There is a significant difference between coverage during drought and flood (ANOVA one criteria; Newman-Keuls; Q=4.6046, p<0.01). Some of the lakes were covered up to 70% during the flood. During the drought small patches of floating meadows persist, but usually located at the heads or in small bays of the lakes visited.

Table 2 . Percentage of lake surface covered with floating meadow mattresses (S.C.) and number of species of macrophytes (N.S.) found in the lake during the seasonal cycle at Mamirauá Reserve.

Lake	Drought		Rising Water		Flood		Dropping Water	
	S.C.	N.S.	S.C.	N.S.	S.C.	N.S.	S.C.	N.S.
Maciel	40	18	40	24	50	25	40	7
Sumaumeirinha	20	16	20	27	30	19	30	13
Serapião	10	15	10	18	30	17	40	12
Buá-buá	30	16	50	35	40	21	50	19
Queimado	20	14	50	29	70	23	50	8
Pirarara	20	15	50	18	70	14	40	9
Teiu	30	19	30	19	20	26	30	13
Antônio	20	14	20	29	60	27	50	19
Araué-grande	10	12	30	27	10	17	30	10
Curuçá-redondo	30	12	20	25	30	24	40	16
Moura	20	7	20	18	50	19	30	11

There are exceptions to these general trends, however, and some lakes studied did not show this same pattern, being more stable along the seasonal cycle instead. But the average percentage of surface covered during the drought was around 20%, while the same percentage for the flood was around 40%.

A similar general rule can be applied to the number of species of macrophytes. The number of species found and recognised tends to increase with the water level. However, the end of the rising of water level was more diverse than the flood itself. At this season, 35 species where found in lake Buá-buá, contrasting with 16 species at the same lake during the drought. In some lakes, like the example above, rising of the water was the more diverse season. But in some other lakes, the flood was the more diverse season. Dropping of water level and the drought were, nevertheless, always proved to be low diversity seasons for aquatic macrophytes. Significant differences in the number of aquatic macrophyte species were not found only for comparisons between drought and dropping of water level, and between rising of water level and flood. All other comparisons showed significant differences in variance (ANOVA one criteria, p<001).

Water physical and chemical aspects

Table 3 summarises the main physic-chemical characteristics of the water in the sampled lakes for each of the seasons of this study. Values presented are averages of series of five measurements each. As it can be seen, there is much variation in parameters from one lake to another at any given season, and standard deviations from the average are usually high. This variation, though, is brought to a narrower range during the flood.

During the drought, dissolved oxygen reaches its highest levels, though in some places there are virtually no oxygen dissolved in the water at all. Seasonal differences in dissolved oxygen where significant (ANOVA, one criteria, $p=0.0062$), and drought had waters with more oxygen than any other season ($p<0.01$). Water temperature was little above 30 C almost everywhere, and maybe this warm temperature was responsible for the low readings of oxygen level in shallow lakes.

On the other hand, transparency reaches its lowest levels during the drought, with much sediment revolved in the thin water columns. However, transparency showed similar variances in drought, rising and dropping of the water level. All three showed significant differences to flood (ANOVA, one criteria, $p<0.01$).

Conductivity had intermediate levels during the drought, while pH didn't show much variation from the other seasons. As expected, conductivity and pH were statistically similar between periods of low and high water levels ($p>0.05$).

At the rising of the water period, water was less oxygenated and warmer. An increase in transparency was observed, but there was a decrease in water conductivity. The readings for pH were kept stable as for the previous season.

During the flood, although a substantial decrease in water temperature was observed, the levels of dissolved oxygen reached its lowest point. The great increase in water conductivity indicates the input of white water from the big river floods. But, in contrast, at this point the transparency of the water reached its highest value and the water assumed a black-water appearance.

Finally, at the time of the dropping of the water level, most of the parameters tended to the initial state. The level of dissolved oxygen increased dramatically, and during this time the current exposed the land quickly. Water conductivity and transparency decreased while pH remained

Table 3 . Averages of physical-chemical parameters recorded in the waters of 11 selected lakes during the seasonal cycle of 1994-95 at Mamirauá Reserve.

Lake	Drought					Rising Water					Flood					Dropping Water				
	O_2 (%)	Temp (°C)	Cond (mS)	Trans (cm)	pH	O_2 (%)	Temp (°C)	Cond (mS)	Trans (cm)	pH	O_2 (%)	Temp (°C)	Cond (mS)	Trans (cm)	pH	O_2 (%)	Temp (°C)	Cond (mS)	Trans (cm)	pH
Maciel	0	29.5	122	70	6.4	1.5	33.6	101	75	6.9	0.6	27.2	126	160	6.8	3.4	31.4	159	100	6.7
Sumaumeirinha	6.7	30.6	148	130	6.4	0.8	30.7	73.8	70	6.8	0.6	27.3	118	160	6.6	5.2	28.5	152	145	7.0
Serapião	7.5	32.1	67.7	90	6.8	1.9	32.0	52.8	60	6.8	0.6	27.3	116	190	6.8	5.5	28.7	158	110	6.9
Buá-buá	0	28.8	107	25	6.6	2.3	36.0	82.6	110	7.0	0.5	27.9	120	200	6.5	1.8	27.9	157	115	6.9
Queimado	3.5	30.8	118	75	6.6	1.2	30.3	60.7	65	6.4	0.5	28.1	138	210	6.5	0.7	30.9	167	65	6.5
Pirarara	3.8	29.2	55.7	20	6.9	2.6	30.3	98.8	30	7.3	0.3	27.5	120	75	6.4	2.2	29.5	67.6	45	6.8
Teiu	0	29.2	79.9	80	6.3	1.2	29.8	86.5	135	6.7	0	28.3	121	160	6.6	1.5	28.9	139	90	6.6
Antônio	0	31.4	116	85	6.6	1.0	30.8	53.6	85	6.5	0.3	28.1	107	220	7.3	0.1	29.2	133	70	6.2
Araué-grande	3.4	31.7	122	100	6.9	2.1	31.8	67.5	105	6.7	0	27.4	138	145	6.7	2.8	28.9	127	125	6.9
Curuçá-redondo	2.8	30.7	84.3	70	6.5	1.4	33.1	81.5	70	6.6	0.1	27.6	115	160	6.6	0	29.8	158	60	6.6
Moura	3.8	29.6	121	55	6.7	2.1	33.0	42.2	90	6.7	0	27.6	119	155	6.5	1.9	28.7	155	115	7.0
Average	2.86	30.33	103.78	72.7	6.61	1.64	31.94	72.82	81.4	6.76	0.32	27.66	121.64	166.8	6.66	2.28	29.31	142.96	94.5	6.74
s.d.	2.67	1.12	28	31.5	0.2	0.58	1.86	19.26	28.3	0.25	0.26	0.38	9.33	39.4	0.25	1.84	1.04	27.86	31.2	0.25

O_2 is saturation of oxygen dissolved in percentage (%); Temp. is temperature in degrees (°C); Cond. is conductivity in micro-Siems (S); Trans. is transparency in centimetres (cm). Each value represents the average of five measurements. And s.d. is standard deviation.

roughly in the same level. Temperature increases, though not as warm as during the drought, and was again around 30 C.

As a general rule, during the flood all parameters showed the smallest deviation from the average, with exception of water transparency. These parameters vary the most from the averages in times associated with low water levels.

Invertebrate aquatic fauna

Tables 4 to 7 present a summarised account of invertebrates found in one square meter of the root zone of floating meadows, for each of the seasons considered.

Table 4 . Invertebrates in root zone of floating meadows during the Drought at Mamirauá Reserve.

Lakes	Molluscs	Micro-crust.	Macro-crust.	Insects	Other invert.	Unidenti-fied	Total per lake
Maciel	12	38	7	49	2	4	112
Sumaumeirinha	6	8	15	28	1	6	64
Serapião	14	1	376	33	1	5	430
Buá-buá	22	5	21	27	1	5	81
Queimado	51	13	65	36	2	4	171
Pirarara	3	1	9	9	3	0	25
Teiu	22	10	21	42	4	0	99
Antônio	64	192	1	70	13	6	346
Araué-grande	21	37	461	39	1	2	561
Curuçá-redondo	0	12	0	7	1	1	21
Moura	54	2	110	50	5	5	226
Σ	269	319	1086	390	34	38	2136

Table 5 . Invertebrates in root zone of floating meadows during the Rising of the Water Level at Mamirauá Reserve.

Lakes	Molluscs	Micro-crust.	Macro-crust.	Insects	Other invert.	Unidenti-fied	Total per lake
Maciel	13	11	3	58	1	8	94
Sumaumeirinha	33	46	1	58	2	0	140
Serapião	0	14	10	54	0	0	78
Buá-buá	7	7	2	85	4	3	108
Queimado	0	30	0	41	1	5	77
Pirarara	2	2	2	18	0	1	25
Teiu	0	2	1	24	1	2	30
Antônio	8	43	0	38	1	6	96
Araué-grande	10	1	14	27	1	3	56
Curuçá-redondo	3	4	0	20	2	0	29
Moura	10	36	1	54	6	0	107
Σ	86	196	34	477	19	28	840

Table 6 . Invertebrates in root zone of floating meadows during the Flood at Mamirauá Reserve.

Lakes	Molluscs	Micro-crust.	Macro-crust.	Insects	Other invert.	Unidenti-fied	Total per lake
Maciel	7	73	0	52	1	14	147
Sumaumeirinha	7	94	0	57	1	5	164
Serapião	6	91	1	22	5	3	128
Buá-buá	49	26	2	31	3	7	118
Queimado	56	17	3	53	1	5	135
Pirarara	4	42	0	46	2	7	101
Teiu	12	35	8	29	5	16	105
Antônio	56	28	0	67	2	11	164
Araué-grande	0	36	4	37	2	9	88
Curuçá-redondo	13	42	2	52	5	5	119
Moura	36	6	2	32	3	2	81
Σ	246	490	22	478	30	84	1350

Table 7. Invertebrates in root zone of floating meadows during the Dropping of the Water Level at Mamirauá Reserve. Results are grouped in broad categories of invertebrates.

Lakes	Molluscs	Micro-crust.	Macro-crust.	Insects	Other invert.	Unidenti-fied	Total per lake
Maciel	6	17	3	31	2	0	59
Sumaumeirinha	1	23	4	46	3	8	85
Serapião	2	27	3	37	2	5	76
Buá-buá	6	41	6	31	0	4	88
Queimado	2	5	3	26	0	1	37
Pirarara	6	8	3	20	6	1	44
Teiu	8	57	12	48	7	0	132
Antônio	16	7	0	117	1	1	142
Araué-grande	5	23	1	20	0	0	49
Curuçá-redondo	11	7	7	47	2	3	77
Moura	20	5	1	62	1	0	89
Σ	83	220	43	485	24	23	878

Under the general name Molluscs, only univalve members of gatropoda were recorded. Micro-crustaceans represented the groups Ostrachoda, Conchostracha and Amphipoda. Macro-crustaceans were always Decapoda, and included prawns and crabs. The insect orders identified were Odonata, Choleoptera, Hemiptera, Lepidoptera, Diptera, Orthoptera, Trichoptera and Hymenoptera. However, many insects were not identified at the order level, and were thus grouped with other unidentified invertebrates. The group named "Other invertebrates" included, apart of unknown insects, helminthos (especially Aschelminthos), leeches (Annelida, Hirudina), Acari and Arachnidae.

More than 5,200 individuals were accounted and grouped in the categories presented at tables 4 to 7. The intermediate seasons of rising and dropping of the water level presented similar harvests (either on the total number of invertebrates found, or on the dominance of insects and micro-crustaceans in the sample). The extreme seasons of drought and flood sustain two different invertebrate communities. In both seasons molluscs are more represented (ANOVA one criteria, $p=0.02$), but, above all, the droughts are dominated by macro-crustaceans. Decapoda frequencies were significantly higher at this season, (ANOVA one criteria, $p<0.01$). And the flood was dominated by micro-crustaceans. The general variance for micro-crustaceans did not vary through seasons, but statistically significant differences were found in frequencies of Amphipoda ($p<0.01$). Conchostracha and Ostrachoda showed less significant variation through seasons ($p=0.05$ and $p=0.21$, respectively). In both seasons insects are ranked in second place. Of course, when identification at lower taxonomic level is employed, differences between seasons and among lakes in a same season would be more pronounced.

The same strong variation among lakes observed in relation to physical and chemical parameters can be seen here concerning the invertebrates living at the root zone of floating meadows.

Grouping Mamirauá lakes

As mentioned before, almost all the seasonal aspects recorded for the sampled lakes showed a considerable variation, both inter and intra-seasons. The information, as presented, does not allow a straightforward comprehension of habitat evolution, structure and categorisation.

All information gathered were used in detail to determine similarities and dissimilarities among the lakes sampled, in a attempt to revel any natural grouping based in convergence and divergence of some of their morphological/structural, limnological and biological aspects.

The Euclidean Multivariate Distance test, a multivariate analyses based on co-relations among variables, was employed to show any possible natural lake groups or categories (AYRES et al, 1998).

Table 8 presents a matrix of Euclidean distances between the sampled lakes at Mamirauá. This table can be better understood through the graphic representation of a Cluster Analysis (MCALEECE, 1997) made with the similarity among lakes, calculated from the same data set, shown at Figure 1.

Table 8 . Euclidean distances between the sampled lakes at Mamirauá, as a result from an Euclidean Multivariate Distance Test.

Lakes	MAC	SUM	SER	BUA	QUE	PIR	TEI	ANT	ARA	CUR	MOU
MAC	0	-	-	-	-	-	-	-	-	-	-
SUM	9.982	0	-	-	-	-	-	-	-	-	-
SER	11.949	10.613	0	-	-	-	-	-	-	-	-
BUA	11.633	14.246	14.729	0	-	-	-	-	-	-	-
QUE	11,962	13.704	14.073	13.806	0	-	-	-	-	-	-
PIR	12.783	15.639	14.716	15.384	14.848	0	-	-	-	-	-
TEI	11.828	13.764	13.595	13.453	13.374	14.992	0	-	-	-	-
ANT	12.733	13.592	14.304	13.752	11.045	16.211	13.826	0	-	-	-
ARA	13.032	12.923	11.237	14.666	14.234	15.256	13.484	15.149	0	-	-
CUR	11.583	13.648	13.815	14.535	12.527	13.636	13.579	12.196	13.518	0	-
MOU	11.786	13.086	12.411	12.942	12.590	14.460	13.540	12.998	12.769	13.225	0

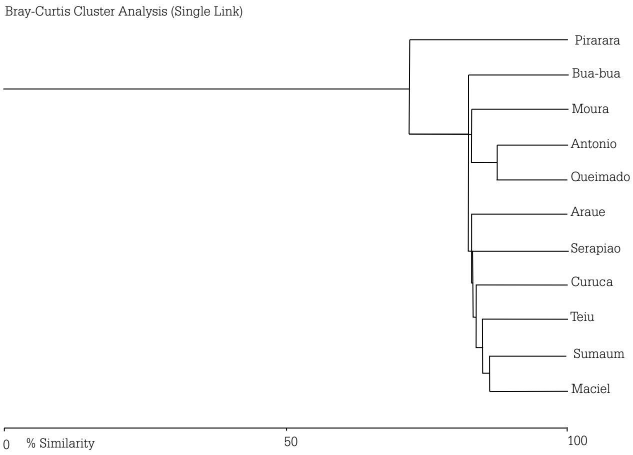

Figure 1. Bray-Curtis Cluster Analysis shows two natural groupings of lake types, and one isolated out-group lake above.

The resulting groups of lakes from all multivariate analysis performed can be described simply as the formation of two main groups. One group is made of four water bodies (Buá-buá, Moura, Antônio and Queimado), more closely related. The second group, not as closely similar with one another as in the first group, is made of six lakes (Araué-grande, Serapião, Curuçá-redondo, Teiu, Sumaumeirinha and Maciel). It is important to mention that this grouping was not influenced by the lake system where the lakes are located, but only by the characteristics measured. One distinctive out-group is observed, made of only one lake (Pirarara), the one still strongly linked to the closest main river, the Japurá.

DISCUSSION

Lake structure and morphology

Since satellite imagery was used to measure lake areas, a tendency of underestimating lake surface was introduced, due to the fact that pixel size in Landsat sensors refer to a 30m side square of the surface of Earth. This usually leads to a bad definition of feature edges (like land/water, for instance). Each group of 100 misinterpreted pixels may leads to an error of 1 ha. As most of the lakes under analysis were between 1 and 20 hectares, major errors were avoided. Size distribution of lakes seems to agree with the predicted in Henderson et al. (1998), and average area was between 10 and 20 hectares.

All lakes sampled fit in one of the Henderson (1999) categories of lake structure; and 6 can be considered oxbow lakes (3 of them belonging to a single ridge-and-swale succession structure) and the other 4 can be considered swampy lakes. This is also reflected in the morphology of their shores. Swampy lakes were surrounded by low land, dominated by chavascais, after gentle slopes. On the other hand, oxbow lakes tended to be surrounded by levees where restinga taller forests can stand. The one remaining lake (Pirarara) is a new lake, in formation in an area of sedimentation close to the main river, and still linked directly with the river. During most part of the year this particular lake behaves as the Japurá River itself, located only 50 meters upstream.

Floating meadow coverage

As expected, the floating vegetation boomed along the seasonal cycle, as the water level increased. This is well known for the Amazon region and is much better described elsewhere (JUNK, 1970), based in i29nformation from other várzea sites in the Brazilian Amazon. Also expected was the increase in number of species of macrophytes found as the water level increases. The bulk of the biomass was due to a few species (mainly Gramineae and Cyperaceae), but the increased amount of nutrients dissolved in the incoming water made other species increase in numbers to the point of been encountered again. This same effect is known in other flooded forests outside the Amazon as well (CARLOS et al., 1993). This represents a general trend for tropical flooded environments (MITSCH; GOSSELINK, 1986).

Water physical and chemical aspects

Data presented at Table 3 allows the interpretation of general trends of how the water bodies at Mamirauá behave throughout the seasons. However, monthly records would be more useful, since sudden changes in water level can transform lakes profiles quickly. But they are not available in this study.

The water temperature is obviously dependent on the volume of the water bodies, given that sun radiation and temperature of the atmosphere don't vary much during seasonal cycle (QUEIROZ, 1994). So, during times of flood or the end of the period of rising of water level, water temperatures drop in almost 3 Celsius degrees. And at times of low water, water temperature can rise as much as 3 Celsius degrees, from a average annual temperature of 29.8 C. Neither of the variances mentioned was significant statistically, though.

High water temperatures in shallow water bodies can explain why low levels of dissolved oxygen are detected in some lakes during the drought, while in some others the opposite situation is found. Anoxic situations are not unusual in lakes where stratification cannot take place (HENDERSON, 1999). On the other hand, low levels of dissolved oxygen in almost all lakes during high water periods can be explained differently. This seems to be associated with the decaying of litter material recently flooded at this time of the seasonal cycle, a process that consumes almost all oxygen available in the water. In general, it can be said that the waters of várzea are very poor in dissolved oxygen.

The great input of water and nutrients into várzea environment is made by the floods, which bring the sediment particles from the Andes and from recently destroyed banks upstream. And it is during the times of high water levels that higher records of water conductivity are obtained at Mamirauá lakes. In contrast, this is the time when water transparency reaches its highest values. These two apparently contrasting parameters can be explained simply by the growing of floating meadows and its large lake coverage. Most of the particles of sediment stays, retained by the root zone of floating meadows, and creates a singular and very nutrient rich environment for lots of different species. Some other sediment particles can alternatively deposit on the bottom of the lakes, since the presence of big blocks of floating vegetation interrupt water current and wind effects on the surface of the water. Thus, high conductivity and nutrient rich waters can be much more transparent than the expected in a várzea lake.

All physical or chemical parameters recorded tended to present a great deal of variation among lakes into the same season, with the exception of the flood, when all water bodies become one. Even then, variation on the amount of dissolved oxygen, conductivity or in water transparency from lake to lake is considerable. Even more striking spatial or temporal variations (between sites apart only a few meters from each other, or between different moments of a same day in a same site) can be described if frequency of data collection is improved (HENDERSON et al, 1998). Lots of different factors lead to this variation at Mamirauá, but the most important of them is the seasonal variation of the water level (HENDERSON, 1999).

Invertebrate aquatic fauna

The same variation among lakes found in physical and chemical aspects of the water can be also found in the faunal composition and abundance of invertebrates at the root zone of floating vegetation. Either between seasons or between lakes in a same season, variation can be observed at Mamirauá and at other white water Amazonian sites (JUNK, 1973). But, as the author points out, not all sites studied presented such seasonal variation in invertebrate total abundance, but variation on composition of invertebrate community in floating meadows through seasons can always be detected. The main cause of that seems to be the variation of available habitat, with the annual increase and decrease of sizes of mats of floating vegetation.

Data suggests that Mamirauá lakes can be accommodated in Junk's category 3, a white-water sedimented environment, with low dissolved oxygen levels (JUNK, 1973). In this type of lake, seasonal variation in abundance and composition of floating vegetation and in invertebrate fauna of its root zone are expected.

Grouping Mamirauá lakes

The final grouping of lakes obtained produced two main groups, and excluded Pirarara. As this lake is linked to Japurá River for most of the year, its limnological aspects are more related to the river, than to the other lakes at Mamirauá Reserve.

The first group of lakes will be here called lakes Type A, was made of Buá-buá, Moura, Antônio and Queimado lakes. All these lakes have high amounts of floating vegetation, waters tend to be more transparent than in other lakes, lower oxygen levels and invertebrate fauna dominated by insects and molluscs.

In contrast, the second group of lakes, called here lakes Type B, made of Araué, Serapião, Curuçá, Teiu, Sumaumeirinha and Maciel lakes. This group shows the mats of floating vegetation more concentrated in their extremities, higher levels of oxygen and invertebrate fauna dominated by insects and crustaceans.

Figures 2 to 7 present different comparisons of some important lake traits between Type A and Type B lakes. The examples given in these figures show how most of the traits do not vary between the group types. Some of them, however, show some degree of variation in one or two seasons only. Some other present a clear distinction between lake types in all seasons.

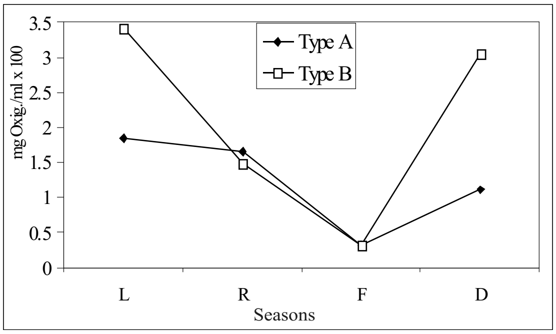

Figure 2. Averages of dissolved oxygen (in mgO_2/ml of water) in lakes Type A and Type B throughout the seasonal cycle at the study site. L is low water level; R is rising of the water level; F is flood; D is dropping of the water level.

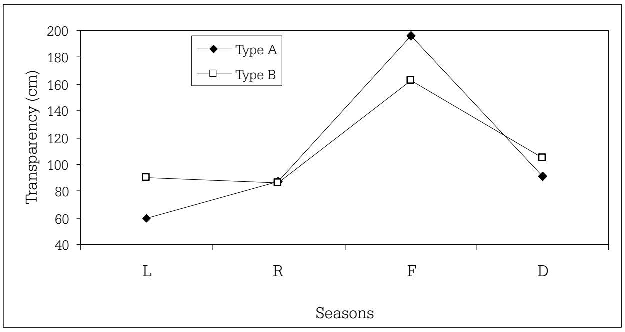

Figure 3 - Averages of water transparency (in cm) in lakes Type A and Type B throughout the seasonal cycle at the study site. L is low water level; R is rising of the water level; F is flood; D is dropping of the water level.

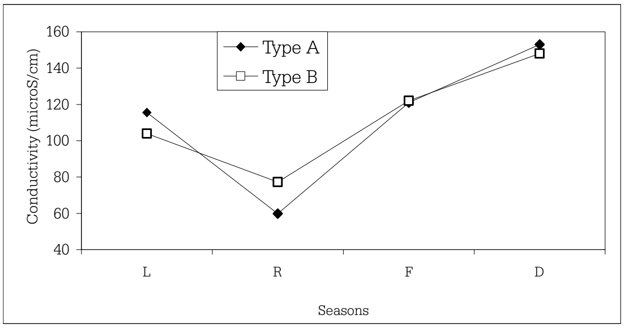

Figure 4 . Averages of water conductivity (in S/cm) in lakes Type A and Type B throughout the seasonal cycle at the study site. L is low water level; R is rising of the water level; F is flood; D is dropping of the water level.

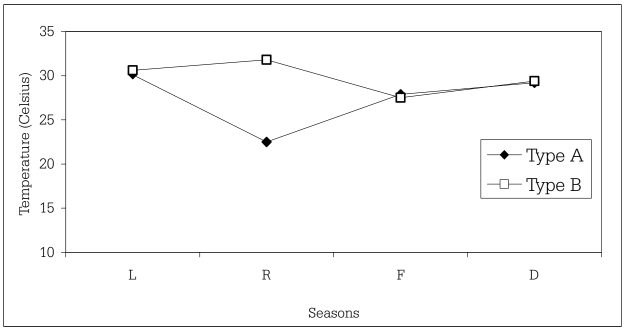

Figure 5 . Averages of water temperature (in C) in lakes Type A and Type B throughout the seasonal cycle at the study site. L is low water level; R is rising of the water level; F is flood; D is dropping of the water level.

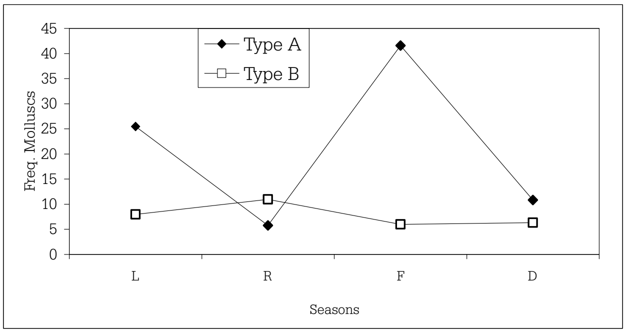

Figure 6 . Averages frequencies of molluscs in lakes Type A and Type B throughout the seasonal cycle at the study site. L is low water level; R is rising of the water level; F is flood; D is dropping of the water level.

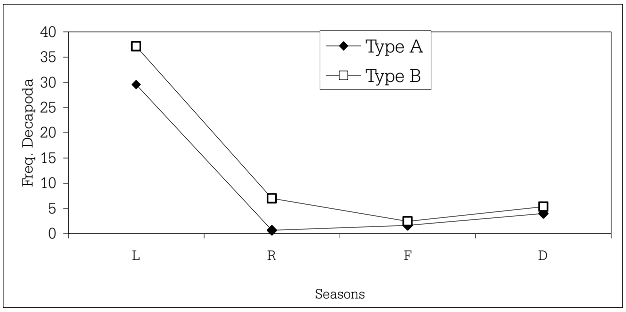

Figure 7. Averages frequencies of macro-crustaceans in lakes Type A and Type B throughout the seasonal cycle at the study site. L is low water level; R is rising of the water level; F is flood; D is dropping of the water level.

Differences in the contents of dissolved oxygen between both types of lakes are not statistically significant (ANOVA, two tailed samples, $p=0.17$). The situation is similar with the water transparency between both lake types ($p=0.03$).

Conductivity, on the other hand, is significantly different between types of lakes ($p<0.01$), although it cannot be visually observed in Figure 4. The same cannot be said concerning the water temperature ($p=0.73$), with the exception of water temperatures during the rising of the water level ($p<0.01$). A similar situation is observed in the frequencies of molluscs between de two types of lake, where the general annual difference is not significant, but during the flood it is ($p<0.01$). There is a statistically significant difference between both types of lake in respect of the frequencies of prawns and crabs for all seasons ($p=0.002$).

Some significant difference in variation can be found here and there, but in general it is not possible to distinguish a set of diagnostic traits for lake Types A or B from the single information on limnology and invertebrate fauna. But the structural/morphologic data (shape, forest types and bank) can be much more reliable as diagnostic features.

CONCLUSIONS

Lakes in Type A are all surrounded by chavascais, with small patches of restingas, present long extents of mud or sand beaches, and located in low terrain. Lakes in Type B have long extents of levees covered with restingas, with small patches of chavascais, and are generally long and narrow water bodies. Type A lakes fall into Henderson's (1999) central or swampy lakes, while Type B lakes fall more or less into the oxbow lake category, with the exception of Maciel. Although Curuçá-redondo is not long and narrow in shape, its banks are mainly formed by levees with restingas, and have comparatively small amounts of floating vegetation. Maybe, Pirarara can be considered to be now in process of formation, and segregating from the main river. As part of the river's old abandoned channel, Pirarara seems not to fall in one of those categories.

It is suggested here, then, that the broad categories of lakes described at Mamirauá Reserve accordingly with their ecological aspects and size, correspond to the broad categories of várzea lakes described elsewhere (HENDERSON, 1999; PUHAKKA et al, 1992) accordingly with their geomorphologic origin and structure. Lake structure is a consequence of geomorphologic history, and this is a consequence of the physical dynamics of várzea (formation and destruction of land due to the water current during floods and differential sediment deposition), a typically stochastic factor. As a result, the diversity of communities found in lakes and their ecology depends on a highly diverse patchwork of available but short living habitats in várzea, in agreement with other studies in várzea lake categorization (JUNK, 1970 and 1973). And this depends on a very stochastic process that involve lake formation and modification, a process that takes something from 100 to 10,000 years (HENDERSON et al, 1998) and may or may not repeat itself through time.

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