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The influence of rain in limnological characteristics of Viruá wetlands, Brazilian Amazon

A influência da chuva nas características limnológicas das áreas alagáveis do Viruá, Amazônia brasileira

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Abstract: Aim: Floodplains occupy a vast area of the Amazon basin but little is known of how their physical and limnological characteristics respond to local and regional ecological processes. In the Negro River basin and its main tributary, the Branco River, there are large areas that are seasonally flooded by water from local rainfall and that are not directly connected to major rivers. One such area is the floodplain of Viruá National Park, in Roraima state, northern Brazil. **Methods**: The physical and chemical limnological characteristics of 19 plots in this area were monitored over three years (2008-2010), with samples collected each year at the beginning and end of the rainy season (May to August). **Results**: The water bodies studied had low mean values for electrical conductivity (22.0 ± 14.0 $\mu S{*}cm^{-1}$) and pH (4.8 ± 0.7), relatively high temperatures (26.6 ± 2.7 °C), and moderate values for dissolved oxygen saturation (43.0 ± 21.5%) and water transparency (87.9 ± 38.7 cm). There was no significant difference in the limnological characteristics of the aquatic plots between the beginning and end of the rainy seasons in 2008 and 2010, but there were significant differences in 2009 due to an atypical rainfall pattern with two short dry spells during the rainy season. Multivariate analysis showed that the highest temporal variations in the limnological characteristics of the aquatic plots resulted from changes in water transparency, and these changes were related to soil type, elevation of the plot, and the particular micro-basins to which they were connected. **Conclusions**: This dynamic is different from that of most floodplains in the Amazon region, where the limnological pattern is well-defined seasonally and strongly dependent on the direct connectivity to large river systems. Floodplains not connected to large rivers should receive special attention in relation to the expected impacts of global climate change because of their high dependence on local rainfall.

Keywords: water transparency, seasonal variation, wetland, Branco River basin, Viruá National Park, temporary ponds.

Resumo: Objetivos: As planícies alagáveis da Amazônia ocupam uma vasta área e compreender os padrões das características limnológicas dessas planícies é de grande importância para os processos ecológicos locais e regionais. Na bacia do rio Negro e de seu principal afluente, o rio Branco, há grandes áreas sazonalmente alagadas que são abastecidas principalmente por chuvas locais e não são conectadas diretamente com grandes rios. Uma dessas áreas é a planície alagável do Parque Nacional do Viruá, em Roraima, no extremo norte do Brasil. **Métodos**: Foram monitoradas as características físicas e limnológicas de 19 parcelas durante três anos (2008 - 2010), com coletas realizadas no início e no fim do período de chuvas (maio - agosto). **Resultados**: Os corpos d'água estudados apresentaram baixos valores médios de condutividade elétrica (22.0 ± 14,0 $\mu S{*}cm^{-1}$) e pH (4.8 ± 0.7). A temperatura foi relativamente alta (26.6 ± 2.7 °C) e o oxigênio dissolvido teve valores moderados de saturação (43.0 ± 21.5%). A transparência da água apresentou grande oscilação espacial e temporal (87.9 ± 38.7 cm). Não houve diferenças significativas nas características limnológicas das parcelas aquáticas entre o início e o fim dos períodos chuvosos de 2008 e 2010, mas houveram em 2009 devido a um regime de chuvas atípico. Análises multivariadas evidenciaram que as maiores variações temporais nas características limnológicas das parcelas aquáticas são resultantes de mudanças estocásticas da transparência da água, o que está relacionado com o tipo de solo, altitude das parcelas e com a microbacia à qual está conectada. **Conclusões**: Essa dinâmica é diferente da maioria dos ambientes de várzea da região, onde o padrão da dinâmica limnológica é fortemente dependente de uma conexão direta com grandes sistemas fluviais. Planícies alagáveis não conectadas a grandes rios deveriam receber especial atenção em relação aos impactos esperados decorrentes das mudanças climáticas devido à sua grande dependência do regime de precipitação local.

Palavras-chave: transparência da água, variação sazonal, área alagável, bacia do rio Branco, Parque Nacional do Viruá, poças temporárias.

1. Introduction

More than a third of the Amazon basin is composed of floodplains (Keddy et al., 2009). Floods in this area generally result from overflow of the main rivers and/or local rainfall (Junk et al., 1989; Mertes, 1997). Amazon floodplains and other large wetlands in South America usually have a single annual flood pulse that lasts for months and is highly predictable (Hamilton et al., 2002). Smaller systems undergo fast changes in water level directly related to rainfall in the watershed, resulting in multiple short flood peaks of low predictability. Therefore, the flood pulse comes increasingly later in the season as the drainage area increases and local differences in rainfall among sites are buffered (Poff et al., 1997; Allan and Castillo, 2007).

The inundation dynamics have a direct relationship with limnological features in the wetlands. River overflow adds nutrients to soils on floodplains, but there is little nutrient input where the major source of water is local rainfall (Junk and Silva, 1995). Thus, landscape and regional rainfall regimes are the main determinants of biogeochemical cycles in aquatic environments (Hess et al., 1995; Melack and Forsberg, 2001), with direct and indirect effects on the local biota.

The Flood Pulse Concept – FPC (proposed by Junk et al., 1989) associates major ecological events in river-floodplain systems with their seasonal flooding dynamics, and that pattern has been recorded for several floodplains (Thomaz et al., 2007). This process is well described for the Orinoco River floodplain, where seasonal flooding with sediment-rich water causes marginal lakes to become turbid at the beginning of the flood period, and later to become transparent with the sedimentation of the suspended material. The high predictability and relative stability of the amplitude of annual floods allows for a wide variety of organisms to have life cycles closely adapted to these drastic seasonal changes in environmental conditions (Rodriguez and Lewis, 1997; Lewis Junior et al., 2000).

Many studies have been conducted in the Amazon floodplains, mostly focusing on lowlands associated with large rivers and tributaries of the middle and lower Amazon River (e.g., Melack and Fisher, 1983; Junk and Furch, 1993; Sippel et al., 1994; Junk, 1997; and Affonso et al., 2011). These aquatic systems carry high suspended-sediment loads because their waters originate from recent geological formations in the Andean region. Waters that drain more weathered areas, such as the Branco River basin, are much poorer in nutrients, have lower loads of suspended solids, and differ from typical whitewater rivers in their physical and chemical characteristics (Ferreira et al., 2007). Despite the name, Branco [= white] River waters do not properly meet the classical definition of so-called white water in the Amazon (Sioli, 1968; Santos et al., 1984; Ferreira et al., 2007). They have a much lower quantity of suspended matter than the water of the Amazon River, but it is not as low or poor in nutrients as the Negro River (to which it is connected) and not as clear as the waters of the Xingu and Tapajós Rivers (Forsberg et al., 1988; Ferreira et al., 2007). Moreover, the length of flooding in its plain is approximately four months, considerably less than that in most of the remaining Amazon sub-basins (Hamilton et al., 2002).

In the lower Branco River and middle Negro River, there are extensive floodplains along the larger rivers (Frappart et al., 2005). This landscape is very different from those formed by alluvial lands in the middle Amazon River (Melack, 1984). However, in the north of the Amazonian lowlands are large areas of poorly drained areas with hydromorphic soils that remain flooded during the rainy season (Frappart et al., 2005). Due to these characteristics, vast areas of the lower Branco River and the middle Negro River have been called the "Northern Pantanal" (Santos et al., 1993), but scientific knowledge about this region is remarkably scarce due to its geographic isolation and lack of large human settlements in the region. Both of which have contributed to high degree of conservation, a rare situation for aquatic environments (Moulton and Wantzen, 2006).

The Amazon basin is critical for the world's carbon balance (Clark, 2004). In an analysis with various climatic models and scenarios, Marengo et al. (2009) predicted a change in the frequency and duration of dry periods in the Amazon. The interannual variability caused by climate change may alter the dynamics of aquatic ecosystems (Hamilton, 2010). Thus, knowledge of the physical and chemical characteristics of these environments can provide a benchmark for comparisons with future scenarios. The maintenance of the natural flow regime is especially important for the maintenance of these ecosystems (Poff et al., 1997). If climate change forecasts come to pass, floodplains that are not connected to major rivers will probably be more affected by irregular local rainfall than the floodplains of major rivers, where the larger catchment areas act as buffers.

The present study was conducted in wetlands of the Viruá National Park (Parque Nacional do Viruá - PNV) in Roraima State to examine the spatial and temporal variation of its physical and chemical limnological characteristics. Specifically, we seek to answer the following questions: 1) Is there a pattern in the temporal variation (throughout the rainy season and between years) in the limnological characteristics of Viruá wetlands? And; 2) What are the main factors that determine the changes in the water characteristics in this area?

2. Material and Methods

2.1. Study area

PNV is located in the south-central region of Roraima state, Brazilian Amazon, in the municipality of Caracaraí in the RAPELD grid system of the Biodiversity Research Program (Programa de Pesquisas em Biodiversidade – PPBio, more information at http://ppbio.inpa.gov.br/). It has an area of 227,000 ha and is bordered to the southwest by the Barauana River, to the west by the Branco River, and to the south by the Anauá River. The waters in the southeast portion of the park drain into the Barauana River. The Iruá River is located on the central axis of PNV and receives waters from most of the local drainage basin, including waters from the aquatic plots of the research grid at that site (Figure 1).

The PNV region has a humid tropical climate according to the Köppen's classification, with a short dry season between November and February (Barbosa, 1997). Mean annual rainfall varies from 1,700 to 2,000 mm, with a regular period of higher precipitation that occurs between April and August [National Water Agency (Agência Nacional de Águas - ANA); Figure 2]. Fluctuations in water levels in flooded areas are consistent and are directly related to the occurrence of local rainfall or drought periods. On the plains, fluctuations in water levels can last a few hours in areas close to higher-elevation lands and up to two days in the lower areas (JDV, pers. obs.). Since early 2009, flooding within the grid area has been monitored using automatic probes (level loggers) (Figure 3).

Much of PNV consists of plains that remain dry during most of the year and flood during the rainy season. The soils have a gradient associated with elevation; the higher areas are composed of litholic neosols, latosols, and cambisols, and the lowlands have a predominance of hydromorphic sandy soils (Mendonça et al., 2013). These soils are extremely poor in nutrients and are periodically subjected to water stress. According to the IBGE classification (2005), the vegetation that covers these areas is of the "campinarana" type, which can be either "forested campinarana" (with low and sparse trees) or "grassy-woody campinarana" (with or without palm forests along drainages). There are few permanent streams in these areas, but drainage networks with lotic characteristics form during the rainy season. Depth is slightly greater (≈ 50 cm) in these drainage networks than in the surrounding wetland where flow is extremely low or even undetectable. These drainage channels (called "*igarapés*" locally) have widths ranging from 1.0 m to over 100 m. Forested campinaranas (riparian forest) predominate in these areas, with trees up to 20 m tall. In some areas where the soil remains flooded for a relatively long period, *Mauritia flexuosa* palms predominate. Thus, the topography and type of soil define the local phytophysiognomy.

During the rainy season, many areas along the grid's trail system are flooded. The waters that flood the system originate from three main sources: rainwater draining from plains located in the north and south of the grid; waters that descend from the Serra da Perdida, which is located on the eastern edge of the area; and rainfall over the grid area itself. These wetlands vary in size from small puddles and ponds to flooded areas over 1.0 km^2.

2.2. Sampling points

The RAPELD system research grid (Magnusson et al., 2005; Magnusson et al., 2013) used at the PPBio sites in PNV is composed of a set of 12 trails of 5 km each, with six having a north - south orientation and six with an east - west orientation and intersections every kilometer. For each east - west trail, there are five uniformly distributed plots located at 1-km intervals along the trails. These plots are 250 m in length and follow the altitudinal contour lines [for more details on this sampling design see Magnusson et al. (2008) and Costa and Magnusson (2010)]. Of the 30 evenly distributed plots in the grid, 19 are seasonally

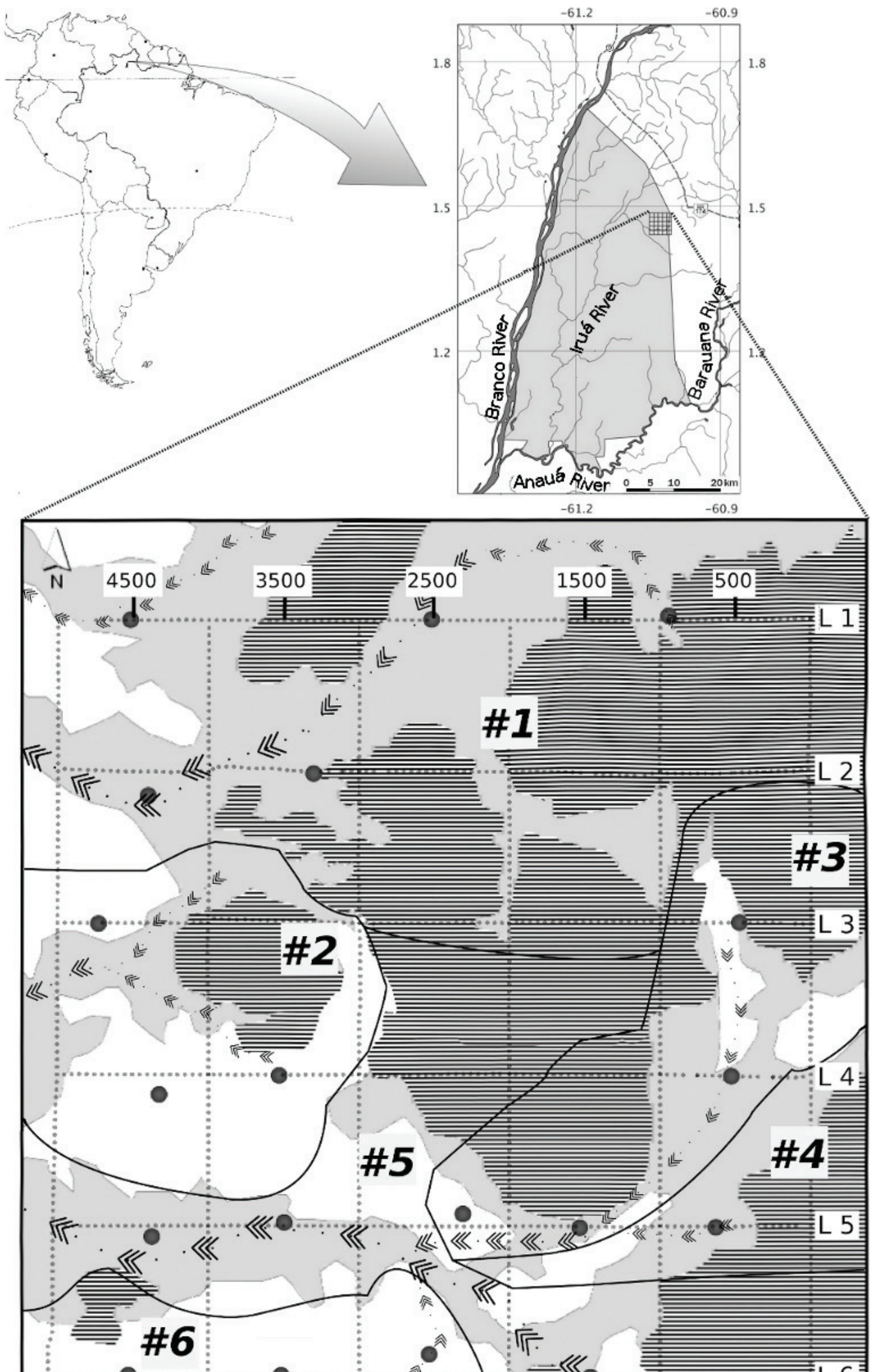

Figure 1. Localization of the Viruá National Park, central region of Roraima State, Brazil, and the grid system. Black dots on the trail system indicate the location of plots, segments "<<" are drainage channels. White areas are grassy campinas, gray area are wooded campinaranas, and hatched areas indicate forest that is not flooded. Black lines delineate the micro-basins.

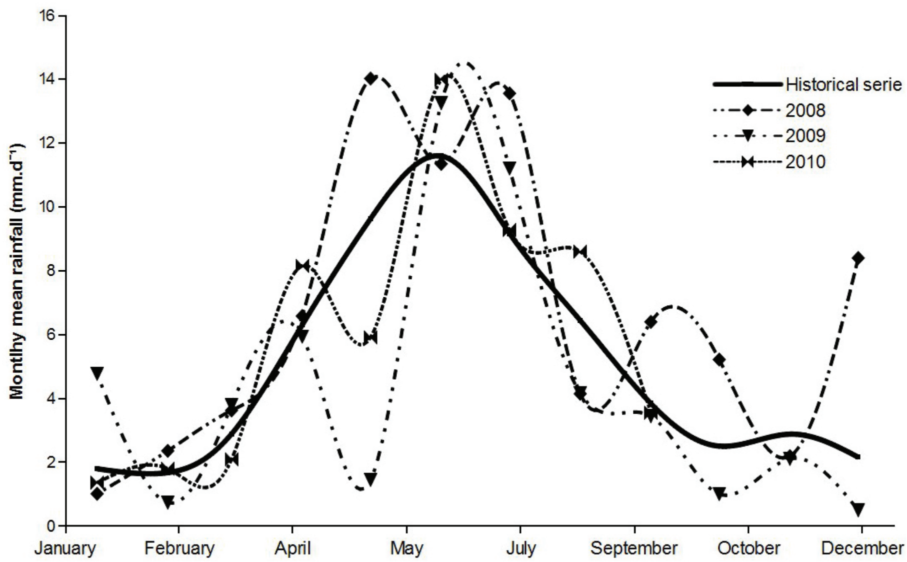

Figure 2. Daily rainfall in the municipality of Caracaraí - RR (ANA, 2010). The solid black line represents the trend of rainfall based on the monthly means of the last 34 years (1976 - 2010), and the remaining lines represent the rainfall of the three years of sampling in the present study.

flooded, and are considered aquatic plots in this study (Figure 1).

2.3. Physical and chemical variables

Water samples were collected during the flood period from aquatic plots of 2,500 m^2 (50 × 50 m) established 50-m from each of the 19 uniformly distributed plots. The samples were taken twice each year, at the beginning and end of the rainy season, for three consecutive years (28/May to 21/June and 15/July to 25/July 2008, 11/June to 02/July and 22/July to 04/August 2009, and 31/May to 22/June and 12/July to 04/August 2010). The environmental variables measured in the aquatic plots were temperature, pH, electrical conductivity, dissolved oxygen, transparency and depth. With the exception of two plots that were dry during July 2009, all of the plots were sampled six times.

Physical and chemical parameters were measured immediately below the surface, always at the same locations within the plots. A potentiometer/digital conductivity meter (Yellow Springs Inst., model 63) was used to measure conductivity, pH, and temperature. The dissolved oxygen saturation percentage was measured using a digital oxymeter (Yellow Springs Inst., model 58). Due to the shallow depths of the sampling sites, water transparency was measured using a graduated transparent tube (3 cm diameter, 150 cm height) that was open at the top and fitted with a small Secchi disk covering the bottom. After being filled with water from the plot, the tube was emptied slowly using a small hole in the bottom until the Secchi disk could be viewed from the upper opening of the tube, and the height of the remaining water column was recorded in cm (Bales et al., 1998).

In each plot at 47 uniformly distributed points we measured the following variables: 1- Mean Depth of the Flooded Area (mean of the flooded points), 2- Percentage of Flooded Area (proportion of 47 points below water), and 3- Substrate (relative frequency at the 47 points in June 2010 of the following types of substrate: sand, fine litter, litter, grass, roots, soil and trunk – adapted from Mendonça et al., 2005).

Elevation was measured by a professional surveyor using a theodolite and geodesic GPS (methodological details and original data available at http://ppbio.inpa.gov.br/). IBGE (1974) charts, SRTM (Shuttle Radar Topographic Mission) data, topographic images, and field observations were used to define divisions among the small catchments that drain the trail grid. These procedures resulted in division of the study area into six catchments (Figure 1).

Soil samples were collected at six points every 50 m in the 30 permanent plots to a depth of 15 cm. After the samples were dried, cleaned, and crushed, EMBRAPA (1997) methodology was used to determine the proportions of clay, silt and sand. Analyses were undertaken in the Plant and Soil Thematic Laboratory (Laboratório Temático de Solos e Plantas - LTSP / INPA) in Manaus, Amazonas state, Brazil (data available at http://ppbio.inpa.gov.br/).

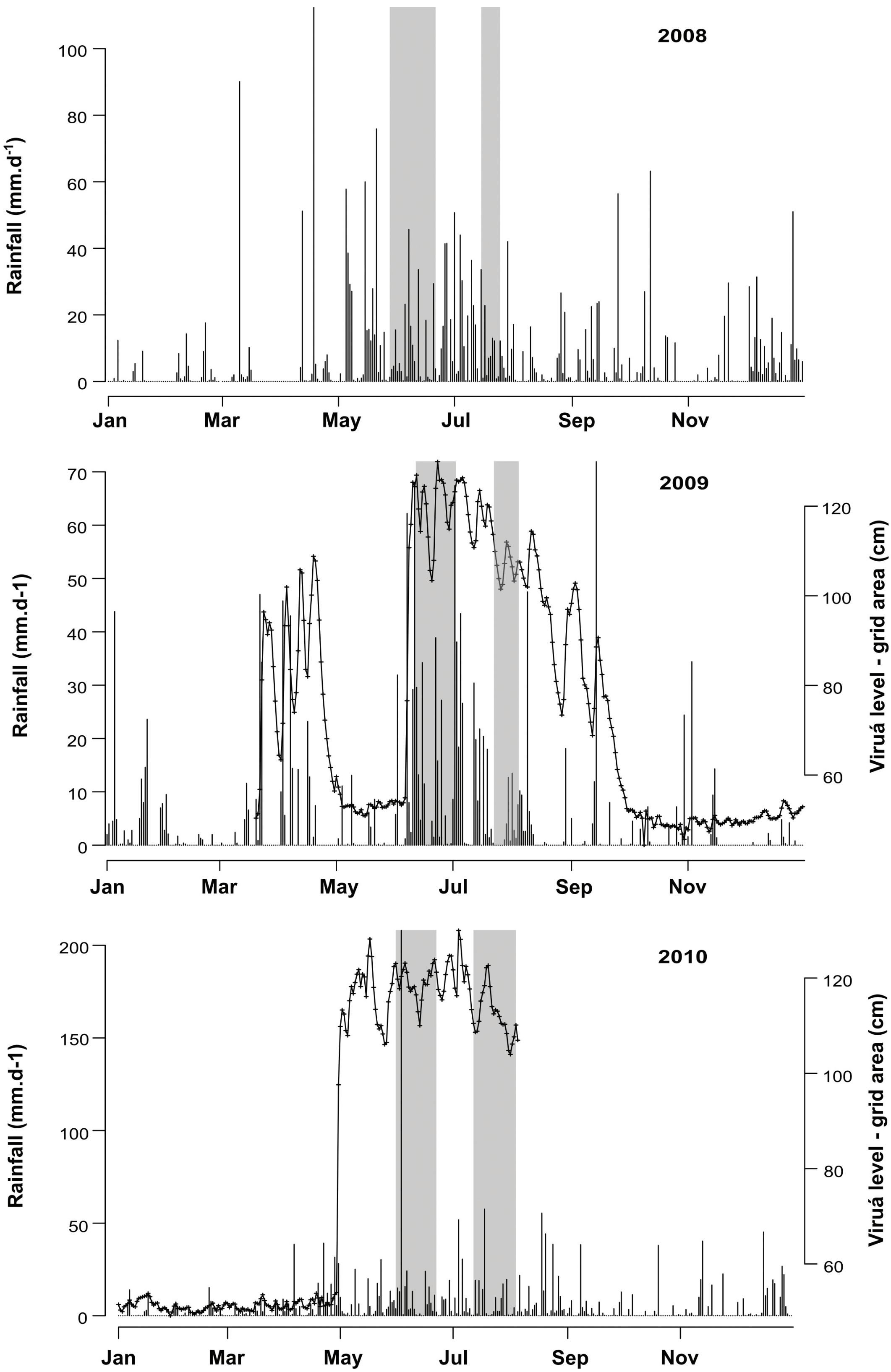

Figure 3. Daily rainfall during the three years of sampling (2008-2010) and water levels in the flooded areas of the Viruá National Park research grid (narrow line - probe values for the data logger on trail L2 at 4,250 m; there was no probe data for 2008). The gray areas represent the period of the first and second sampling each year.

2.4. Statistical analysis

The statistical significance of differences for each variable between the beginning and end of the rainy season was determined by a Student's paired t-test. To test the effects of the elevation, soil clay content, season (start or end of rainy season), and substrate the variables mean depth, temperature, oxygen concentration, and transparency were combined in a principal component analysis (PCA). Conductivity and pH were excluded from the analyses since they could not be measured in 21 of 112 samples; moreover, in preliminary PCA analyses their loadings were the lowest and contributed little to the pattern of variation in the plots. The PCA1 and PCA2 axes were tested using non-parametric multivariate analysis of variance (MANOVA-Np; Anderson, 2001) to assess whether the limnological variables were related to elevation, soil clay content, season or substrate (another PCA was used to summarize substrate composition in a single axis).

To investigate the occurrence of patterns in the limnological characteristics of the plots between the beginning and end of the rainy season, the PCA results were analyzed separately for each year. Therefore, after plotting the PCA scores for each sampling site in a temporal sequence (2008-2010), the values of the angles of the segments formed by the points corresponding to the beginning and end of each rainy season were compared to the ordinal axis of each plot. The Rayleigh Test for Uniformity was used to test whether the variation in the angles of the segments differed from that expected from random data. Deviations from random indicate predictable changes in the limnological characteristics of the aquatic plots. A similar test was applied by Espírito-Santo et al. (2009) to assess seasonal trends in changes in the composition of stream fish community assemblies.

The relationships between the physical and limnological characteristics of the aquatic plots (mean depth, pH, conductivity, temperature, oxygen, and transparency) and soil particle sizes were assessed using Spearman correlations.

The tests and transformations were undertaken with the base package of the R 3.0.2 software (R Development Core Team, 2013); the Adonis function from the vegan package was used for MANOVA-Np (Oksanen et al., 2011), and the CircStats package was used for the Rayleigh test (Agostinelli, 2009).

3. Results

A total of 112 samples were taken, six in each plot, but plots L3-4500 and L4-4500 were sampled only five times because they were dry during July 2009 due to an unusually short rainy season that year. Conductivity and pH were not measured during the first sampling in 2010 due to problems with the equipment. Limnological characteristics varied among plots; physical and chemical variables are presented in Figure 4. At the end of the rainy season in 2009 there was an increase in water temperature and decrease in depth and dissolved oxygen content, which resulted in significant differences in the limnological characteristics between the beginning and end of the rainy season for all the variables tested. In the remaining years (2008 and 2010), only mean depth showed significant differences between the beginning and end of the rainy season.

Most plots were located at elevations of approximately 50 m with a variation of only 1 m. Only three plots were above 51 m: L1-1000 (54.6 m), L3-500 (55.1 m), and L4-500 (52.4 m). The mean depth of the water column in the plots was 23.5 cm (max: 94.5, min: 0.6 cm). However, in the plots below 49.5 m, the mean value was 39.0 cm, and in the plots above this threshold, the mean was 14.1 cm (Figure 5).

The proportion of land flooded within the 2,500 m^2 of each plot varied widely among locations and among the six samples of the same plot over the 3-year sampling period. Plots that were situated near the drainage channels (L5-4500, L6-1500, L5-3500, and L2-4500) or in a lake-like area (L6-3500) had greater mean depths. Larger surface flow areas were also observed in these five plots compared to the other plots.

The first two axes of the PCA of limnological characteristic captured 88% of the variance in the original data for limnological characteristics (Table 1). The variable most related to the ordination axes was transparency, followed by oxygen and mean depth. The limnological characteristics of the plots varied significantly with elevation (MANOVA-Np: $F = 9.2$, $p < 0.001$), percentage of clay ($F = 31.2$, $p < 0.001$), sampling year ($F = 5.4$, $p = 0.001$), and substrate ($F = 3.21$, $p = 0.047$ – by first axis substrate PCA, Table 2), but not in relation to season ($F = 1.8$, $p = 0.167$).

The limnological characteristics of the plots between the beginning and end of the rainy season in samples taken in 2008 and 2010 (Figure 6) varied stochastically (Rayleigh test, $p = 0.366$ and $p = 0.708$, respectively). However, in 2009, there was a consistent pattern of change in the limnological characteristics of the plots between the beginning and end of the rainy season (Rayleigh test, $p < 0.001$).

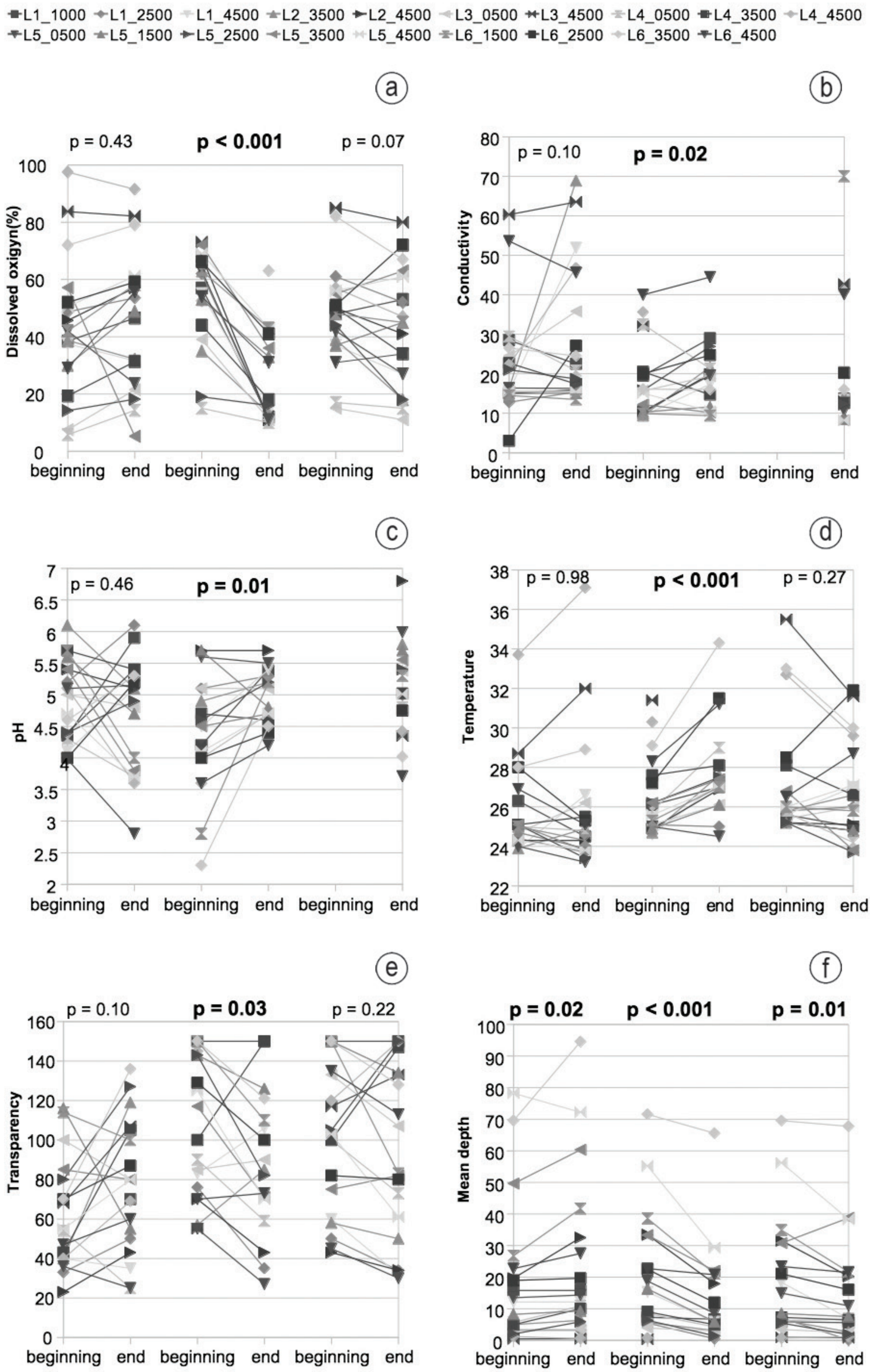

Figure 4. Physical and chemical variables measured in the Viruá National Park aquatic plots, with values for the beginning and end of the rainy season in the three years of sampling (2008-2010) for (a) oxygen, (b) conductivity, (c) pH, (d) temperature, (e) transparency, and (f) mean depth. The values of p refer to the paired t tests applied to the comparisons between the beginning and end of the rainy season in each sampling year.

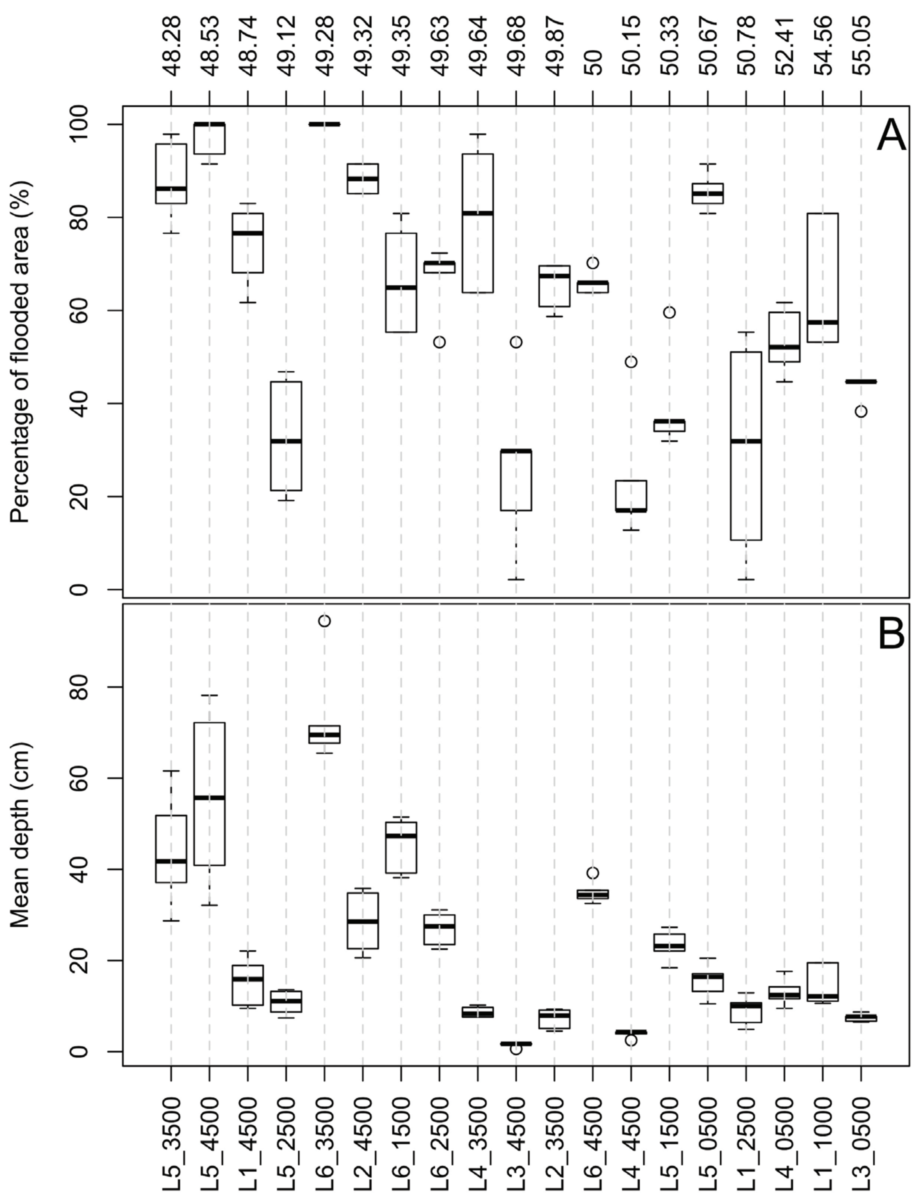

Figure 5. Percentage of flooded area and mean depth of aquatic plots, sorted according to the elevation of the terrain. In Figures A and B, the circles represent outliers, the dotted lines show the upper and/or lower quartiles +1.5*IQR (interquartile range), and the box represents the upper and lower quartiles around the median based on the six samples taken in each plot.

Transparency, pH, electrical conductivity, and water temperature showed moderate to high correlations with soil particle size, but this trend was not observed for oxygen and mean plot depth (Table 3).

Based on median transparency by plot and the relationship with proportion of clay in the soil, the Viruá aquatic plots can be separated into two groups. The first comprised the two-thirds of the plots located in the southern micro-basins with transparency values above 70 cm and containing soils with less than 15% of clay. The second group has more turbid water (less than 70 cm transparency) and proportion of clay in the soil between 15% and 36% (Figure 7).

4. Discussion

The plains of the Viruá National Park showed overall temporal variation in their physical and chemical limnological characteristics that conform to predictions of the flood pulse concept (FPC) (q.v., Junk and Wantzen, 2004). However, the measured limnological variables showed different dynamics from those in other Amazonian floodplains. In

Table 1. Loadings of the limnological variables on the first three components of a Principal Components Analysis of aquatic plots. Values ≥ 0.70 are highlighted in bold.

	PC1	PC2	PC3
Mean depth	0.10	0.57	**–0.81**
Temperature	0.02	0.03	0.07
Oxygen saturation	0.10	**0.80**	0.58
Transparency	**0.99**	–0.14	0.02
Variance explained (%)	64	24	12
Cumulative variance (%)	64	88	99

Table 2. Loadings of substrate categories on the first three components of a Principal Components Analysis. Values ≥ 0.70 are highlighted in bold.

	PC1	PC2	PC3
Sand	0.12	–0.17	0.19
Fine litter	0.31	0.47	**–0.71**
Litter	**–0.88**	0.08	–0.13
Grasses	0.18	0.55	0.64
Roots	0.00	–0.36	0.12
Soil	0.28	–0.56	–0.13
Trunk	–0.02	–0.03	–0.01
Variance explained (%)	57	24	9
Cumulative variance (%)	57	81	90

most floodplains studied to date, there is a tendency for lower transparency values to occur during the early period of flooding (*e. g.* Lewis Junior et al., 2000; Thomaz et al., 2007), but this pattern was not observed in the Viruá floodplain, where local conditions, such as the type of soil in the micro-basin, had greater effect on transparency. A similar trend was observed in the Pantanal region of Mato Grosso State in Brazil (Oliveira and Calheiros, 2000; Hamilton, 2002), where seasonal differences in limnological variables, such as those between the beginning and end of the rainy season in 2009, were most related to mean depth and oxygen rather than transparency.

Highest turbidity was found in micro-basins with high clay soil contents whose waters drain from low hills or pediplains with vegetation transitioning from forested campinarana to rain forest. In places where the water was more transparent and the soils exhibited lower clay content, the land was predominantly characterized by sandy plains covered with mosaics of forested campinaranas, shrubs, and open formations in which grasses predominated.

The low vegetation is evidence that geological formations of these sandy plains differ from most floodplains of major rivers in central Amazonia. The Viruá plains are paleochannels remnants of Quaternary megafans (Zani and Rossetti, 2012) with highly leached and nutrient-poor soils that provides little material to water bodies, in contrast to areas flooded

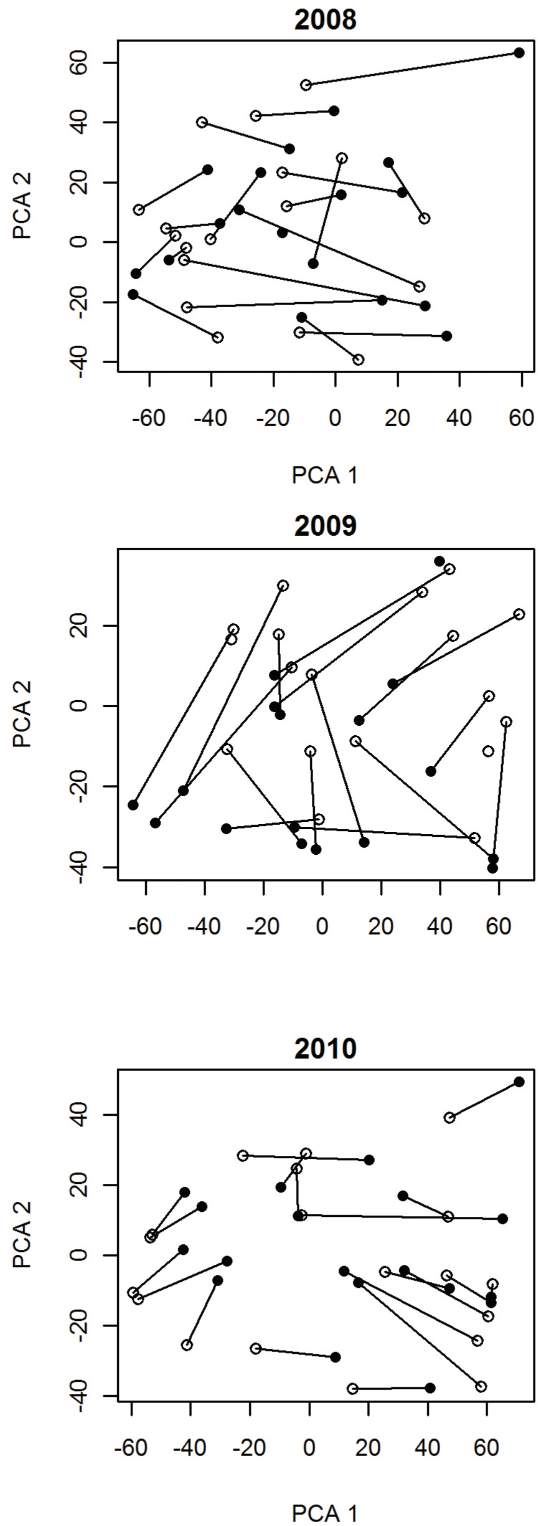

Figure 6. Two-dimensional representation of the Principal Component Analysis (PCA) of limnological data for the three sampling years (2008-2010) in the Viruá National Park research grid. The white and black circles represent the beginning and end of the rainy seasons, respectively. Lines connect the samples from the same plot.

Table 3. Spearman correlations between the median values of the limnological parameters and substrate composition (by first two PCA axes) in plots across percent soil-texture composition of soils. Correlations with R values greater than 0.5 are highlighted in bold, and n = 18 for all comparisons.

		Soil Characteristics		
		Clay	**Silt**	**Sand**
Water characteristics	pH	0.41 (0.09)	**0.57** (0.01)	**–0.56** (0.02)
	Conductivity	–0.31 (0.15)	**–0.49** (0.04)	**0.50** (0.03)
	Temperature	**–0.68** (<0.01)	**–0.56** (0.01)	**0.67** (<0.01)
	Oxygen	–0.34 (0.16)	–0.06 (0.82)	0.14 (0.57)
	Transparency	**–0.68** (<0.01)	**–0.52** (0.02)	**0.61** (0.01)
	Mean depth	–0.02 (0.92)	–0.10 (0.68)	0.03 (0.91)

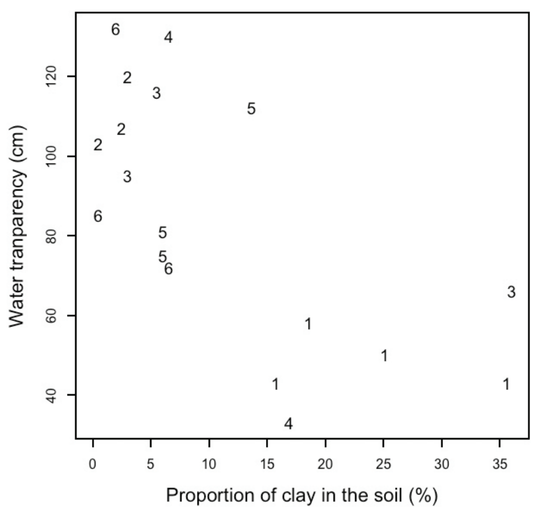

Figure 7. Relationships between the median water transparency of the aquatic plots and the proportion of clay in the soil. Numbers indicate the micro-basin.

by lateral overflow of the major rivers (Melack and Fisher, 1990; Amoros and Bornette, 2002).

Dissolved oxygen, an essential parameter for the survival of most aquatic organisms, showed strong variation between the beginning and end of the rainy season and especially between the sampling sites associated with different combinations of soil characteristics and phytophysiognomies. The highest oxygen values occurred predominantly in plots associated to grassy-woody campinarana vegetation, where there is a reduced amount of organic matter in the soil, possibly resulting in a lower amount of decomposing organic matter and contributing to a lower seasonal depletion of dissolved oxygen (Hamilton et al., 1995; Sabo et al., 1999).

Plots located in higher areas had small pools or, more rarely, small streams. These water bodies were shallow and poor in nutrients and had low concentrations of dissolved oxygen, which are characteristics similar to the pools studied by Pazin et al. (2006) in a terra-firme area (not flooded by the seasonal flood pulse) in the Ducke Forest Reserve in Manaus, Central Brazilian Amazonia. Plot L3-500 was the only one with well-defined pools. Other plots with general limnological characteristics similar to those described above are a little different because they were associated with streams draining terra-firme forest, had larger and deeper pools, creating anastomosed networks in the irregular terrain. The remaining plots, situated at elevations below 49.5 m, showed patterns of more extensive and widespread flooding, similar to the dynamics observed in the Pantanal in western Brazil (Hamilton, 2002; Fernandes et al., 2010).

Although the lower areas showed higher levels of flooding, most of the water bodies in the Viruá research grid were shallow, which makes them more susceptible to disruption due to regional and global climate changes. In Amazon wetlands, decomposition processes in the aquatic system cause seasonal hypoxia or even anoxia (Meade et al., 1979; Melack and Fisher, 1990; Furch and Junk, 1997). However, these unfavorable conditions for most aquatic biota are often confined to the hypolimnion, which restrict its negative effects to some events of thermocline disruption and water mixing that may kill thousands of fish (Tundisi et al., 1984). In areas such as PNV, the shallower water bodies and the accumulation of organic matter produced by the forest may promote the formation of hypoxic conditions, especially at high temperatures, which can severely compromise aquatic organisms.

When a floodplain is located downstream of a major drainage basin, the effects of atypical climactic events are mitigated because irregularities in rainfall in a given area is offset by rains that fall in other river sources (see Poff et al., 1997), buffering the direct effects of local climate changes. However, for basins located in plains that are not connected to large river systems, and where the rainy season is shorter, atypical periods of drought (such as that which occurred in 2009 in Viruá region) can have strong impacts on aquatic environments and the local biota. Hamilton et al. (2002) showed that many of the

Branco River floodplains can vary greatly regarding time of flooding, which also directly influences the dynamics of the aquatic ecosystems, reducing the variability of water-body types and therefore the diversity of available niches for local biota.

In summary, floodplains, such as that in the Viruá National Park that are not connected to major rivers and are regulated by local rains, have several characteristics similar to those experienced by environments regulated by the flood pulse. Nevertheless, rainfall-filled floodplains such as those in PNV show peculiarities that must be considered when establishing conservation and management strategies for these areas. Under many scenarios predicted for global climate change (e.g. Marengo et al., 2009) events such as the atypical dry spells observed in 2009 are hypothesized to become more frequent and intense. These events could represent a strong selection pressure for the local biota, and should be considered in predictions of local and regional biotic responses to climate change.

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