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Research Article

Ecological Gradients Influencing Waterbird Communities in Black Water Lakes in the Anavilhanas Archipelago, Central Amazonia

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For the first time, and in a large spatial scale, the influence of ecological properties on the aquatic bird community of black water lakes in Brazilian Amazonia is evaluated. Bird surveys were conducted in 45 lakes. A total of 3626 individuals in 48 bird species were recorded; of these, 31 are aquatic, and 18 of these are primarily piscivorous. Bird richness and abundance were not significantly related to lake shape and productivity but were influenced by hydrological period (low versus high), water depth, transparency, lake isolation, and habitat richness. Matrices of bird species by lake were subjected to multivariate analyses (NMDS) to evaluate how these parameters influence bird community. The variation in bird species composition was positively correlated to lake depth and isolation and negatively correlated to water transparency and habitat richness. The results indicate that period, lake physical characteristics (depth, water transparency), isolation, and habitat richness are determinants of aquatic bird community composition in the black water lake systems of Amazonia.

1. Introduction

Ecological studies on the composition and structure of biological communities are critical to understanding the interactions between the species and populations that comprise them, to explain local and regional biodiversity [1, 2], and are essential to guiding management actions and conservation policies.

Tropical wetlands provide habitats for a wide variety of plants, fishes, birds, and mammals. Aquatic environments (rivers, lakes, and wetlands) represent 6% of Brazilian Amazonia, and over 100,000 km^2 of lakes and swamps [3].

Aquatic birds are ubiquitous components of Amazonian freshwater systems. However, their role in the ecological dynamics of these systems has often been overlooked, as in other rainforest areas in the Neotropics (but see [4–6]). In order to evaluate the impacts of human activities on freshwater systems and improve their conservation value, the status and trends of freshwater biodiversity need to be monitored [7].

Because many aquatic birds are top predators in the aquatic environments, they can affect the distribution and abundance of fish [8], and presumably other biota. Both in tropical and temperate wetlands, aquatic bird communities have been demonstrated to be influenced by their environment (lake features such as their degree of isolation, depth, physical-chemical properties, and habitat availability) or/and by their own interaction and population dynamics (see below). For instance, in southern Brazil in fragmented wetlands, it has been recently found that some aquatic birds are more abundant in small and isolated lakes [6]. The authors defend the idea that the physicochemical conditions, type of landscape, together with food resources, and habitat might influence ecological gradients in the bird communities and therefore deserve further analysis.

Bird assemblage structure and composition can also be influenced by local ecological interactions such as predation and competition, and by large-scale environmental factors, such as the degree of habitat isolation and structure [1, 5, 6]. Considering only internal mechanisms, population structure and consequently community composition can result from a link in processes operating at the local and regional scales, which suggests that the locally most abundant species tend to have larger or extended distributions, and the replacement of individuals can be a result of immigration from the regional species pool [9]. For example, a positive relationship between the locally most abundant species and the range of their distributions across a given wetland area can indicate population dispersal as predicted by the neutral theory of biodiversity [9]. Nevertheless, weak correlations between spatial variation in bird community composition and geographical distances (distances between lakes) can be taken as evidence against the distance decay predicted by Hubbell's theory [9]. Although the present study is within this theoretical framework and presents results on these relationships, the main purpose is not to test the theory.

Similar to those of other neotropical wetlands (the Everglades, Llanos and Pantanal), the aquatic bird communities in the Amazonian lakes are composed by grebes, cormorants, anhingas, herons, egrets, ibises, storks, waterfowl such as ducks, kingfishers, skimmers, terns, hawks and kites, rails, and jacanas [5, 6]. Some species seem to privilege lakes with shallow water, with shrubs and grasses along the shore, to forage and nest, while others use deep open waters with abundant trees in the margins. Because lake features (isolation from other lakes, water transparency, productivity) and habitat richness also vary spatially, bird species composition may also differ through many lakes over a large area, probably following gradients of spatial variation in ecological and environmental factors [5].

Only two studies of birds associated with Amazonian aquatic environments analyzed how bird community composition varies with water body characteristics and ecological gradients [4, 5]. These and other good descriptive studies [9–13] have dealt with bird communities of white water systems (várzea), which supposedly would have more aquatic bird species than black water (igapó) wetland systems, because they are more productive. However, investigation of other local ecological factors such as lake features (i.e., water transparency, depth, productivity, habitat richness at lake margins) and geographical position (lake isolation in relation to other lakes and to river margins) has never been undertaken for the entire Amazon region.

In a previous study, it was demonstrated that variations in white water lake shape produced ecological gradients, resulting in spatial variation in aquatic bird communities [5]. The study was made during the period of highest waters in Amazonian lakes (July). The study indicates that bird richness and abundance tend to decrease with the increase in lake shape complexity, certainly influencing the variation that bird community composition also undergoes with lake shape. The authors were surprised with these results, because they believed that the more complex the shape of a lake, the higher the diversity of microhabitats, and in consequence, the higher the species richness and abundance. However, aquatic birds are very territorial during the high water season, when most food resources are dispersed throughout the landscape. Their territories tend to be linear, located in the forest-water ecotone. In elongated lakes, opposite margins are usually closer than in roundish ones, and aquatic birds tend to defend both margins instead of only one. This inter- and intraspecific competition for space (to gain access to food resources) may make habitats more difficult to colonize by dispersers coming from other lakes. This may help explain the differences in waterbird species richness and composition between long and round lakes. Although they have not analyzed the spatial distribution of each individual species, during their surveys they noticed an "even distribution" of several egrets, herons, kingfishers, and allies in the margins of long water bodies.

My expectation is that lake shape in Anavilhanas will not influence bird communities, since most of them tend to be elliptical and not so variable (rounded to amoeboid or even dendritic) such as those that have influenced and form white water systems [5]. However, because the variation on habitat richness at lake shore may be independent of lake shape, I expect it will influence bird community.

Due to high seasonal precipitation over the Amazon basin, associated with very low inclination of the terrain, the wetlands on the margins of the large rivers are annually flooded up to 12 m depth, and this scenario may last for months [14]. Therefore, the várzeas flooded by white waters, receiving annually high amounts of sediments rich in nutrients and supporting high productivity, are historically the most heavily occupied and with the highest human densities [15]. On the other hand, the black water areas of igapó are inundated by rivers that originate in geologically older areas and therefore are acidic, with low sediment loads, and poor in nutrients (see below) resulting in low human occupation.

Together, várzeas and igapós cover about 400,000 km^2 (up to 300,000 for várzea and 100,000 for igapó) among the 1.5 million km^2 of wetland area estimated for the Amazonian region [16]. Both várzea and igapó have a high diversity of herbaceous plants [17] and are the richest flooded forests in tree species in the planet [14].

Because black water systems have lower productivity, it is expected that bird richness and assemblages differ from those that have been described previously for white waters, showing a gradient in community structure and composition from black to neighboring white water systems due to lake shape, and probably due to lake to lake spatial differences in habitat richness and water productivity [5]. What is not so clear yet is how bird communities respond to variation in lakes within black water systems themselves, principally in those areas with similar lake shape and no influence of white water wetlands. Although black waters are the most acidic in Amazonia and are much less productive than white waters, they still seem to have similar and high biodiversity, as indicated by their high fish and aquatic and forest bird richness [4, 18, 19]. However, the investigation on factors influencing aquatic bird communities in black water lakes needs to be made to confirm these expectations.

The black water lakes of Anavilhanas are located in islands in the second largest fresh water archipelago in the planet; the first is located upwards in the same Rio Negro, a typical representative of Amazonian black waters, and floods huge areas of forest, providing the environment for endemic and rare taxa, including recently described fish families and lizard genera.

Although more recently the knowledge has substantially increased on biology and ecology of many aquatic bird species [5, 6, 10–13], studies are lacking on the function of species in black water systems and how their communities are influenced by local variation in the physical and biological features observed in black water lakes.

This is the first ecological study in the Amazon on the aquatic bird community of a system composed exclusively of black water lakes. This study is an overview of the system and investigates how richness, abundance, and species composition of aquatic bird communities differ over a large spatial scale among lakes and is locally influenced by lake features and seasonality.

The black water wetlands of the Anavilhanas Archipelago, central Brazilian Amazonia, are composed of about 70 lakes differing in size and several features, distributed over the landscape (about 140 km long and up to 20 km wide in the middle of the archipelago). Lake systems are useful to evaluate whether ecological factors (as possible underlying mechanisms) and differences in spatial scale influence aquatic bird community. Relating the environmental continuum and lake characteristics of the Anavilhanas to attributes of bird species, such as variation in presence/absence and abundance, and/or species composition across the archipelago, may help understand how lake ecological components influence their community.

In this study, I selected eight variables, including lake shape, depth, productivity (nitrogen and phosphorus concentration), water transparency, isolation (distance to river margins and distance to nearest lake), and habitat richness, that may be important because (i) many bird species (ducks, egrets, herons, storks, and allies) rely on lakes with complex shapes, transparent, and shallow waters [3, 5, 6, 13] for foraging, and lakes with more habitats can offer a more complex structure, sustaining more species [6], and may provide more area for feeding and nesting, while providing spots for sexual display for some species; for example, males of Muscovy duck use patches of grass near the shore as arenas where they fight for females [R. Cintra unpublished observations]; (ii) lakes bearing more productive waters may provide higher food availability [20–23]; the abundance of small vertebrates such as small fishes and large invertebrates such as large arthropods, crabs, and snails (prime avian food resources) is directly related to water productivity [20, 23]; (iii) degree of isolation is an important component of wetlands; for example, more isolated lakes may increase breeding success because they are located further away from access of terrestrial predators [6].

Although in recent years a great body of knowledge has been gathered on general aspects of the biology and behaviour of many tropical species, little is known about the behaviour and distribution of species in wetland ecosystems, and how a significant part of the aquatic bird community responds to the local variation observed in the physical and biological characteristics of tropical lakes, mainly of black waters. Within- and among-year climatic seasonality can also be determinant in the spatial distribution of bird species richness, so I also evaluated its effects on the bird community.

Since most aquatic birds are good colonizers, opportunistic, and widespread in the Amazonian basin [24], the main prediction of this study is that differences in species composition in relation to lake features is relatively similar among black water lakes throughout the Anavilhanas Archipelago. However, because lakes vary in their features, and because bird species differ in their habitat preferences and ability to occupy the complex environment, some direct relationships are expected, for example, ecological turnover in bird species composition with concomitant variation in lake habitat richness. Because the locally abundant species seem to have ample distribution, I also predict that aquatic bird density in each lake will correlate strongly with the frequency of lakes used by the species.

I verified the effect of the eight variables on bird community using data based on speedboat transect surveys. Specifically, I tested the hypothesis that spatial variation in lake characteristics should influence the richness (total number of bird species/lake), abundance, and variation in bird species' composition (i.e., how bird community undergoes species substitution across lakes), in a tropical black water wetland system.

The main questions I am asking are the following. (1) Does bird community composition change seasonally (low versus high water period) and among years in the black water lakes of Anavilhanas archipelago? (2) Does bird richness, abundance and species composition vary along a lake gradient that includes lake shape, water transparency, depth, productivity, isolation, and habitat richness?

2. Material and Methods

2.1. Study Area. Bird surveys were conducted on the black water lakes of Anavilhanas Archipelago, state of Amazonas, Brazil (Figures 1 and 2, 2°3′ S and 3°2′ S, 60°22′ W, and 61°12′ W), a National Park administered by Instituto Chico Mendes (ICMBio-MMA, Brazil), located 40 km northwest of Manaus, the Amazonas state capital. Anavilhanas National Park has an area of 350,000 ha, including the entire archipelago, in the Rio Negro, and a continuous and extensive area covered with terra firme (upland) rainforest on its left margin (Figure 1). The Archipelago itself is mainly covered by 100,000 ha of igapó, a forest seasonally inundated by black water relatively poor in nutrients [25–27]. The mean annual temperature is 25°C. Rainfall is about 2500 mm/year, most of it between November and May, with a short dry season between June and October [4].

There are three main kinds of Amazonian aquatic systems according to water type: white-, black-, and clear-water systems [28, 29]. White waters originate in the Andes, are turbid and muddy due to high loads of inorganic particles and suspended minerals, with transparency no greater than 20 cm, and more productive because of high nutrient concentration; their pH is almost neutral (6.6 to 7) due to dissolved bicarbonates and high conductivity (above 60 μS/cm). Clear waters originate in the pre-Cambrian crystalline

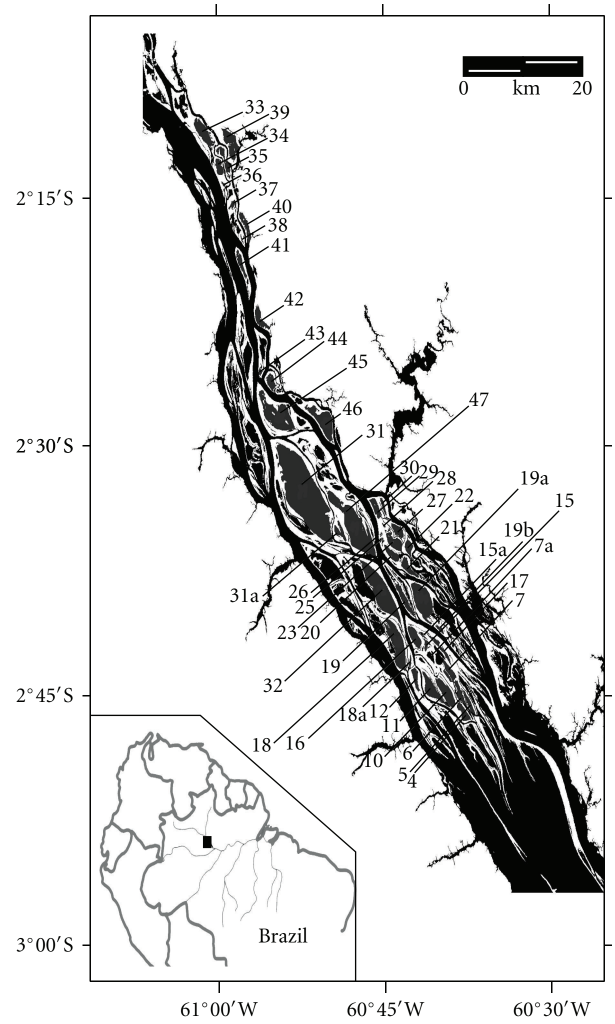


Figure 1: Location of the study area in Brazilian Amazonia. Map made from satellite image showing the location of the Anavilhanas Archipelago with the 45 black water lakes where bird surveys were conducted.

Photo: L.C. marigo

Figure 2: Aerial view of the southern part of the Anavilhanas Archipelago during high waters, showing some of the lakes visited in this study. Note at the lower part of the figure, in a long channel, the Chico Mendes Institute (ICMBio, Brazil) floating house used as field research base.

central Brazilian plateau and Guiana shield. They are greenish and transparent, they can have low to high concentration of dissolved and suspended minerals, water transparency is very high (5-6 m), their pH is acid to neutral (5 to 6), and their conductivity (6 to 50 μS/cm) and productivity are low. Black waters originate in washed sands and podzols in Central Amazonian lowlands, in crystalline shields and sedimentary basins. They drain from Campina vegetation (with incomplete decomposition of organic matter) in very porous soils, facilitating the transport of humic acids to the main rivers and lakes. Black waters are acidic, with high concentration of humic acids in a colloidal form and fulvic acids (contents, resp., ten and three times higher than in white waters); consequently, they are dark-brown coffee in color, and their transparency is up to 1 m. The low nutrient concentration probably makes them the poorest in nutrients and electrolytes in Amazonia, and accordingly, conductivity is very low (8 μS/cm) [21, 22, 29, 30].

The lakes of Anavilhanas are delimited by forest, usually in the form of levees. Their sediments originate in the Guianan Shield and in Central Amazonia uplands of the late Cretaceous and the early Tertiary/Quaternary periods [29]. The water is poor in nutrients, with high transparency and low pH (<5). The dark water color is due to dissolved humic and fulvic acids from the forest litter during processes of decomposition [29, 30].

Filoso and Williams [30] provided a characterization of the lakes' hydrology; for this study, some more data were collected as a complement. The lakes receive water from the Rio Negro, and those located close to river margins, also from terra firme forest streams, locally known as igarapés. The frequency and duration of the floods, depending on the area, vary from 75 to 250 days [31]. They have ecological importance and great impact on the local biota, determining large spatial-temporal variation in the aquatic and terrestrial phases of plant and animal communities [21, 23, 31]. The Rio Negro water level in Anavilhanas varies between 8 and 12 m, with the highest flooding in June-July and the lowest waters in October-November. At the time when the main bird surveys in this study were conducted, lake depth varied from 0.88 to 7 m. In Anavilhanas, during the period of the highest waters, the igapó forest is submerged, with water level fluctuating between 1 and 20 m, depending on the distance to the Rio Negro [18]. During the low water period, macrophytes abound, especially *Utricullaria foliosa*, *Salvinia auriculata*, *Pistia stratioites*, free floating *Paspalum repens*, *Eichhornia crassipes*, and *Oryza perennis*. More information on typical plant species of the area are presented below and in [17]. The vegetation along lake shores allows the coexistence of terrestrial forest and aquatic birds. Long-distance migrant birds from the northern hemisphere annually find along the white sands and muddy beaches of the Anavilhanas lakes a temporary feeding area and refuge [32].

2.2. Bird Surveys. Bird surveys were conducted twice a day, between 6.30 and 10.00 h, and between 16.00 and 18.00 h, in 45 lakes, from 14 November to 17 December 2007. In this period of the annual inundation cycle, water level is low, and starting to rise. At this time, the forest floor of the igapó (black water flooded forest) is not submerged yet, and most Nearctic migrant birds (shorebirds, and allies) are no longer present in the area. Although wading and probably most other aquatic birds often move from a foraging spot to another as the water table drops in the dry season, in response to water recession and prey availability, they were sedentary in the area in this period, using the same lake for weeks (R. Cintra unpublished data). The large size and/or conspicuous foraging behavior of most bird species results in high detection probability. Therefore, for this study, the data were not adjusted for false absences [33]. Water level was typical for the area and the period of the year [29]. For the purpose of investigating the effects of lake features on bird communities (see Section 2.4), the surveys were conducted only once in each of the 45 lakes, in a very short period, but covered a large area; hence, a snapshot of the aquatic bird community in the study area could be obtained. This approach is convenient in studies where birds are not captured and marked and avoids recording the same bird twice, overestimating count numbers.

To investigate potential seasonal effects on the bird community, two additional surveys were done at maximum water level (July 2007 and July 2008) and two at low water level (November-December 2007 and November-December 2009). Because during high flooding bird abundance was very low in both years, and during the shallow waters of 2009 the majority of the lakes were inaccessible, only a subsample of 16 small- and medium-sized lakes was surveyed, between 6.30 and 10.00 h. Also, because bird abundance during the high-water periods is too low, for this part of the study only species presence/absence data was used in the analyses to compare seasonal species richness and community composition between the high- and low-water periods.

All surveys were done aboard a 30 hp outboard speedboat driven by a field assistant, most of the time at a speed of 15–20 km/h. Birds were observed with 10 × 50 and 8–20 × 50 binoculars, sometimes using a portable counter.

The sample unit was the lake, which was completely circumnavigated, travelling at a distance of about 10–15 m from the shore. A Garmin 76 GPS was used to record geographical coordinates in order to obtain lake positions (Table 2); because lakes can have several names, they were identified by numbers instead of names.

Lakes of several sizes were sampled (see Figures 1, 2, Table 2). The influence of lake size was already considered when I estimated and used the lake shape (which includes lake area in the formula). Because of this, I did not evaluate the effects of lake area on birds using rarefaction curves which would be an obvious thing to do, but when various bird surveys are made per lake, which is not the case. However, rarefaction curves were constructed and presented but for the entire lake system.

Although it would not be necessary because none of lakes had an exaggeratedly higher number of birds than the rest (e.g., hundreds of species or thousands of individuals, see Table 2), I followed an earlier protocol of data standardization [4, 5] in order to be able to make regional comparisons with an ongoing study. Therefore, to make bird species richness and abundance, and community composition, comparable among lakes of different sizes, and with other studies, the data were standardized by dividing the number of individuals of each species by the sizes (areas) of the lakes in which the species occurred. The densities obtained were then used in the quantitative statistical analyses. Rarefaction curves of bird richness in relation to number of lakes sampled and to bird number were constructed using "R" program [34] and are also presented.

The density approach assumes that birds potentially could use the entire lake area. However, kingfishers and other birds commonly use trees along lake margins; herons and egrets (Rufescent Tiger-Heron *Tigrisoma lineatum*; Striated Heron *Butorides striatus*; Great Egret *Ardea alba*), rails (Gray-necked Wood-Rail *Aramides cajanea*), and Sungrebe *Heliornis fulica,* use floating meadows along the margins and in the central part of the lakes; cormorants (Neotropic Cormorant *Phalacrocorax brasilianus*), Anhinga *Anhinga anhinga*, piscivorous hawks (e.g., Black-collared Hawk *Busarellus nigricollis* and Osprey *Pandion haliaetus*) are commonly observed perched in dead trees, wherever they are located, and fishing over the entire lake area; and terns (Large-billed Tern *Phaetusa simplex* and Yellow-billed Tern *Sternula superciliaris*) use the center and margins of lakes and rivers. Any bird-counting method in Amazonian aquatic systems needs to consider differences in species distribution in relation to habitats. Since the surveys were made in the central and marginal parts of lakes alike, the influence of differences in their habitat use (birds that use trees along lake margins and those that use floating meadows along the margins and in the central part of the lakes) in local species distribution on the results is likely negligible.

The marginal habitat data (see below) were also standardized for the same reasons as above by dividing the number of times each habitat was recorded at lake margins by the perimeter of the lakes in which the habitat occurred. Information on biology of the bird species is available in Del Hoyo et al. [35].

2.3. Lake Characteristics Sampling. Lake depth was recorded at the center of each lake using a 5 kg weight attached to a 20 m rope graduated in meters, with a precision of 0.25 m. Water transparency was measured with a secchi disc. At the same spot, at a depth of 20 cm, a 50 ml water sample was collected in a sterile plastic vial to analyze water productivity. Total nitrogen (N) and total phosphorus (P) concentrations (μmol l^{-1}) in water samples were determined through simultaneous analyses [36] conducted at INPA's laboratory. A recent study in 20 lakes around Manaus (including three in Anavilhanas) showed significant correlations between both and chlorophyll-a [22], so they were used as indices of lake productivity in this study. Several experienced Amazonian limnologists informed that variation in lake water depth, water transparency, and productivity is very low, and one sample in the centre would represent adequately each lake. Therefore, lakes were sampled for these parameters only once.

The aquatic bird community composition was also compared among lakes of different shapes. The Global Mapper Program [37] was used to estimate lake dimensions (area and perimeter) on a satellite image. To estimate lake shape, or deviation from a circle (a circular lake assuming an shape index, SI = 1.0, and all other shapes assuming higher values), the shape index (SI) of Patton [38] was used as follows: $SI = (P/200)(\pi A)^{0.5}$, where SI = lake shape index; P = perimeter of the lake in km; $\pi = 3.1416$; A = area of the lake in km^2.

Microhabitat surveys (lake marginal vegetation), hereafter called habitat, were conducted concomitantly with the bird surveys. With the speedboat in motion every 10 s, an assistant (Jessica Cancelli), with extensive experience in the region, looked at the lake margin and recorded habitat type on a form containing habitat names. As the lake littoral strip can vary substantially in area, only the habitats located in the immediate vicinity of water were considered; these are the ones most often used by birds (personal observations). Habitats were named based on physiognomy, complemented with the presence of some dominant plant species. Eleven habitats along lake margins were identified: (1) stands of wild rice (*Oryza perennis*), sometimes partially submerged and forming small "peninsulas" in lakes; (2) stands of shrubs dominated by araçá-do-igapó (*Eugenia inundata*) and camu-camu (*Myrciaria dubia*); (3) stands of carauaçu (*Symmeria panicullata*); (4) stands of the tree macacarecuia (*Eichweilera tenuifolia*); (5) groups of snags (standing dead trees); (6) groups of dead logs; (7) secondary forest dominated by the embaúba tree (*Cecropia* spp.); (8) secondary forests dominated by jauari palms (*Astrocaryum jauari*); (9) igapó forest (with typical and some of the abundant flood-tolerant trees *Alchornea schomburgkiana, Leopoldinia pulchra,* arapari (*Macrolobium acacifolium*), macucu-do-igapó *(Aldina latifolia), Mabea nitida,* and *Hevea spruceana,* ipê (*Tabebuia barbata*) [31, 39]; (10) muddy beaches with no vegetation; (11) muddy beaches covered with scattered patches of grass (*Oryza perennis*) and rush (Cyperaceae). After standardization (see bird survey data above), habitat richness was used in the analyses to evaluate its influence on the bird community. Piedade and Junk [17, 40] presented information on herbaceous plants of the Amazonian floodplain, some of which occur in Anavilhanas.

2.4. Statistical Analysis. Aquatic bird richness, abundance, and community composition were compared among 45 lakes within the Anavilhanas Archipelago. Of the total community (birds associated with aquatic environments), only a group of 31 species was subjected to statistical analyses: those always associated with the aquatic environment, hereafter called the aquatic bird community, which includes the nine species considered piscivorous by Petermann [11]. They are marked as A (aquatic) and P (piscivorous) in the "Aq./Pisc." column of Table 2, which lists all the birds associated with aquatic environments in the study area.

Mantel tests, available in PC-ORD [41], were run to verify spatial autocorrelation of the quantitative aquatic bird community (matrix of species abundance by lakes) and lake location (matrix of Euclidian distances with geographical coordinates by sites (lakes), using latitude and longitude metric (UTM) values. The method chosen for the test was Mantel's asymptotic approximation [41].

To investigate whether the most abundant species were also the most widely distributed in the lakes, a simple linear statistical model was used to verify the relationship between bird abundance (mean bird density, which was log-transformed before analysis), and bird distribution in the Archipelago (number of lakes in which they occur). In this specific analysis, only species occurring in at least five lakes (21 of the 31 bird species) were included.

Multiple linear statistical models were used to look for relationships between qualitative and quantitative bird community composition (NMDS axes, see below) and the independent variables of lake shape, degree of isolation (distances from the centre of a given lake to the centre of the nearest neighbouring lake and to river margins), depth, water transparency, habitat richness, and lake productivity. Simple linear models were used to verify relationships between bird richness and abundance and the same independent variables. Before running the analyses, a Pearson correlation matrix was used to verify the significance of correlations among the independent variables. Only those that were not significantly correlated were considered in the same statistical models.

Qualitative matrices with species presence/absence, and quantitative matrices with species abundance, by lake, were constructed for the aquatic bird communities. In the matrices, the quantitative values (number of birds recorded) for each species were divided by lake area to obtain bird densities, which were then used as dependent variables in models of multiple linear statistical models to test the null hypothesis that bird community composition is similar among lakes.

To compare bird species composition among lakes, all quantitative and qualitative data matrices constructed from the bird surveys were subjected to nonmetric multidimensional scaling (NMDS), an multivariate ordination analysis available in the program PC-ORD [41, 42]. An advantage of using NMDS is that it is based on ranked distances and tends to linearize the relationship between environmental distance and biological distance [43], a procedure that alleviates the "zero truncation problem," which plagues all ordinations of heterogeneous datasets [41, 44]. According to these authors, NMDS has performed well with both simulated gradients and field data.

The distributions of species densities generally do not conform to the assumptions of multivariate inferential analyses such as multivariate analysis of variance [45]. Therefore, NMDS was performed on the data matrices to obtain linear, orthogonal variables (axes) describing the bird community composition that met the assumptions of the multivariate inferential analyses [46].

Throughout the study, I used two NMDS axes for quantitative data and three axes for qualitative data as dependent variables. For community data from 45 lakes, two NMDS axes captured most of the variance in the original variables for quantitative data in the bird species matrix (cumulative proportion of total variance, $C_{PV} = 0.83$), whereas three axes were enough for the presence/absence data matrix ($C_{PV} = 0.82$). Similarly, for the seasonal data, three axes captured most of the variance for presence/absence data ($C_{PV} = 0.85$).

The Bray-Curtis index was used to describe dissimilarity between lakes. This index is available in PC-ORD program [41], and was used on abundance and presence/absence data. The use of quantitative data may lead to patterns influenced by the higher contribution of the most abundant species to the ordination; however, for qualitative ordination, they contribute less to dissimilarities in the bird communities among lakes because qualitative ordination tends to capture mainly the patterns of the rarest species. The Bray-Curtis coefficient has been recommended and used in ecological gradient studies [42, 43, 47, 48], and, in Amazonia, with birds [4, 5, 49]. Finally, the resulting NMDS axes were used as dependent variables in models of multiple linear statistical models.

A comparison between both bird richness and species composition in the community was made using analysis of variance (ANOVA) and multiple linear statistical models, respectively, to evaluate whether and/or how the bird community changes between high-water and low-water periods. *A posteriori* Pillai-Trace tests were used to verify whether there were significant differences in bird species composition among the 45 lakes and also when 16 of the 45 lakes during the low-water period (November-December 2007, November-December 2009) were compared with the same 16 lakes for the high-water period (July 2007, July 2008, see bird survey data). The Pillai-Trace statistic has been shown to be less sensitive to deviations from assumptions than other multivariate statistics [50, 51]. To make the water periods comparable, only the morning surveys (6.00 to 10.00 h) were considered. The abundances of most bird species were too low during the peak of flooding; therefore, only a qualitative matrix (presence/absence data) including the two periods of high water and one of low water was used for NMDS. The resulting NMDS axes were also used as dependent variables in models of multiple linear statistical models. The General Linear Model (GLM) procedure available in the program SYSTAT [52] was used to run the analyses.

Multiple linear models followed by Pillai-Trace tests were used to evaluate the effects of lake shape, isolation, and physicochemical characteristics (depth, water transparency, productivity) on the bird qualitative and quantitative community composition, now using data from all 45 lakes (November-December 2007). To verify potential problems of residual analysis in multiple regressions, a graphic method called partial residual plot, available in R (Core Development Team 2008) was used. To verify possible linear relationships among predicting variables, I also used R to estimate the variance inflation factor, which calculates the level of multicolinearity.

3. Results

3.1. Avian Surveys. In this study, the Anavilhanas Archipelago landscape was surveyed along a large gradient of 45 lakes, varying in size (area) from 0.29 km^2 (Lake 26) to over 60 km^2 (Lake 31), to obtain a nearly complete survey of the aquatic bird community. Lake perimeter ranged from 4 km (Lake 28) to 43.7 km (Lake 31). The lakes were distributed within an archipelago extending 140 km along the Negro River (Figure 1). Since the survey was conducted mostly from a distance of approximately 20 m from lake margins (but most of the time crossing each lake when visiting the central areas to get the geographical coordinates for its position), a minimum of 1,300 km in the 45 lakes was surveyed by speedboat.

A total of 3,626 individuals of 48 species associated with 45 lake environments were recorded at Anavilhanas (Table 2). None are endemic to the Archipelago, and none are listed as threatened. The Fasciated Tiger-Heron (*Tigrisoma fasciatum*), a bird extinct in southern Brazil, is a new record for the area. During the surveys, three individuals were registered (one in a lake). Most species recorded are permanent residents. One is considered a northern neotropical migrant (the Osprey *Pandion haliaetus*). The families Ardeidae and Alcedinidae had the highest species richness, with 8 (16.6%) and 5 (10.4%) species, respectively.

The rarefaction curves of aquatic bird species increased until they reached a plateau after 20 lakes (about half of the total) were surveyed, after which they continued to increase, but less than before (Figure 3).

Nine of the ten most abundant aquatic and piscivorous species are among the ten most abundant of the 48 species associated with aquatic environments (Table 2). These species (Neotropic Cormorant *Phalacrocorax brasilianus*; Black-bellied Whistling-Duck *Dendrocygna autumnalis*; Greater Ani *Crotophaga major;* Muscovy Duck *Cairina moschata*; Cocoi Heron *Ardea cocoi*; Great Egret *Ardea alba*; Anhinga; Large-billed Tern *Phaetusa simplex*; Ringed Kingfisher *Megaceryle torquata*) summed up 2,567 individuals, representing over four fifths (82.7%) of the 3,105 aquatic birds recorded for the 31 species used in the analyses.

In the 45 lakes, considering the 31 species used in the analyses, the aquatic bird species richness ranged from four (Lakes 19-B and 38) to 19 (Lakes 15 and 38), and the total community abundance ranged from four individuals (Lake 4) to 603 (Lake 12).

3.2. Lake Characteristics. Lake shape (SI) ranged from 1.183 (close to round) to 2.749 (elliptical). Lake distances from river margins ranged from 0.306 km (Lake 40) to 10.4 km (Lakes 5 and 6), and distances to the nearest lake ranged from 0.688 km (Lakes 25 and 26) to 6.3 km (Lakes 42 and 43). Lake depth ranged from 0.88 m (Lake 12) to 7.0 m (Lake 42), and water transparency ranged from 0.47 m (Lake 25) to 1.1 m (Lakes 42 and 46). Lake productivity variation considering nitrogen concentration was higher (from 0.18 in Lakes 21 and 22, to 0.81 mg/L in Lake 16) than for phosphorus (from 0.020 in Lakes 6 and 18 to 0.060 mg/L in Lake 25). Habitat richness (marginal vegetation) ranged from 3 (Lake 12) to 11 habitats (Lake 31). See more detailed information in Table 3.

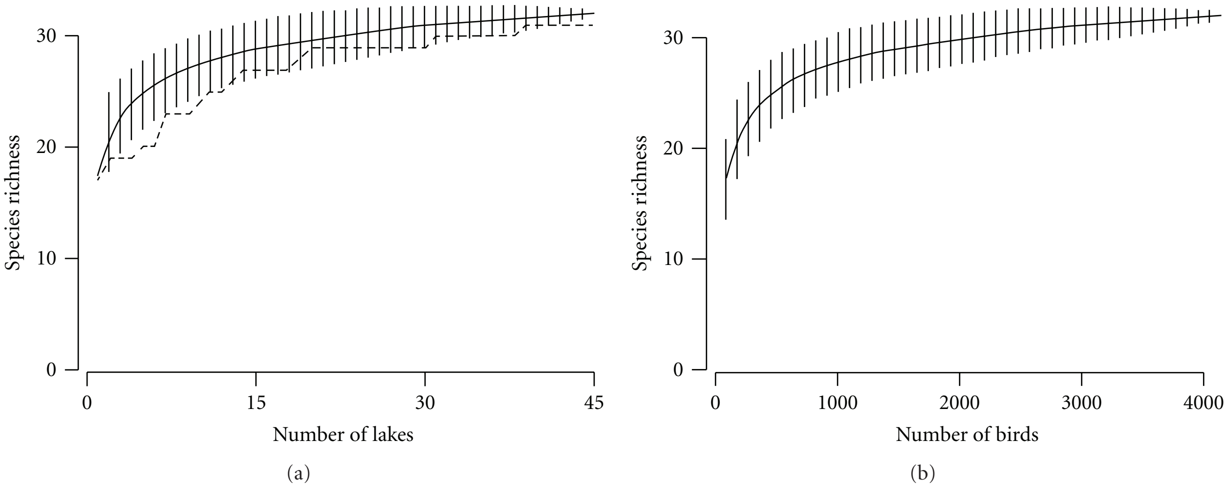


FIGURE 3: Rarefaction curves for the survey data from Anavilhanas Archipelago, showing bird species richness in relation to (a) number of lakes surveyed (sampling effort) and (b) number of birds. Continuous lines are rarefaction curves; the hatched line depicts observed data.

The correlation between lake habitat richness and distance to nearest lake was significant ($r = -0.560$, $N = 45$, $P < 0.002$), and so was that between lake shape and phosphorus concentration ($r = -0.487$, $N = 45$, $P < 0.019$). Therefore, these two variables (habitat richness and lake shape) were not included together with the others in the same statistical models, in which the response variables of bird richness, abundance, and community composition were evaluated. The other independent variables were not significantly correlated among them.

The relationship between distances in the quantitative aquatic bird community composition and distances between lakes was not significant (Mantel test, $r = 0.071$; $P < 0.264$), indicating absence of spatial autocorrelation, or that bird species composition of the lakes was not grouped by spatial proximity. The relationship between distances in the qualitative aquatic bird community composition and distances between lakes was very weak, although significant (Mantel test, $r = 0.148$; $P = 0.029$), indicating some degree of spatial autocorrelation.

Because the correlations for quantitative aquatic bird community composition were not significant, and the relationship between the qualitative aquatic bird community composition and distance between lakes were so weak, multivariate analyses were run to compare the quantitative and qualitative bird community composition among lakes, and to evaluate the effects of lake characteristics on them.

There was a positive and highly significant relationship between bird species abundance (mean bird density) and bird species distribution, or the number of lakes in which they occurred (simple linear regression, $r^2 = 0.833$, $F_{1,19} = 94.459$, $P = 0.0001$; Figure 4). The number of lakes in which birds occurred explained 91% of the total variation, indicating that the most abundant species were the ones with the most extensive distribution in the archipelago.

3.3. Effects of Seasonality on Bird Species Composition. The aquatic bird species richness changed significantly among the high-water periods and the low-water periods (ANOVA, $F_{3,60} = 22.972$; $P = 0.0001$), with more species occurring at low water. The species composition of the aquatic bird community during high water (July 2007 and July 2008) was more similar between them than to that during low water (November-December 2007 and November-December 2009, Figure 5) and changed significantly between high- and low- water periods (Pillai-Trace = 0.744, $F_{3,60} = 9.280$, $P = 0.0001$, Figure 5).

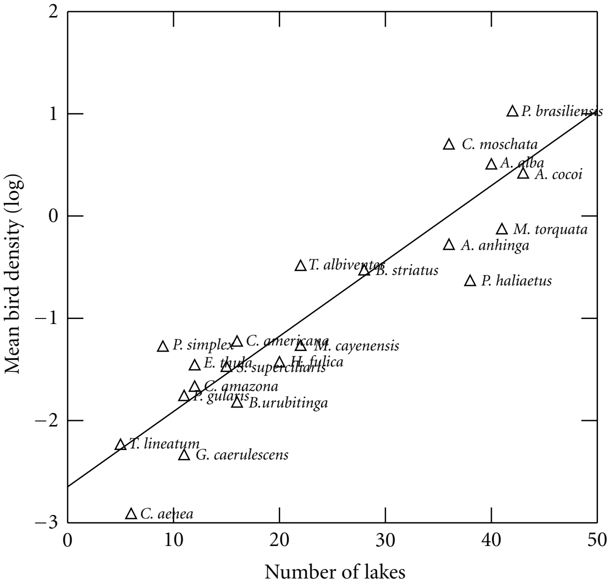


FIGURE 4: Relationship between the aquatic bird species (mean bird density) and their distribution (number of lakes they occur) within the Anavilhanas Archipelago (see Section 2).

3.4. Bird Species Composition along Gradients Produced by Lake Characteristics. In Figures 6(a) and 6(b), the aquatic bird species are ordered by relative density (bars) along the

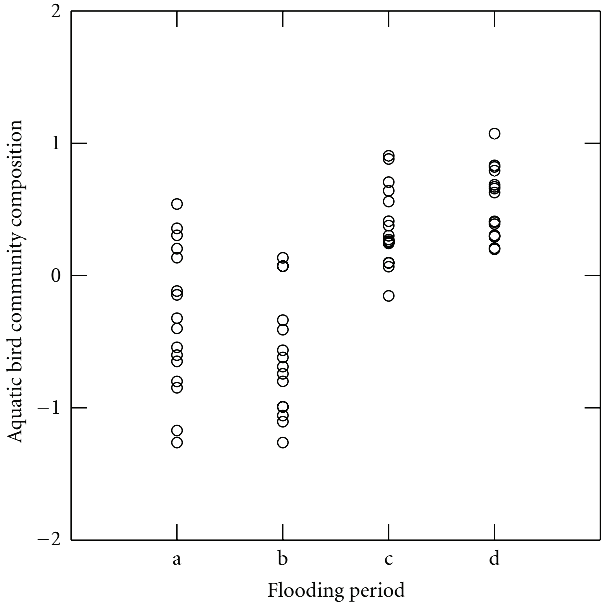


Figure 5: Seasonal changes in aquatic bird community composition (represented by score values of NMDS-axes, see Section 2 for more explanations). Bird community composition differed significantly between high-water periods (a = July 2007; b = July 2008) and low-water periods (c = November-December 2007; d = November-December 2009).

ecological gradients of lake depth and habitat richness, which influenced significantly bird community composition (see below). Because it depicts a similar pattern to those of Figures 6(a) and 6(b), a figure with the ordination of bird species in relation to that of lake distance to river margins and distance to the nearest neighboring lakes is not shown.

Bird community composition was significantly influenced by lake depth, water transparency, lake isolation, and habitat richness (Table 1). However, in all cases, few species were strongly associated with the limits of the gradients, and most species occurred across the gradients of these variables (Figures 6(a), 6(b)). Differences in species composition (qualitative data) were significantly correlated with lake water transparency, lake isolation and habitat richness (Table 1, Figures 6(a), 6(b)). However, when abundance of individuals was added to the community data (quantitative data), lake depth was also an important determinant and all relations were significant except for water transparency (Table 1).

3.5. Effects of Lake Characteristics on the Aquatic Avifauna. The aquatic bird species richness was not significantly related to lake shape (simple linear regression, $r^2 = 0.003$; $F_{1,43} = 0.121$; $P = 0.730$); however, it was significantly higher in lakes bearing higher habitat richness ($r^2 = 0.741$, $F_{1,43} = 53.429$; $P = 0.0001$), and significantly lower in more isolated lakes, or those located farther away in relation to neighbouring lakes ($R^2 = 0.341$, $t = -2.690$; $P = 0.011$). It was not significantly related to any other lake physicochemical properties.

Bird abundance was significantly lower in deeper lakes ($R^2 = 0.327$, $t = -3.316$; $P = 0.002$). However, it was not significantly related to lake shape ($r^2 = 0.019$; $F_{1,43} = 0.831$; $P = 0.367$), habitat richness of lake margins ($r^2 = 0.008$, $F_{1,43} = 0.349$; $P = 0.558$), or any other lake physicochemical properties or isolation.

For the quantitative data (species abundance), the aquatic bird community composition (NMDS axes) differed significantly with lake isolation (distance to river margins and to the neighbouring lake) and lake depth. Differences in the aquatic bird community composition were not significantly related to water transparency or lake productivity (*N* and *P*, Table 1).

For the qualitative data (species presence/absence), bird community composition also differed significantly with lake isolation (distance to river margins and to neighbouring lake) and water transparency. However, differences in bird community composition were not significantly related to lake depth and lake productivity (*N* and *P*, Table 1).

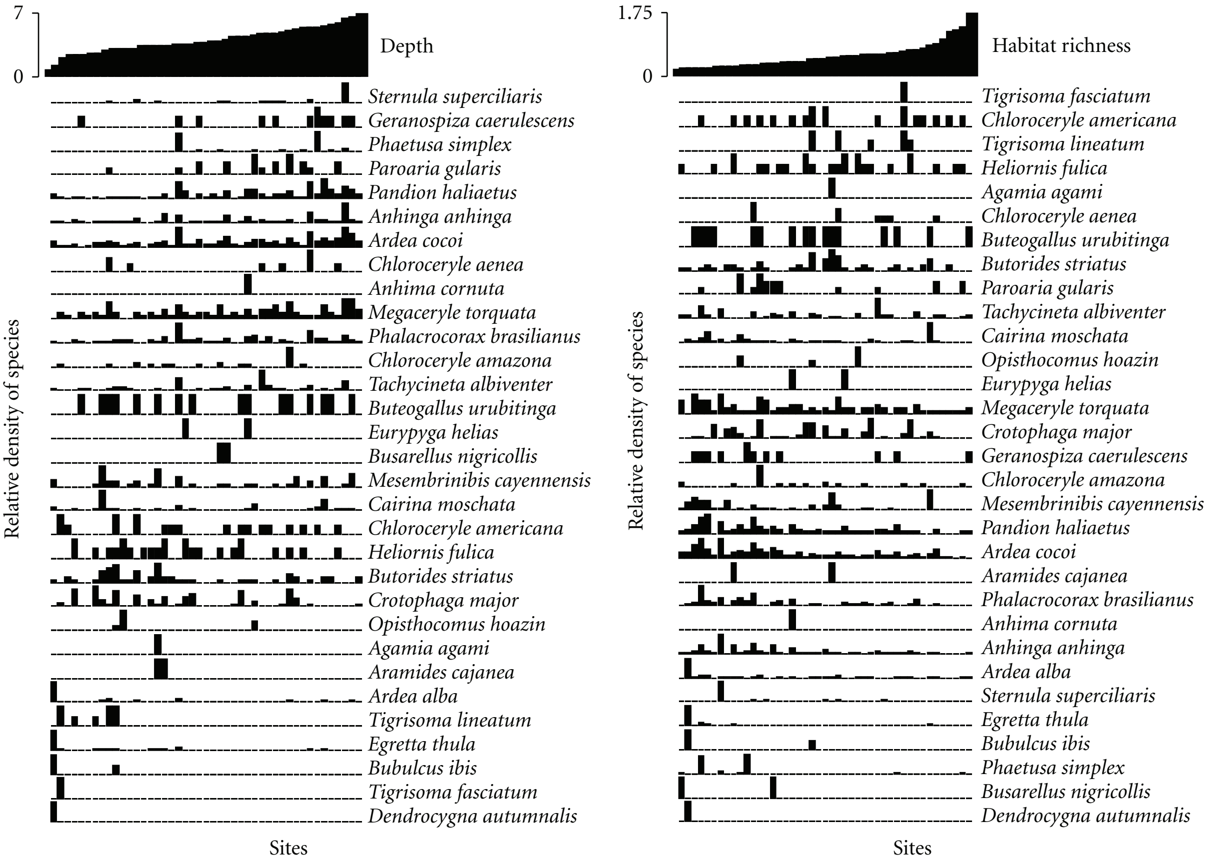
The differences in both quantitative and qualitative aquatic community composition were consistent, and probably, as a result of the degree of lake isolation, decreased significantly with the increase in distance to river margins (Table 1, Figure 7), and increased with the increase in distance to the nearest neighbouring lake (Figure 7). The differences in quantitative community composition increased with lake water depth and decreased with water transparency (Table 1, Figure 7), indicating that aquatic birds use shallow lakes with somewhat turbid waters more often.

Because lake shape and habitat richness were significantly correlated to other variables (see data on correlation between variables), they were included in separate models. For the quantitative data (species abundances), the differences in aquatic bird community composition decreased significantly with the increase in habitat richness. However, differences in the aquatic bird community composition were not significantly related to lake shape (Table 1, Figure 7). For the qualitative data (species presence/absence), the differences in the aquatic bird community composition also decreased significantly as habitat richness increased. However, those differences were not significantly related to lake shape as well (Table 1, Figure 7).

4. Discussion

Several factors have been investigated as determinants in the composition of aquatic bird communities in Brazil. Guadagnin et al. [6] showed the importance of α- and β diversity influencing aquatic bird communities in fragmented wetlands in southern Rio Grande do Sul. They found that some aquatic birds favour small, isolated lakes and suggested among other parameters that waterbody physicochemical conditions, food resources, and habitat, may influence ecological gradients and therefore deserve further investigation.

This study clearly provides further evidence that the natural limnological heterogeneity and flood dynamics of Amazonian black water lakes can affect the local composition of animal and plant communities [5, 39, 53, 54]. In addition



(a)

(b)

Figure 6: Aquatic bird species distribution in relation to lake (sites) properties: (a) water depth and (b) habitat richness. The right side of the lake properties axis represents higher values of the properties.

to some variables significantly associated with the number of bird species (richness) and individuals (abundance), there were strong and significant relationships between lake depth, isolation, water transparency and bird community composition. Furthermore, I also found that variation in bird community composition can, in part, be attributed to a habitat richness gradient, and the phases of the annual hydrological cycle in Anavilhanas.

Most of the findings were in community composition and fewer in variation in species richness and bird abundance. This can be attributed to species turnover within the archipelago of Anavilhanas, which is not related to regional variation in the aquatic avifauna (unpublished data), but to local differences in the avian communities. The surveys indicate that most bird species occur throughout the lakes of the Anavilhanas and are tracking differences in the archipelago's landscape and the characteristics of the lakes.

In the study area, there is a strong and significant relationship between the locally most abundant species and the range of their distributions across the Archipelago (Figure 4), which can be related to population dispersion as predicted by the neutral theory of biodiversity [9, 55, 56]. Nevertheless, in the Anavilhanas, the weak correlations between the spatial variation in the bird community composition and geographical distances (distances between lakes, see Section 3 on spatial autocorrelation) can be taken as evidence against the distance decay predicted by Hubbell's theory [9]. Therefore, long-term studies are needed to specifically test this theory for the lake bird community in the Anavilhanas. In European wetlands, abundance has been considered a good predictor of the ability of species to colonize lakes, with the less abundant being less able to occupy distinct areas and occurring in few large ponds [57], a pattern that seems valid for the Anavilhanas. For example, the Agami Heron, the Sunbittern, and the Horned Screamer, among others, were all very scarce in the surveys (see Table 2) but occurred in a small number of medium to large lakes.

Some lakes were not visited because access was blocked by shallow waters. However, 60–70% of all lakes in the archipelago were surveyed. Therefore, the sampling was extensive and representative of this enormous black water system (Figures 1 and 2). In addition, over 95% of the bird species associated with aquatic environments previously recorded in the archipelago [4] were recorded in this study.

Of the ten most abundant species in lakes, six are piscivorous (Neotropic Cormorant, Cocoi Heron, Great Egret, Anhinga, Large-billed Tern and Ringed Kingfisher), and one is a migrant, piscivorous species (Osprey) whose juveniles

Table 1: Results of the multiple linear models performed to test the effect of lake shape, physicochemical properties—depth, water transparency, and productivity (nitrogen and phosphorus concentration)—isolation (distance to river margin and distance to nearest lake), and habitat richness provided by marginal vegetation, on the qualitative and quantitative composition of the communities of aquatic birds. The first figures in the DF columns are the degrees of freedom of the treatment; the second, those of lakes. The analyses were performed on scores resultant from nonmetric multidimensional scaling (NMDS). See Section 2 for details.

Ecological variables	Qualitative				Quantitative			
	Pillai-Trace	F	DF	*P*	Pillai-Trace	F	DF	*P*
Lake shape*	0.075	1.115	3; 41	0.354	0.034	0.483	3; 41	0.696
Lake depth	0.056	0.716	3; 36	0.549	0.239	3.779	3; 36	**0.019**
Lake productivity								
Nitrogen	0.005	0.058	3; 36	0.981	0.100	1.335	3; 36	0.278
Phosphorus	0.091	1.199	3; 36	0.324	0.146	2.047	3; 36	0.125
Water transparency	0.216	3.306	3; 36	**0.002**	0.109	1.464	3; 36	0.240
Distance to river margins	0.274	4.534	3; 36	**0.009**	0.325	5.768	3; 36	**0.003**
Distance to nearest lake	0.329	5.883	3; 36	**0.002**	0.257	4.159	3; 36	**0.013**
Habitat richness*	0.394	8.890	3; 41	**0.0001**	0.598	20.334	3; 41	**0.0001**

[*] Lake shape and habitat richness were significantly correlated to other variables, and therefore analyzed in separate models (see Section 3 and also Figure 7).

can stay in the area for a year or more before they migrate to the Northern Hemisphere (unpublished data). Six also showed ample distribution in the archipelago, with records in more than 80% of the lakes (see Table 2). The Neotropic Cormorant was the most abundant species (nearly 500 individuals). The Black-collared Hawk and the Horned Screamer (abundant in white water Lakes), the Gray-necked Wood-Rail, the Agamia Heron *Agamia agami*; the Fasciated Tiger-Heron *Tigrisoma fasciatum*; the Sunbittern *Eurypyga helias*; were among the ten rarest species (Table 2).

With similar species composition, but lower bird abundance than those from Amazonian white water lakes [5], the communities of birds associated with black water environments at Anavilhanas comprise a few abundant and a higher number of rare species. This is a typical pattern of large animal communities, not only in the tropics, but also in other latitudes [1, 58, 59].

In this study, the aquatic bird species accumulation curve did not reach an asymptote, and more species were being added even after 40 lakes (Figure 3). This indicates that other species that are present in the area could potentially have been added. Indeed, some species unrecorded in the survey have been seen in the area, and also in other conservation units in central and western Brazilian Amazonia [4, 5, 9, 19]. This notwithstanding, most species (30, or 96.8% of the aquatic; 17, or 94.4% of the piscivorous) were found before less than half of the lakes (20, or 44.4%) were surveyed (Figure 3), and several lakes had to be visited before another new species was added. In white water lakes in western Brazilian Amazonia, a similar number of bird species were recorded after surveying only five lakes [5]. This difference may be due to the higher lake productivity of the várzea wetlands.

In the Anavilhanas, there were significant changes in species composition between periods of high and low water, with less variation in low-water than in high-water season (Figure 5). Although species richness is similar between these two periods, only slightly lower during high water, abundance is notably higher during low water. This may result from some species having nonresident individuals which are, therefore, transient in the area, for example, Anhinga, terns, egrets, herons, and ducks (Black-bellied Whistling-Duck). During low waters food resources are more abundant and concentrated because the lakes are drying out, and probably more accessible. In his intensive and detailed study at Marchantaria Island, Central Amazonia, Petermann [11] also found seasonal changes in the composition of the wetland bird fauna, with lower numbers of species occurring during the high water period (flood pulse).

The results of multivariate analyses suggest that, in general, the aquatic bird community composition varies considerably with a gradient in ecological factors across the Archipelago, such as lake depth, lake isolation, and habitat richness (Table 1). Morphometric features of lakes are important determinants of bird and fish community structure in north-central Alberta, Canada [60]; probably, environmental conditions at the margins of round and shallow lakes are more homogeneous, and littoral production higher, than in deeper lakes that have a greater amount of pelagic habitat relative to the littoral zone [55, 61]. Considering the entire bird assemblage, there were no effects of lake shape on the community, contrary to another recent study in western Brazilian Amazonia (Amanã and Mamirauá Reserves), where lake morphometry influenced variation in the avian community [5]. This difference probably is due to the lower heterogeneity in the shapes of the Anavilhanas lakes, which tend to be more elliptical, whereas the ones from Amanã and Mamirauá vary from circular to elongated, and dendritic [5].

There was a trend of higher bird richness and abundance and larger variation in bird community composition in shallower lakes (see Section 3, Figures 6(a) and 7), likely linked to the fact that many piscivorous and omnivorous birds, such as egrets, herons, terns, and ducks (Figure 8), capture prey (aquatic insects, crabs, snails, and small fish) more easily in shallow than in deeper lakes ([55], see also [62]). Higher light

Table 2: The species of birds associated with aquatic environments at the Anavilhanas Archipelago, central Brazilian Amazonia, total numbers recorded in lakes (NB), body weights in grams (Wt.), the strictly aquatic and/or piscivorous (Aq./Pisc.) species used in statistical analyses, their statuses in the study area, the designations and numbers (NL) of lakes in which they occurred, and the percentages (%) of these numbers relative to the total numbers of lakes (= $N \times 100/45$), see code meanings at the end of the table.

	Scientific name	Bird species Portuguese common and/or local (*) name	English name	NB	Wt.	Aq./Pisc.	Status	Lakes in which birds occurred (see names, types, and locations in Table 3)	NL	(%)
1	*Phalacrocorax brasilianus*	Biguá, miuá*	Neotropic Cormorant	499	1,300	A, P	r, b	4–7, 7-A,10–12,15,15-A,16–23, 19-A, 19-B, 25, 27–31, 31-A, 32–47	42	93.3
2	*Dendrocygna autumnalis*	Marrequinha*	Black-bellied Whistling-duck	474	740	A	ps+, b	5, 12, 15, 19-A	04	8.8
3	*Crotophaga major*	Coroca*	Greater Ani	383	170	A	r, b	4–7, 7-A, 10–12, 15–18, 15-A, 18-A, 19, 19-A, 20, 25, 27–32, 31-A, 27, 29–31, 33–35, 37, 40–42, 45, 46	31	68.8
4	*Cairina moschata*	Pato-selvagem*	Muscovy Duck	352	3,000	A	r, b	4–7, 7-A, 10–12, 15–19, 15-A, 18-A, 19-A, 21, 22, 25, 27, 29–32, 31-A, 33–35, 39–43, 45–47	36	80.0
5	*Ardea cocoi*	Maguari*	White-necked Heron	271	2,100	A, P	r, b	4–7, 7-A, 10–12, 15–19, 15-A, 18-A, 19–23, 19-A, 25–27, 29–32, 31-A, 33–47	43	95.5
6	*Ardea alba*	Garça-branca-grande	Great Egret	235	885	A, P	ps+, b	4, 5, 7, 7-A, 10–12, 15–23, 15-A, 18-A, 19-A, 19-B, 25, 26, 27–36, 31-A, 40–42, 44–47	40	85.1
7	*Anhinga anhinga*	Anhinga, Carará*	Anhinga	138	1,200	A, P	ps+	5, 10–12, 15–19, 15-A, 18-A, 19-A, 21–23, 25, 27–35, 31-A, 37, 39–47	36	80.0
8	*Phaetusa simplex*	Gaivota*	Large-billed Tern	121	240	A, P	r, b	19-A, 23, 31, 35–37, 39, 46, 47	9	20.0
9	*Progne subis*	Andorinha-púrpura	Purple Matrin	103	47		vn	47	1	2.2
10	*Megaceryle torquata*	Ariramba-grande*	Ringed Kingfisher	94	300	A, P	r	4–7, 7-A, 10, 11, 15–21, 15-A, 18-A, 19-A,19-B, 23, 26, 28–47, 31-A	41	91.1
11	*Pandion haliaetus*	Gavião-caipira	Osprey	89	1,500	A, P	vn	4, 5, 7, 7-A, 10, 12, 15–23, 15-A, 18-A, 19-A, 25, 27, 28, 30–37, 31-A, 39, 47	38	84.4
12	*Progne tapera*	Andorinha-do-campo	Brown-chested Martin	89	32		u	6, 7-A, 11, 15, 18, 18-A, 19, 19-A, 22, 25, 28–34, 31-A, 36, 37, 39–41, 43–47	27	60.0
13	*Coragyps atratus*	Urubu	Black Vulture	87	1,350		r, b	5–7, 10, 11, 15-A, 16–20, 18-A, 22, 23, 25, 29–33, 31-A, 35, 39, 41, 45, 47	26	57.7
14	*Tachycineta albiventer*	Andorinha-de-rio	White-winged Swallow	75	17	A	r, b	10, 12, 15, 16, 21, 22, 27, 28, 31, 31-A, 32, 33–41, 44, 45, 47	23	51.1
15	*Progne chalybea*	Andorinha-grande	Gray-breasted Martin	62	39		u	10,11, 31, 31-A, 32, 34, 40, 42, 45, 47	10	22.2
16	*Butorides striatus*	Socozinho	Striated Heron	59	175	A, P	r, b	4, 5, 7, 10–12, 15, 15-A, 19, 19-A, 20, 22, 23, 25–27, 29–32, 39, 41, 42, 45	28	62.2
17	*Sternula superciliaris*	Gaivotinha*	Yellow-billed Tern	58	46	A, P	r, b	10, 16, 30, 31, 31-A, 33, 35, 37, 39, 40, 44, 45, 47	13	28.8
18	*Mesembrinibis cayennensis*	Corocoró, curubá*	Green Ibis	54	720	A	r, b	4, 7, 10–12, 15, 15-A, 16, 18, 19, 19-A, 27, 29–33, 31-A, 39, 41, 45, 47	22	48.8

Table 2: Continued.

	Scientific name	Bird species Portuguese common and/or local (*) name	English name	NB	Wt.	Aq./Pisc.	Status	Lakes in which birds occurred (see names, types, and locations in Table 3)	NL	(%)
19	*Amazona festiva*	Paqpagaio-da-várzea	Festive Parrot	54	400		u	6, 7, 15, 16, 18, 19, 32, 33, 39, 40, 45, 47	12	26.6
20	*Patagioenas cayennensis*	Pomba-galega	Pale-vented Pigion	41	260		r	5, 7, 10, 15–19, 23, 25, 29, 30, 31-A, 32, 34, 39, 40, 45, 46, 47	21	44.7
21	*Egretta thula*	Garça-branca-pequena	Snowy Egret	39	330	A, P	ps+, b	4, 12, 15, 15-A, 16, 17, 18-A, 29, 31, 31-A, 32, 45	12	26.6
22	*Heliornis fulica*	Patinha-do-igapó*	Sungrebe	25	130	A	r, b	4–6, 10, 11, 15, 15-A, 16, 17, 19, 19-B, 20, 22, 25, 27, 31-A, 34–36, 39	20	44.4
23	*Cathartes melambrotus*	Urubu-da-mata	Greater Yellow-headed Vulture	24	1600		r	6, 11, 18, 19, 22, 25, 27, 31, 31-A, 34, 40–41, 47	13	28.8
24	*Chloroceryle amazona*	Ariramba-média*	Amazon Kingfisher	24	110	A, P	r	4, 5, 7-A, 17, 18-A, 19, 30, 31-A, 35, 36, 39, 41	12	26.6
25	*Ara ararauna*	Arara-canindé	Blue-and-yellow Macaw	23	1300		u	6, 15-A, 16, 19, 23, 33, 41	7	15.5
26	*Paroaria gularis*	Cardeal-da-Amazônia	Red-capped Cardinal	20	22		r, b	10, 19, 19-A, 31, 31-A, 33–36, 40, 45	11	24.4
27	*Chloroceryle americana*	Ariramba-pequena*	Green Kingfisher	19	27	A, P	r	5, 7-A, 15, 17, 18-A, 19, 26, 30, 31, 33, 34, 36, 40, 41, 44, 46	16	35.5
28	*Buteogallus urubitinga*	Gavião-preto	Black Hawk	16	1,100	A	r, b	5, 11, 15, 16, 18, 19, 23, 28–32, 31-A, 37, 41, 45	16	35.5
29	*Geranospiza caerulescens*	Gavião-pernilongo, gavião	Crane Hawk	12	330	A	r	10, 18, 23, 28, 31, 32, 35, 40, 45–47	11	24.4
30	*Buteo magnirostris*	Gavião-pega-pinto*	Roadside Hawk	11	265		r, b	4, 7, 15, 18, 18-A, 22, 30, 35, 39, 46	10	22.2
31	*Bubulcus ibis*	Garça-dos-bois*	Cattle Egret	10	340	A	r, b	12, 15	2	4.4
32	*Chloroceryle aenea*	Ariramba-miudinha*	American Pygmy Kingfisher	9	15	A, P	r	27, 31-A, 34, 37, 40, 45	6	13.3
33	*Milvago chimachima*	Caracaraí*	Yellow-headed Caracara	9	325		r, b	10,11,16,21, 31, 32, 33, 45, 47	9	20.0
34	*Tigrisoma lineatum*	Socó-boi, socó-onça*	Rufescent Tiger-Heron	8	840	A, P	r, b	15,15-A,18-A, 25, 31-A	5	10.6
35	*Opisthocomus hoazin*	Cigana	Hoatzin	7	820	A	r, b	15, 19-A, 22	3	6.6
36	*Actitis macularia*	Maçarico-pintado	Spotted sandpiper	5	60		vn	18, 32	2	4.4
37	*Crotophaga ani*	Anu-preto	Smooth-billed Ani	4	95		r, b	15-A, 33, 43	3	6.6
38	*Callidris fuscicollis*	Maçarico-de-sobre-branco	White-rumped sandpiper	3	60		vn	12, 30	2	4.4
39	*Sturnella militaris*	Polícia-inglesa-do-norte	Red-breasted Blackbird	3	48		v	12, 22	2	4.4
40	*Limosa haemastica*	Maçarico	Hudsonian Godwit	3	270		vn	12	1	2.2
41	*Ramphastos tucanus*	Tucano-de-papo-branco	White-throated toucan	3	600		r	16, 33, 46	3	6.6

Table 2: Continued.

Scientific name	Bird species Portuguese common and/or local (*) name	English name	NB	Wt.	Aq./Pisc.	Status	Lakes in which birds occurred (see names, types, and locations in Table 3)	NL	(%)
42 *Aramides cajanea*	Saracura-três-potes	Gray-necked wood-rail	2	410	A	r	16, 17	2	4.4
43 *Busarellus nigricollis*	Gavião-panema*	Black-collared Hawk	2	650	A, P	r, b	33, 39	2	4.4
44 *Chloroceryle inda*	Martim-pescador-da-mata	Green-and-rufous Kingfisher	2	52	A	r, b	36	1	2.2
45 *Eurypyga helias*	Pavãozinho*	Sunbittern	2	220	A	r	20, 41	2	4.4
46 *Agamia agami*	Garça-da-mata	Chesnut-bellied heron	1	580	A, P	r	16	1	2.2
47 *Anhima cornuta*	Alencorne*	Horned Screamer	1	3,100	A	r, b	41	1	2.2
48 *Tigrisoma fasciatum* NR	Socó-boi-cinza	Fasciated Tiger -Heron	1	850	A, P	r	18-A	1	2.2
			Total: 3626						

Bird species, NR: new record for the Anavilhanas; Wt.: weight data for bird species taken from [35]; Aq./Pisc.: A: species strictly associated with aquatic environments (aquatic bird community); P: primarily piscivorous species. Status in the study area [67]; b: breeding confirmed; ps+: resident year-round, but related mostly with the low-water season; r: resident year-round; u: unknown; v: vagrant; vn: boreal migrant.

Table 3: Information on Anavilhanas lakes location and characteristics (see codes at end).

Lake	Latitude	Longitud	DRM	DNL	A	LP	LS	LD	WT	N	P	HR	HRS
16	270524	6075329	6.81	1.7	447	8.87	1.184	3.5	75	0.81	0.04	5	0.564
17	272502	6070316	9.98	1.31	336	17.3	2.663	3.5	68.5	0.24	0.03	5	0.289
7	272985	6071308	9.09	1.05	673	17.6	1.914	5.45	65	0.27	0.03	5	0.284
6	273987	6069996	10.4	2.32	429	14.9	2.03	4.45	69	0.26	0.02	6	0.403
5	274765	6068959	10.4	1.45	266	9.6	1.661	4.6	82	0.23	0.03	4	0.417
4	274966	6069798	8.52	2.47	299	8.22	1.341	3.46	82	0.22	0.04	5	0.608
15	271439	6073440	7.55	1.28	156	10.5	2.372	3.15	52	0.19	0.03	5	0.476
7-A	274260	6071206	7.49	1.35	144	5.03	1.183	3.5	78	0.23	0.05	4	0.795
15-A	270308	6074032	8.11	1.35	83	8.21	2.543	2.6	59	0.19	0.03	5	0.609
18	272711	6077293	4.17	3.22	1411	36.6	2.749	6.65	59	0.25	0.02	9	0.246
18-A	273380	6076324	3.96	3.11	129	5.64	1.401	1.25	65	0.27	0.03	4	0.709
12	276608	6070643	3.4	3.11	396	12.7	1.801	0.88	86	0.25	0.04	3	0.236
19	267662	6075957	7.63	2.75	1037	20	1.752	5.25	80	0.27	0.04	7	0.35
20	260874	6079476	5.91	1.56	330	10.4	1.615	3.75	92	0.22	0.04	6	0.577
21	262724	6076403	5.09	1.8	326	10.2	1.594	4	100	0.18	0.04	5	0.49
22	260850	6076438	2.98	2.53	275	9.92	1.688	3.15	94	0.18	0.03	6	0.605
25	259281	6081004	6.62	0.67	623	5.38	0.608	2.45	47	0.49	0.06	4	0.743
26	263482	6075347	6.57	0.67	29	3.15	1.651	2.25	57	0.31	0.03	4	1.27
23	259862	6078536	5.03	1.7	450	10.4	1.383	5.95	85	0.27	0.04	7	0.673
27	258592	6077953	3.68	1.65	289	7.66	1.271	3.25	73	0.19	0.03	5	0.653
28	267706	6080493	4.88	1.04	33	4	1.965	2.45	64	0.21	0.03	7	1.75
29	255689	6081857	2.05	1.33	294	9.29	1.529	2.65	60	0.35	0.04	8	0.861
30	255183	6080771	1.67	1.33	122	7.66	1.957	3.25	70	0.3	0.04	4	0.522
19-A	266621	6073741	6.99	3.76	1419	26.7	2	4.65	85	0.24	0.04	8	0.3
31	257568	6091014	6.47	3.45	6064	43.7	1.583	3.65	85	0.2	0.03	11	0.252
31-A	258865	6087138	6.45	2.57	316	14.3	2.27	2.95	84	0.24	0.03	8	0.559
32	266281	6080381	7.68	4.53	3129	40.7	2.053	5.65	85	0.29	0.03	10	0.246
11	274942	6069858	6.02	2.82	731	15.6	1.628	3.75	79	0.23	0.03	4	0.256
10	273946	6069984	8.21	2.45	640	16.1	1.796	4.85	83	0.21	0.03	6	0.373
19-B	270297	6069628	5.88	0.95	97	5.32	1.524	3.45	94	0.25	0.02	7	1.316
33	211955	6110926	1.34	4.45	782	21.6	2.179	4.15	90	0.3	0.03	8	0.37
34	216847	6107868	2.76	1.25	245	7.52	1.356	6	90	0.36	0.03	7	0.931
35	216705	6106408	2.22	1.17	334	16.1	2.486	3.9	80	0.27	0.03	6	0.373
36	218403	6107169	1.84	1.57	43	3.61	1.553	5.5	90	0.25	0.03	5	1.385
37	220764	6105609	0.8	2.09	157	9.48	2.135	5	80	0.36	0.03	6	0.633
38	224759	6104093	1.7	1.12	53	5.76	2.232	2.5	100	0.35	0.04	6	1.042
39	214000	6105279	1.21	2.65	1617	37.4	2.624	4	75	0.33	0.03	7	0.187
40	224750	6102939	0.31	1.43	383	13.2	1.903	4.8	80	0.28	0.03	8	0.606
41	227679	6104293	1.59	2.02	346	14.5	2.2	4.6	70	0.35	0.05	6	0.414
42	234218	6101085	0.43	3.17	391	14.8	2.112	7	110	0.33	0.03	6	0.405
43	239985	6101019	2.03	2.29	71	6.92	2.317	3.9	90	0.29	0.03	4	0.578
44	241764	6099168	1.83	1.18	286	8.08	1.348	4.8	90	0.39	0.04	6	0.743
45	246095	6097620	3.53	1.87	1765	28.1	1.887	5.5	90	0.25	0.03	9	0.32
46	245802	6090167	2	2.28	1084	22.6	1.937	5.6	110	0.23	0.03	7	0.31
47	259990	6083629	4.93	2.57	2522	33.8	1.899	6.5	70	0.23	0.03	9	0.266

Codes: DRM: lake distance to river margins (km); DNL: lake distance to the nearest lake (km); A: lake area (ha); LP: lake perimeter (km); LS: lake shape; LD: lake depth (m); WT: water transparency (cm); N: nitrogen concentration (μmol l−1); P: phosphorus concentration (μmol l−1); HR: habitat richness at lake margins; HRS: habitat richness standardized.

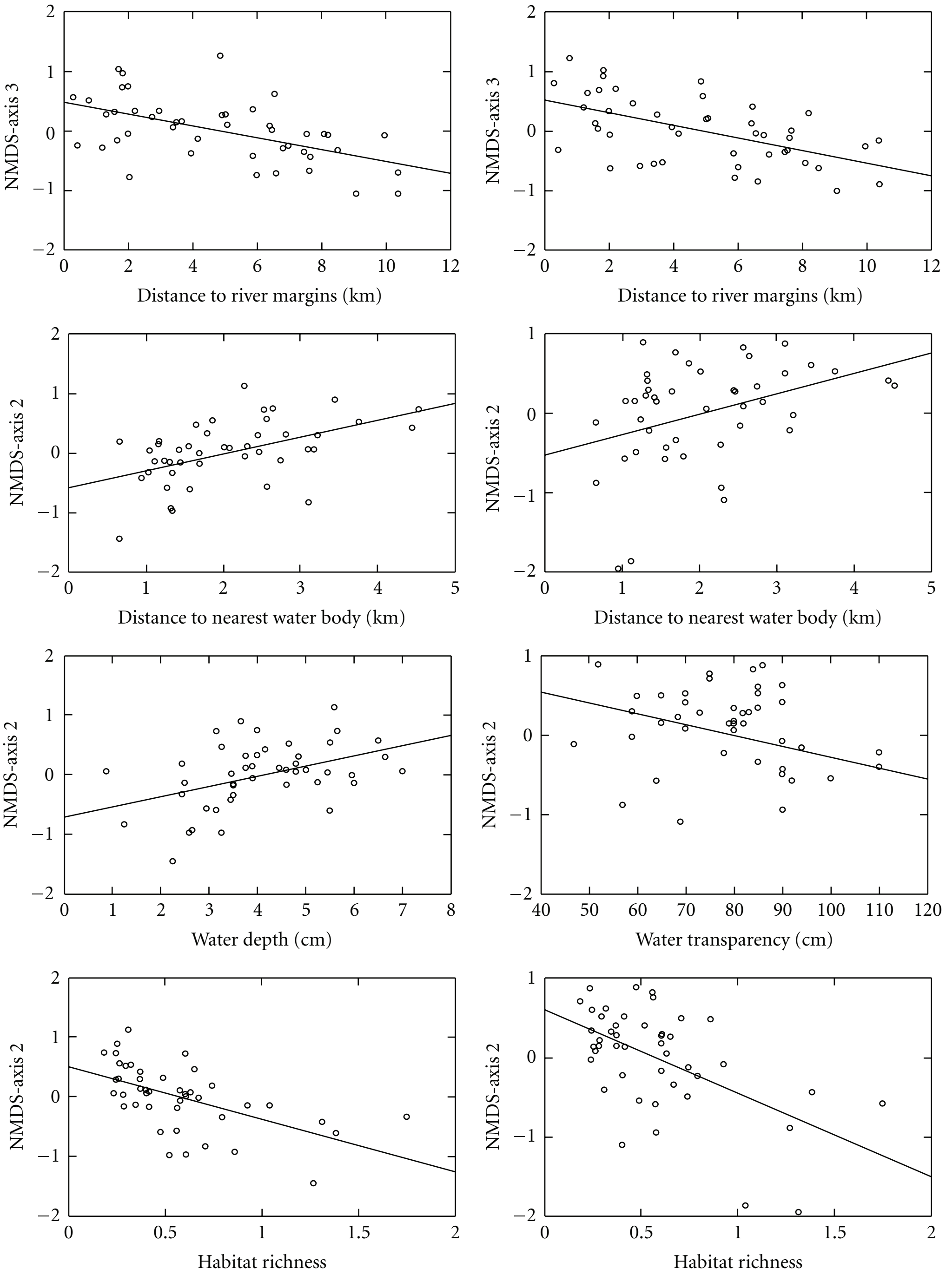


FIGURE 7: Partial residual plots showing the relationships from multiple linear models of aquatic bird quantitative community composition (left graphs) and qualitative community composition (right graphs). The figures show only the relationships that were significant in the multiple regression model, that is, between bird community composition (represented by score values of NMDS-axes) and lake physical properties (water depth, water transparency), lake isolation (distance to river margins), and habitat richness. Sample size is 45 lakes. Some numbers in the axes are negative because the partial regression represents the deviation of the expected results if all the other independent variables are kept in their observed means (see also Section 3). The results are from the analysis in the Table 1.

penetration in shallow lakes may increase prey detectability, principally for visually oriented predators. In this sense, the lack of relationship observed between bird richness and abundance and water transparency was an unexpected result, but one that can be derived from the fact that some waders and piscivorous birds (egrets, herons, and others) forage more often in relatively turbid waters or shady spots, possibly to avoid being visually detected by their prey (personal observations) and/or because prey biomass tends to be higher in these waters. However, variation in aquatic bird

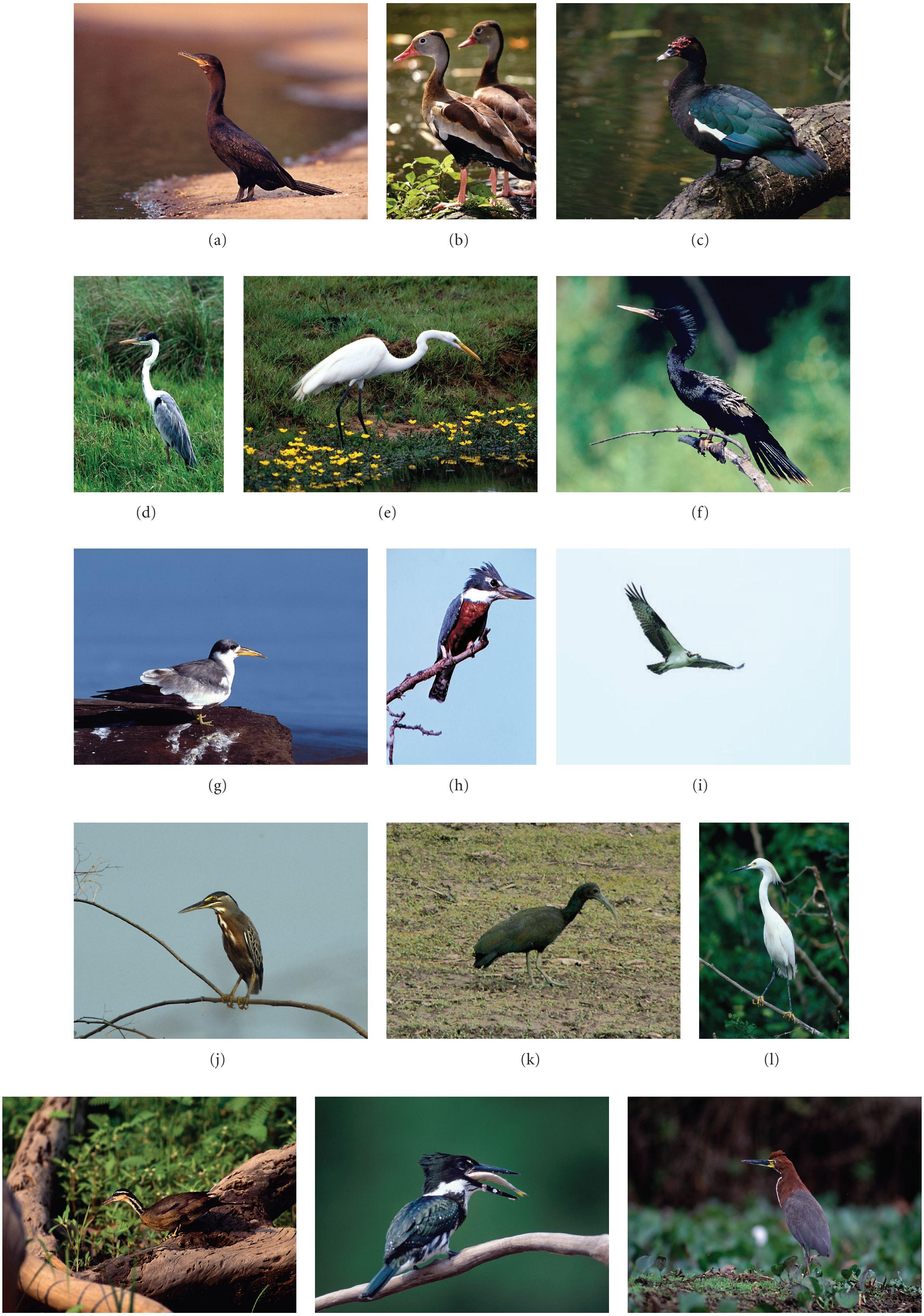

(a) (b) (c)
(d) (e) (f)
(g) (h) (i)
(j) (k) (l)
(m) (n) (o)

Figure 8: Continued.

(p) (q) (r)

(s)

Figure 8: Some aquatic bird species typical of Anavilhanas blake water lakes. The sequence starts with the most abundant, as following that showed in Table 2: (a) *Phalacrocorax brasilianus*; (b) *Dendrocygna autumnalis*; (c) *Cairina moschata*; (d) *Ardea cocoi*; (e) *Ardea alba*; (f) *Anhinga anhinga*; (g) *Phaetusa simplex*; (h) *Megaceryle torquata*; (i) *Pandion haliaetus*; (j) *Butorides striatus*; (k) *Mesembrinibis cayenensis*; (l) *Egretta thula*; (m) *Heliornis fulica*; (n) *Chloroceryle americana*; (o) *Tigrisoma lineatum*; (p) *Aramides cajanea*; (q) *Eurypyga helias*; (r) *Agamia agami*; (s) *Anhima cornuta*. The majority of photos were made by: L. C. Marigo, except the following: *Agami agami* (Photo by: Renato Cintra); *Megaceryle torquata* (Photo by: A. Sucksdorff); *Mesembrinibis cayenensis* (Photo by: Luiz A. T. Barros); *Pandion haliaetus* Photo by: Alsemo D'Áffonseca).

qualitative community composition significantly decreased with increasing water transparency (Table 1, Figure 7) indicating lower species turnover in clearer lakes.

Opposite to studies in North America and Europe [62, 63], in the Anavilhanas, lake productivity did not influence variation in bird community composition, although it may affect bird species individually [64].

Lake isolation was another important determinant of the ecological gradient in the aquatic community of the Anavilhanas. Aquatic bird richness was higher in more isolated lakes. Isolation also influenced bird community composition (Table 1, Figure 7), which showed the highest variation in species in lakes closer to river margins, as expected due to more potential bird colonization from the "mainland" (lakes along river margins). In the Anavilhanas, differences in bird occurrence may stem from differential vagility and ability to colonize lakes farther away from river margins. For example, the Sunbittern, the Sungrebe, the Black-collared Hawk, and the American Pygmy Kingfisher, have small territories; the Striated Heron and the Rufescent Tiger-Heron are quite sedentary.

The distribution of species' relative densities along, (Figures 6(a), 6(b)) and species variation in relation to, ecological gradients (Figure 7) suggest that some species prefer one side of the gradients (e.g., deeper water, higher habitat richness, and greater isolation), which is one of the reasons why bird richness and abundance were weakly affected by them.

In this study, habitat richness of marginal vegetation emerged as one of the most important lake properties affecting aquatic bird community composition; similar results were found in temperate regions [62, 63, 65]. At the Anavilhanas, aquatic birds forage more frequently in lakes than along river margins (personal observations). This may stem from differences in water flow (slower waters favouring feeding success) and to a greater heterogeneity of lake margin vegetation [66]. Habitat diversity may be especially important in the prebreeding season, since a more complex structure may provide more isolated spots for social reproductive behaviour, such as display and courtship, as Turnbull and Baldassarre [65] found for Mallards and American Wigeons in the Northern Hemisphere.

Higher bird species richness and abundances are consistently found in lakes with higher habitat richness along the margins. Anavilhanas lakes differ in their potential to provide adequate habitat to aquatic birds because species have different biological needs which may influence the way each uses the lakes. For some species (e.g., Horned Screamer, Hoatzin, Rufescent Tiger Heron, Gray-necked Wood-Rail, Green, Black-bellied Whistling-Duck, Muscovy Duck, Greater Ani), habitat preference is likely related to local vegetation type and structure within the lakes; the occurrence of other species (e.g., Anhinga, Neotropic Cormorant, Great Egret, Sunbittern) is related to landscape features at larger spatial scales, while others (Large-billed Tern, Yellow-billed Tern, Ringed Kingfisher, Osprey and swallows) do not depend so much on lake habitat attributes because they use mainly open waters and beaches [66]. These differences in habitat use may contribute to maintain alpha diversity and produce spatial gradients [6].

This study's findings strongly suggest that the environmental heterogeneities created by differences in lake isolation, physical properties, and habitat richness are important determinants of ecological gradients in aquatic avian richness, abundance, and community composition in the black water systems of Central Amazonia, particularly in the Anavilhanas archipelago.

An enormous archipelago comprised of hundreds of beautiful lakes stretching throughout its area in the middle of a National Park is a unique situation in the entire Amazon region. Since the distribution and abundance of fish is influenced by waterbirds [8], a long-term basis monitoring program of the bird community dynamics will be important to improve the lakes' conservation value, and to analyze human impacts on them. Future analysis of multiyear data will allow to make temporal comparisons among lakes and to assess if trends reflect local and/or regional patterns of community change in the Amazonian black water system of Anavilhanas.

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References

[1] M. R. Willig, D. M. Kaufman, and R. D. Stevens, "Latitudinal gradients of biodiversity: pattern, process, scale, and synthesis," *Annual Review of Ecology, Evolution, and˜Systematics*, vol. 34, pp. 273–309, 2003.

[2] R. Ricklefs and D. Schluter, *Species Diversity in Ecological Communities: Historical and Geographical Perspectives*, University of Chicago Press, Chicago, Ill, USA, 1993.

[3] D. A. Scott and M. Carbonell, *A Directory of Neotropical Wetlands*, IUCN Cambridge CB3 0DL, Cambridge, UK, 1986.

[4] R. Cintra, T. M. Sanaiotti, and M. Cohn-Haft, "Spatial distribution and habitat of the Anavilhanas Archipelago bird community in the Brazilian Amazon," *Biodiversity and Conservation*, vol. 16, no. 2, pp. 313–336, 2007.

[5] R. Cintra, P. M. R. S. Dos Santos, and C. B. Leite, "Composition and structure of the lacustrine bird communities of seasonally flooded wetlands of Western Brazilian Amazonia at high water," *Waterbirds*, vol. 30, no. 4, pp. 521–540, 2007.

[6] D. L. Guadagnin, A. S. Peter, L. F. Carvalho Perello, and L. Maltchik, "Spatial and temporal patterns of waterbird assemblages in fragmented wetlands of Southern Brazil," *Waterbirds*, vol. 28, no. 3, pp. 261–272, 2005.

[7] C. Lévêque, E. V. Balian, and K. Martens, "An assessment of animal species diversity in continental waters," *Hydrobiologia*, vol. 542, no. 1, pp. 39–67, 2005.

[8] J. Steinmetz, S. L. Kohler, and D. A. Soluk, "Birds are overlooked top predators in aquatic food webs," *Ecology*, vol. 84, no. 5, pp. 1324–1328, 2003.

[9] S. P. Hubbell, *The Unified Neutral Theory of Biodiversity and Biogeography*, Princeton University Press, Princeton, NJ, USA, 2001.

[10] M. A. Cohn-Haft, L. N. Naka, and A. M. Fernandes, "Padrões de distribuição da avifauna da várzea dos rios Solimões e Amazonas," in *Conservação da Várzea: Identificação e Caracterização de Regiões Biogeográficas*, A. L. K. M. Albernaz, Ed., MMA, CNITAE Edições IBAMA, Pró-várzea, Brasília, 2007.

[11] P. Petermann, "The birds," in *The Central Amazon Floodplain: Ecology of a Pulsing System*, W. J. Junk, Ed., Springer, Berlin, Germany, 1997.

[12] G. H. Rosenberg, "Habitat specialization and foraging behavior by birds of Amazonian river islands in northeastern Peru," *Condor*, vol. 92, pp. 427–443, 1990.

[13] D. E. Willard, "Comparative feeding ecology of twenty-two tropical piscivores," *Ornithological Monographs*, vol. 36, pp. 788–797, 1985.

[14] F. Wittmann, J. Schöngart, J. C. Montero et al., "Tree species composition and diversity gradients in white-water forests across the Amazon Basin," *Journal of Biogeography*, vol. 33, no. 8, pp. 1334–1347, 2006.

[15] W. M. Denevan, "The aboriginal population of Amazonia," in *The Native Population of the Americas*, W. M. Denevan, Ed., pp. 205–234, University of Wisconsin Press, Madison, Wis, USA, 1976.

[16] J. M. Melack and L. L. Hess, "Remote sensing of the distribution and extent of wetlands in the Amazon basin," in *Amazonian Floodplain Forests: Ecophysiology, Biodiversity and Sustainable Management*, W. J. Junk, M. T. F. Piedade, F. Wittmann, J. Schöngart, and P. Parolin, Eds., Springer, 2010.

[17] M. T. F. Piedade, W. Junk, S. A. D'Ângelo et al., "Aquatic herbaceous plants of the Amazon floodplains: state of the art and research needed," *Acta Limnologica Brasiliensis*, vol. 22, no. 2, pp. 178–165, 2010.

[18] M. Goulding, M. L. Carvalho, and E. G. Ferreira, *Rio Negro, Rich Life in Poor Water: Amazonian Diversity and Food chain Ecology as Seen through Fish Communities*, SPB Academic Publishing, The Netherlands, 1988.

[19] S. H. Borges, M. Cohn-Haft, A. M. P. Carvalhaes, L. M. Henriques, J. F. Pacheco, and A. Whittaker, "Birds of Jaú National park, Brazilian Amazon: species chek-list, biogeography and conservation," *Ornithologia Neotropical*, vol. 12, pp. 109–140, 2001.

[20] E. J. Fittkau, U. Irmler, W. J. Junk, F. Reiss, and G. W. Schimdt, "Productivity, biomass and population dynamics in Amazonian waterbodies," in *Tropical Ecological Systems*, F. B. Golley and E. Medina, Eds., vol. 11 of *Ecological Studies*, pp. 289–311, Springer, Heidelberg, Germany, 1975.

[21] W. J. Junk and K. Furch, "The physical and chemical properties of Amazonian waters and their relationships with the biota," in *Key Environments: Amazonia*, G. T. Prance and T. E. Lovejoy, Eds., Pergamon Press, Oxford, UK, 1985.

[22] G. V. Trevisan and B. R. Forsberg, "Relationships among nitrogen and total phosphorus, algal biomass and zooplankton density in the central Amazonia lakes," *Hydrobiologia*, vol. 586, no. 1, pp. 357–365, 2007.

[23] J. Adis, "Seasonal igapó-forests of Central Amazônia blackwater rivers and their terrestrial arthropod fauna," in *The Amazon. Limnology and Landscape Ecology of a Mighty Tropical River and Its Basin, Monographiae Biologicae*, H. Sioli, Ed., pp. 245–268, Junk, Dordrecht, The Netherlands, 1984.

[24] D. F. Stotz, J. W. Fitzpatrick, T. A. Parker III, D. K. Moskovits, and D. K. Moskovits, *Neotropical Birds: Ecology and Conservation*, University of Chicago Press, Chicago, Ill, USA, 1996.

[25] J. M. Ayres, *As Matas de Várzea do Mamirauá*, MCT-CNPq-PTU, SCM, Rio de Janeiro, Brazil, 1993.

[26] G. T. Prance, "A terminologia dos tipos de florestas amazônicas sujeitas a inundação," *Acta Amazônica*, vol. 10, no. 3, pp. 495–504, 1980.

[27] J. M. Pires and G. T. Prance, "The vegetation types of the Brazilian Amazon," in *Key Environments: Amazonia*, G. T. Prance and T. E. Lovejoy, Eds., Pergamon Press, Oxford, UK, 1985.

[28] M. Goulding, R. Bartem, and E. Ferreira, *The Smithsonian Atlas of the Amazon*, Smithsonian Institution, Washington, DC, USA, 2003.

[29] H. Sioli, *The Amazon: Limnology and Landscape Ecology of a Mighty Tropical River and Its Basin*, W. Junk Publishers, Dordrecht, The Netherlands, 1984.

[30] S. Filoso and M. R. Williams, "The hydrochemical influence of the Branco River on the Negro River and Anavilhanas archipelago, Amazonas, Brazil," *Archiv fur Hydrobiologie*, vol. 148, no. 4, pp. 563–585, 2000.

[31] M. Worbes, "The forest Ecosystem of the floodplains," in *The Central Amazon Floodplain—Ecology of a Pulsing System*, W. J. Junk, Ed., vol. 126, Springer, Berlin, Germany, 1997.

[32] R. Cintra and M. Rosas, "As aves migratórias neárticas no Parque Nacional de Anavilhanas," in *Conservação de Espécies Migratórias Neárticas no Brasil*, pp. 55–58, CEMAVE; Conservação Internacional; Sociedade Fritz Müller de Ciências Naturais, 2011.

[33] D. I. MacKenzie, J. D. Nichols, J. E. Hines, M. G. Knutson, and A. B. Franklin, "Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly," *Ecology*, vol. 84, no. 8, pp. 2200–2207, 2003.

[34] J. Oksanen, F. Guillaume Blanchet, R. Kindt et al., vegan: Community Ecology Package. R package version 2.0-0, 2011.

[35] J. Del Hoyo, A. Elliott, and J. Sargatal, *Handbook of the Birds of the World*, vol. 1–16, Linx Editions, Barcelona, Spain, 1992–2011.

[36] J. C. Valderrama, "The simultaneous analysis of total nitrogen and total phosphorus in natural waters," *Marine Chemistry*, vol. 10, no. 2, pp. 109–122, 1981.

[37] Global Mapper, Version 6.09, *Global Mapper Software LLC*, Olathe, Kan, USA, 2004-2005.

[38] D. R. Patton, "A diversity index for quantifying habitat edge," *Wildlife Society Bulletin*, vol. 3, pp. 171–173, 1975.

[39] M. T. F. Piedade, W. J. Junk, J. Adis, and P. Parolin, "Ecologia, zonação e colonização de vegetação arbórea das ilhas Anavilhanas," *Pesquisa Botânica*, vol. 56, pp. 117–144, 2005.

[40] W. J. Junk and M. Piedade, "Plant life in the floodplain with special reference to herbaceous plants," in *The Central Amazon Floodplain—Ecology of a Pulsing System*, W. J. Junk, Ed., vol. 126 of *Ecological Studies*, Springer, Heidelberg, Germany, 1997.

[41] B. McCune and M. J. Mefford, *Multivariate Analysis of Ecological Data*, Version 4.25, MjM Software, Gleneden Beach, Ore, USA, 1999.

[42] I. Borg and P. Groenen, *Modern Multidimensional Scaling*, Springer, New York, NY, USA, 1997.

[43] E. W. Beals, "Bray-Curtis ordinations: an effective strategy for analysis of multivariate ecological data," *Advances in Ecological Research*, vol. 14, no. C, pp. 1–55, 1984.

[44] K. R. Clarke, "Non-parametric multivariate analyses of changes in community structure," *Australian Journal of Ecology*, vol. 18, no. 1, pp. 117–143, 1993.

[45] P. Legendre and L. Legendre, *Numerical Ecology*, Elsevier, Amsterdam, The Netherlands, 1998.

[46] M. J. Anderson and T. J. Willis, "Canonical analysis of principal coordinates: a useful method of constrained ordination for ecology," *Ecology*, vol. 84, no. 2, pp. 511–525, 2003.

[47] R. C. MacNally, "On characterizing foraging versatility, illustrated by using birds," *Oikos*, vol. 69, no. 1, pp. 95–106, 1994.

[48] P. R. Minchin, "An evaluation of the relative robustness of techniques for ecological ordination," *Vegetatio*, vol. 69, no. 1-3, pp. 89–107, 1987.

[49] R. Cintra, "Spatial distribution and foraging tactics of tyrant flycatchers in two habitats in the Brazilian Amazon," *Studies on Neotropical Fauna and Environment*, vol. 32, no. 1, pp. 17–27, 1997.

[50] C. L. Olson, "On choosing a test statistic in multivariate analysis of variance," *Psychological Bulletin*, vol. 83, no. 4, pp. 579–586, 1976.

[51] C. R. Johnson and C. A. Field, "Using fixed-effects model multivariate analysis of variance in marine biology and ecology," *Oceanography and Marine Biology*, vol. 31, pp. 177–221, 1993.

[52] L. Wilkinson, *Systat: The System for Statistics*, version 12, SYSTAT Software Inc., Evanston, Ill, USA, 2007.

[53] C. A. R. M. Araujo-Lima, L. P. S. Portugal, and E. G. Ferreira, "Fish- macrophyte relationship in the Anavilhanas Archipelago, a black water system in the Central Amazon," *Journal of Fish Biology*, vol. 29, no. 1, pp. 1–11, 1986.

[54] C. Granado-Lorencio, C. R. M. Araujo Lima, and J. Lobón-Cerviá, "Abundance—distribution relationships in fish assembly of the Amazonas floodplain lakes," *Ecography*, vol. 28, no. 4, pp. 515–520, 2005.

[55] J. A. Kushlan, J. G. Ogden, and A. L. Higer, "Relation of water level and fish availability to wood stork reproduction in the southern Everglades, Florida," Open File Report 75, U.S. Geological Survey, Tallahassee, Fla, USA, 1975.

[56] R. Tompson and C. Towsend, "A truce with neutral theory: local deterministic factors, special traits and dispersal limitations determine patterns of diversity in streams invertebrates," *Journal of Animal Ecology*, vol. 75, pp. 474–464, 2006.

[57] M. Paracuellos and J. L. Tellería, "Factors affecting the distribution of a waterbird community: the role of habitat configuration and bird abundance," *Waterbirds*, vol. 27, no. 4, pp. 446–453, 2004.

[58] J. Terborgh, S. K. Robinson, T. A. Parker, C. A. Munn, and N. Pierpont, "Structure and organization of an Amazonian forest bird community," *Ecological Monographs*, vol. 60, no. 2, pp. 213–238, 1990.

[59] W. M. Tonn, J. J. Magnuson, M. Rask, and J. Toivonen, "Intercontinental comparison of small-lake fish assemblages: the balance between local and regional processes," *American Naturalist*, vol. 136, no. 3, pp. 345–375, 1990.

[60] C. A. Paszkowski and W. M. Tonn, "Community concordance between the fish and aquatic birds of lakes in northern Alberta, Canada: the relative importance of environmental and biotic factors," *Freshwater Biology*, vol. 43, no. 3, pp. 421–437, 2000.

[61] G. T. Bancroft, D. E. Gawlik, and K. Rutchey, "Distribution of wading birds relative to vegetation and water depths in the northern Everglades of Florida, USA," *Waterbirds*, vol. 25, no. 3, pp. 265–277, 2002.

[62] G. E. Crozier and D. E. Gawlik, "Avian response to nutrient enrichment in an oligotrophic wetland, the Florida Everglades," *Condor*, vol. 104, no. 3, pp. 631–642, 2002.

[63] S. K. Riffell, B. E. Keas, and T. M. Burton, "Area and habitat relationships of birds in Great Lakes coastal wet meadows," *Wetlands*, vol. 21, no. 4, pp. 492–507, 2001.

[64] M. Rosas, *Influência de fatores bióticos e abióticos na ocorrência e abundância de garças e socós em lagos do Arquipélago de Anavilhanas, Amazônia Central*, M.S. dissertation, Universidade do Amazonas, INPA, Manaus, Brazil, 2009.

[65] R. E. Turnbull and G. A. Baldassarre, "Activity budgets of mallards and American wigeon wintering in east-central Alabama," *Wilson Bulletin*, vol. 99, no. 3, pp. 457–464, 1987.

[66] R. Zarza, R. Cintra, and M. Anciaes, "Distribution, influence of site features on the occupancy and abundance estimates of yellow-billed terns (*Sternula superciliaris*), large-billed terns (*Phaetusa simplex*) and black skimmers (*Rynchops niger*) breeding in anavilhanas archipelago, Amazonas, Brazil," Unpublished Manuscript.

[67] J. F. Pacheco, "Avifauna da Estação Ecológica do Projeto Mamirauá," Tech. Rep. 5, 1994.