# Species Richness and Composition of Avifaunal Communities in a Complex Amazonian Landscape

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## Statement of Originality

This is to certify that the content of this thesis is my own work. Any assistance from sources have been cited and acknowledged.

B. Gilmore

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# Abstract

Little research has been undertaken to identify the effect that habitat heterogeneity and seasonality have on the diversity of birds in lowland Amazonia. This study aimed to identify how species richness and composition of avifaunal communities in the lower Rio Purús region of central Amazonia compare across terra firme, whitewater and blackwater seasonally flooded forests and their seasonal variation in water levels. Avifauna was sampled at nine sites (three terra firme, three whitewater and three blackwater) during low water, and repeated during high water. Using ten 15-minute point counts every 200m for each site a total of 284 species were recorded. Species richness in seasonally flooded forest was found to be similar but was significantly lower in terra firme. Almost 17 percent of species were significantly associated with a single habitat, with a further 4 percent associated with two of the three habitats. Species composition was significantly different between all three habitats. Seasonal variation in water levels had no effect on species richness or composition. The results suggest that habitat heterogeneity, caused by seasonal flood waters, contributes to creating unique communities of birds in Amazonian forests. Future conservation planning may need to include both terra firme and seasonally flooded forest in order to safeguard bird diversity.

# Chapter 1 – Introduction

The Amazon basin, covering an area of 6.8million km$^2$, is the largest hydroponic basin in the world (Goulding, Barthem, & Ferreira, 2010). It is generally viewed as one expansive homogenous tropical forest, drained by sizable rivers, however, it is in fact made up of a mosaic of different forest and non-forest vegetation types: terra firme, seasonally flooded forest (hereafter referred to as flooded forest) and more localised habitats such as campina (Pires & Prance, 1985; Prance, 1996; Borges & Carvalhaes, 2000; Borges, 2013; Myster, 2016). This mosaic of habitats at all scales has contributed to the Amazon basin becoming one the richest areas for avifauna in the world (Mittermeier, et al., 2003), as species diversity is intrinsically linked with habitat diversity (Cody, 1985; Rosenzweig, 1995).

This high avifaunal species richness in the Amazon basin can be explained through recognising three levels of diversity throughout the area. Firstly, regional diversity (hereafter, gamma diversity), which is driven by restricted species distributions over a large scale (Whittaker, 1972). The major means of diversification in vertebrates is regarded as being speciation by geographical isolation (Mayr, 1942). An early explanation of this was the Riverine Barrier hypothesis, suggesting rivers within the Amazon basin act as these geographical barriers, driving high levels of species richness (Wallace, 1852). Several studies have shown that these rivers do act as important biogeographic barriers in many species of bird (Eberhard & Bermingham, 2005; Naka, Bechtoldt, Henriques, & Brumfield, 2012) as well as mammals (Peres, Patton, & da Silva, 1996; Boubli, et al., 2008; Boubli, et al., 2015) and flora (Nazareno, Dick, & Lohmann, 2017; Nazareno, Dick, & Lohmann, 2019) increasing overall gamma diversity throughout the region.

Secondly, beta diversity, which is the faunal differences between distinct habitats and the focus of this study (Whittaker, 1972). Terra firme, whitewater flooded forests and blackwater flooded forests represent the main differences in habitats across the Amazon (Haugaasen & Peres, 2008). Many species use a variety of these habitats, whereas others are restricted either wholly or partly to a single habitat (Haugaasen & Peres, 2005; Haugaasen & Peres, 2008). There are over 1300 species of bird in the Amazon (Mittermeier, et al., 2003), of which the majority can be found in terra firme; however, 15% of the overall non-aquatic bird species diversity in the Amazon is restricted to riverine environments (Remsen & Parker III, 1983). Over 100 of these species are restricted to flooded forests, some of which appear to occur solely in either white or blackwater flooded forest (Laranjeiras, Naka, & Cohn-Haft, 2019).

Finally, habitat diversity (hereafter, alpha diversity), which is caused by the use of narrow niches and extreme resource specialisation of species within these habitats (Whittaker, 1972). Species that coexist within a local assemblage occupy different ecological niches by dividing resources either temporally, spatially, or behaviourally (Mohd-Azlan, Noske, & Lawes, 2014). In the neotropics, species of bird are frequently more specialised in their use of resources, partly due to the high number of ecological niches, enabling communities to have higher alpha diversity (Belmaker, Sekercioglu, & Jetz, 2012; Mohd-Azlan, Noske, & Lawes, 2014).

While differences in species composition and richness is generally recognised by researchers (Cody, 1985; Rosenzweig, 1995), little research has been undertaken investigating the composition and richness of avifaunal communities across terra firme, blackwater and whitewater flooded forest in lowland Amazonia. Of the few studies to have looked into this, most have limitations of either number of habitats (Rosenberg, 1990; Cintra, Sanaiotti, & Cohn-Haft, 2007; Laranjeiras, Naka, & Cohn-Haft, 2019), focus on specific species (Haugaasen & Peres, 2008), sampling method (Borges & Carvalhaes, 2000; Beja, et al., 2010; Borges, 2013) or differences in biogeography (Remsen & Parker III, 1983). It is important to study this more thoroughly in order to contribute further to the understanding of how species of birds use habitats in the region. This could help inform future decisions on policy, especially regarding conservation of these habitats and the species that inhabit them.

## Background

### Habitat Descriptions

Terra Firme

Terra firme forest is found above the maximum flood level of rivers and streams, and is the major forest type across the Amazon basin, accounting for an estimated 89% of the forest landscape (Olsen, et al., 2001). These forests lie upon well drained soils that are heavily leached and nutrient poor as they are deprived of sediment from flood waters (Haugaasen & Peres, 2006). Although often thought of as a single type of habitat, analysis of satellite images has indicated terra firme contains several distinct plant communities with high levels of floristic diversity (Tuomisto & Ruokolainen, 1994; Tuomisto, et al., 1995; Tuomisto, Ruokolainen, & Yli-Halla, 2003). This is further supported by studies suggesting high levels of floristic diversity are driven by high levels of habitat heterogeneity in terra firme, resulting from ecological and edaphic conditions (Salo, et al., 1986; Tuomisto, et al., 1995; Haugaasen

& Peres, 2006). However, for this study, terra firme forest was regarded as any area of unflooded forest irrespective of the microhabitats it may contain.

### Seasonally Flooded Forest

The second major habitat found across the Amazon basin is seasonally flooded forests, between 7% and 15% of the basin, of which two thirds are flooded by whitewater with the final third flooded by clear and blackwater (Olsen, et al., 2001; Melack & Hess, 2010). Depending on location and rainfall, these flooded forests can remain inundated for between 50 and 270 days, with yearly water level fluctuations of up to 14 metres (Goulding, 1993). While all seasonally flooded forests are inundated regularly each year, various forest types can be identified by their floristic differences resulting from variations in hydrology and geomorphology (Prance, 1979; Goulding, 1993). As water colour is an indicator of ecologically important characteristics, such as sediment load, the use of flood water colour is an accepted method of quickly identifying the type of flooded forest (Prance, 1979) and was used to identify habitat in this study.

### Whitewater Flooded Forest

Whitewater rivers are defined by their colour, which is a reflection of the high levels of nutrient rich sediment these rivers carry (Goulding, 1993). The source of whitewater rivers can be found in the Andes or pre-Andean regions (Goulding, 1993; Myster, 2016). These regions are distinguished by their easily erodible landscapes (Räsänen, Salo, & Kalliola, 1987; Goulding, 1993) which adds a significant amount of nutrient rich sediment to the rivers.

Whitewater flooded forests are found along whitewater rivers and are the most extensive type of flooded forest in the Amazon basin (Kricher, 2011; Myster, 2016). As a result of the sediment in the seasonal flood waters from the whitewater rivers, whitewater flooded forests are rich in nutrients and highly productive (Junk & Piedade, 1993; Myster, 2016). This means that on the whole, whitewater flooded forests are the tallest and most diverse of all flooded forest (Goulding, 1993; Haugaasen & Peres, 2006; Kricher, 2011). Although whitewater flooded forest is highly productive, multiple studies have shown that diversity of fauna and flora is consistently lower than that of terra firme (Peres, 1997; Haugaasen & Peres, 2005; Haugaasen & Peres, 2006).

### Blackwater Flooded Forest

Blackwater rivers are characterised as nutrient poor and acidic due to the decaying plant material they contain (Goulding, 1993; Haugaasen & Peres, 2006; Myster, 2016). This is a result of organic material washed into their waters from the sandy and well-drained soils of lowland Amazonia where these rivers originate (Goulding, 1993; Myster, 2016).

Forests that are inundated by blackwater on a seasonal basis are known as blackwater flooded forest (Kricher, 2011). Due to the nutrient poor water, blackwater flooded forests are smaller in stature and support a lower diversity of fauna and flora than both whitewater flooded forest and terra firme (Ferreira, 1997; Goulding, 1993; Haugaasen & Peres, 2006; Kricher, 2011). Although not as widespread as whitewater flooded forest, blackwater flooded forests still account for an extensive area of flooded forest in the Amazon (Kricher, 1999; Myster, 2016). Within this study, blackwater flooded forests are classified as those flooded solely by blackwaters.

## Bird Species Richness in Amazonia

Species richness and diversity are fundamentally linked with the interconnected variables of habitat diversity and area (Cody, 1985; Rosenzweig, 1995). The floristic composition and structure of habitat is shaped by a number of abiotic factors, such as flooded forests being strongly influenced by flood water characteristics (Junk, et al., 2011; Junk, Piedade, Schöngart, & Wittmann, 2012; Junk, Wittmann, Schöngart, & Piedade, 2015). The mosaic of wide ranging habitat types in the Amazon basin is one of the major factors contributing to the high species richness of avifauna (Remsen & Parker III, 1983; Rosenberg, 1990; Cohn-Haft, Whittaker, & Stouffer, 1997). While some species are non-selective in their habitat preference, others are wholly limited to individual habitats (Haugaasen & Peres, 2008). Though the floristic diversity and structure of different habitat types in the Amazon is understood, few studies have examined how these differences affect the richness and species of avifauna (Rosenzweig, 1995; Haugaasen & Peres, 2008; Beja, et al., 2010; Borges, 2013; Laranjeiras, Naka, & Cohn-Haft, 2019).

Some research has been undertaken to attempt to identify the effect habitat has upon bird species composition and richness in the Amazon. Remsen & Parker III (1983) identified some differences in the composition of species between river created habitats and terra firme. Furthermore, they identified closely related pairs of species which replace one another at the boundary of terra firme and river created habitats, for example, the black-fronted nunbird

(*Monasa nigrifons*) in riverine habitats was replaced by the white-fronted nunbird (*Monasa morphoeus*) in terra firme (Remsen & Parker III, 1983). However the study used five different types of river created habitat (sandbar, sandbar scrub, river edge forest, whitewater flooded forest and transitional forest), with little focus upon whitewater flooded forest, in order to identify differences between habitats (Remsen & Parker III, 1983). The study was also spread across 12 sites in 2 countries which could lead to species composition differences being driven by geographical effects rather than local differences in habitat (Remsen & Parker III, 1983).

Studies of flooded forests on islands and adjacent terra firme have also identified differences in the composition of bird species (Rosenberg, 1990; Cintra, Sanaiotti, & Cohn-Haft, 2007). Rosenberg (1990) found that the composition of bird species on whitewater inundated islands was different to that of surrounding terra firme. These results were mirrored by Cintra et al. (2007) with a similar study on blackwater inundated islands. While both these studies identified differences in species composition between flooded forest and terra firme in the same region, reducing any possible geographical effects, the flooded forests sampled were restricted to islands. These results allow the interpretation that differences in species composition are due to the islands with rivers acting as barriers rather than differences in forest structure (Cintra, Sanaiotti, & Cohn-Haft, 2007).

Additional studies have attempted to identify differences in not only species composition, but also species richness, between blackwater flooded forest and terra firme in the same region (Borges & Carvalhaes, 2000; Borges, 2013). A study in the Jau National Park by Borges & Carvalhaes (2000) found species composition was different between blackwater flooded forest and terra firme. Further to this, Borges & Carvalhaes (2000) also identified a higher species richness within terra firme than that of blackwater flooded forest. However, mist netting was used as the sampling method, which can affect results through differences in catchability between species (Remsen & Good, 1996). Additionally, the more open understory of blackwater flooded forest led to lower catch rates, which could explain the difference in species richness (Borges & Carvalhaes, 2000). A further study in the same region by Borges (2013) reduced the impact of catchability by using mist netting alongside bird counts at fixed points along a trail. The results again showed higher species diversity in terra firme than blackwater flooded forest alongside a difference in species composition between habitats (Borges, 2013).

While the above studies do identify differences in the composition and richness of species between terra firme and flooded forests, little research has been undertaken to identify these differences in whitewater flooded forest and blackwater flooded forest. A study into this sampled pairs of adjacent rivers of differing types, allowing for direct comparisons between blackwater flooded forest and whitewater flooded forest to be undertaken while reducing geographic effects (Laranjeiras, Naka, & Cohn-Haft, 2019). Using a sampling method of ten, 15 minute point counts along a transect, detecting bird species through sight and sound, allowed for maximum detectability of species (Laranjeiras, Naka, & Cohn-Haft, 2019). There was no difference in overall species richness between the two habitats; however species richness was significantly higher in whitewater flooded forest than blackwater flooded forest for species identified as floodplain specialists (Laranjeiras, Naka, & Cohn-Haft, 2019). Additionally, overall species composition and floodplain specialist species composition were found to be different between habitats (Laranjeiras, Naka, & Cohn-Haft, 2019). These results show the communities of birds found in whitewater flooded forest and blackwater flooded forest are unique, and not just a single community of birds across all types of flooded forest.

Studies by Haugaasen & Peres (2008) and Beja et al. (2010) have endeavoured to identify differences in composition and richness of species among whitewater flooded forest, blackwater flooded forest and terra firme within the same region, eliminating the majority of geographical effects. The first of these found a difference in species composition between all three habitats (Haugaasen & Peres, 2008). Terra firme and whitewater flooded forest showed the most marked divergence in species composition (Haugaasen & Peres, 2008). Blackwater flooded forest sites, whilst still distinct in their grouping, showed less divergence from the other habitats (Haugaasen & Peres, 2008). However, this could be due to a lack of sampling effort as only two sites were sampled in blackwater flooded forest compared to five in whitewater flooded forest and six in terra firme (Haugaasen & Peres, 2008). Another reason for this could be due to focusing only on large bodied birds, a total of 23 species, producing a smaller sample size (Haugaasen & Peres, 2008). While this smaller sample size could have affected overall results, the study identified closely related pairs of species that replaced one another. Blue-and-yellow macaw (*Ara ararauna*) was more abundant in blackwater flooded forest than whitewater flooded forest, whereas both scarlet macaw (*Ara macao*) and red-and-green macaw (*Ara chloropterus*) were more abundant than the former species in whitewater flooded forest, similar to findings by Remsen & Parker III (1983) (Haugaasen & Peres, 2008). The species identified by Haugaasen & Peres (2008) and those identified by Remsen

& Parker III (1983) could act as indicator species of specific habitat types, allowing for more focused conservation efforts.

Beja et al. (2010) found similar results to Haugaasen & Peres (2008) in terms of differences in species composition between habitat types. In addition to this, no differences were found in species richness between habitats (Beja, et al., 2010). These results could have been affected by only using mist nets for sampling species (Beja, et al., 2010), similar to Borges & Carvalhaes (2000). There was a low catch rate for blackwater flooded forest, a higher catch rate in whitewater flooded forest, and a significantly higher catch rate in terra firme, demonstrating how more open habitats result in lower catch rates as identified by Borges & Carvalhaes (2000) and differences in catchability among species can affect results (Remsen & Good, 1996; Beja, et al., 2010). Interestingly, this study, unlike the former studies, resampled the same sites for each season and directly compared them to observe any seasonal variation to both species composition and richness (Beja, et al., 2010). Overall there was a significant seasonal variation in composition, though comparisons for each habitat type did not generate significant differences (Beja, et al., 2010). However, there was no significant difference in species richness due to season (Beja, et al., 2010). The change in composition was mainly seen in flooded forests with ground dwelling species moving in during low water and aquatic species during high water (Beja, et al., 2010). This could indicate species tracking resources that become temporarily available; for example Beja et al. (2010) caught kingfishers (*Alcedines*) more frequently in the interior of flooded forests throughout high water, when fish migrate into floodplain forests. This was also seen with ground dwelling insectivores, which were observed moving from upland to floodplain forests as the water level receded, likely following alterations in resource availability (Beja, et al., 2010). The influx of ground dwelling insectivores from terra firme was only observed in neighbouring blackwater flooded forest, whereas no influx was observed in whitewater flooded forest which were further from terra firme and isolated by river channels (Beja, et al., 2010). The spatial configuration of forests was identified as the key factor in where species moved between seasons.

## Objectives

The aim of this study is to describe the avifauna of a near undisturbed Amazonian landscape composed of different habitat types, aiming to understand how the heterogeneity of habitat affects the species richness and composition of avifaunal communities in the region, by asking the following questions: (1) how does avifaunal species richness and composition differ between terra firme, whitewater flooded forest and blackwater flooded forest?; (2) what effect does seasonal variation in water level have on species richness and composition of avifaunal communities?; (3) which species of bird can be defined as indicators of each habitat?

# Chapter 2 - Methods

## Study Area

The study was conducted from October to November 2018 for low water, and during June 2019 for high water, at Lago Uauaçu in the lower Rio Purús region of central western Brazilian Amazonia (Figure 1). Parts of the study area fall within the Piagaçú-Purús Sustainable Development Reserve with Lago Uauaçu on the northern border of the reserve. The reserve was established in September 2003 and encompasses 4 municipal counties covering 1,008,167 ha inside the lower Rio Purús region (Haugaasen & Peres, 2006). The initial purpose of the reserve was to protect fisheries in the region, owing to their importance to the Manaus fish market, but the reserve now also incorporates crucial breeding sites for threatened species such as manatees (*Trichechus inunguis*) and *Podocnemis* turtles (Haugaasen & Peres, 2006). This new type of reserve was established by the State of Amazonas in Brazil, with an emphasis on the sustainable use of natural resources whilst retaining a relatively intact forest cover. In spite of the study area's proximity to the confluence of the Rio Purús and Solimões, the region remains rather undisturbed, with large mosaics of terra firme, whitewater and blackwater flooded forest largely untouched (Haugaasen & Peres, 2006).

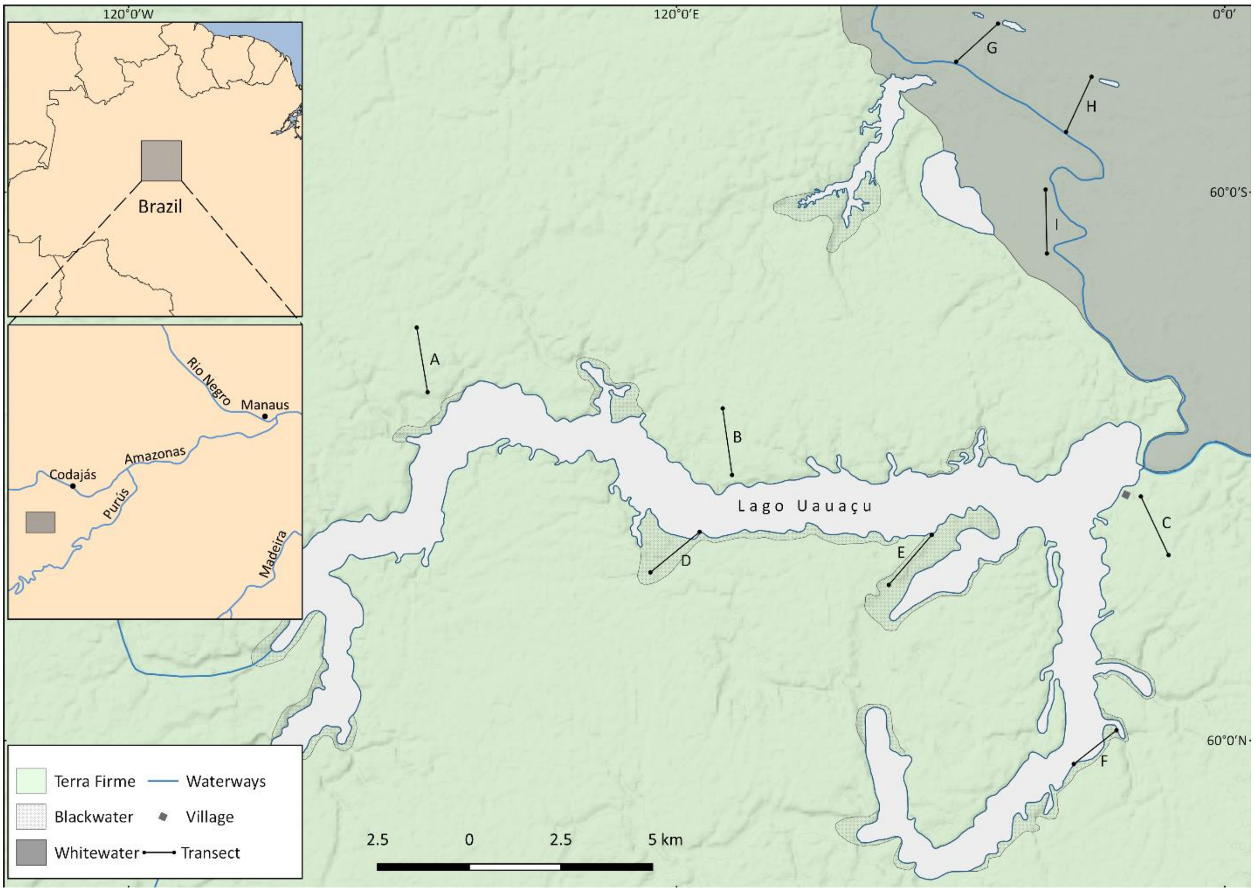

Figure 1. Map of Lago Uauaçú study area. Transects A-C conducted in terra firme, D-F conducted in blackwater flooded forest and G-I conducted in whitewater flooded forest

Lago Uauaçu is a crescent shaped, blackwater lake approximately 32 km long. The lake is fed wholly by rainfall collected in an internal basin composed of mainly terra firme, with blackwater flooded forest occurring on the lakes edge and banks of permanent streams (Haugaasen & Peres, 2006). The study area also included a region to the north east of the lake containing a large swathe of whitewater flooded forest under the influence of both the Rio Purús and Solimões (Haugaasen & Peres, 2006). The area surrounding Lago Uauaçu is unique in its geographical setting where terra firme, whitewater and blackwater flooded forest converge and this is further reflected in the high levels of both fauna and flora species richness (Haugaasen & Peres, 2005; Haugaasen & Peres, 2006; Haugaasen & Peres, 2008).

The study area is subject to little population pressure both locally and from the surrounding area. The area is home to around 30 families whose village is to the east next to the lake’s entrance. These villagers principally depend upon the collection and sale of Brazil nuts from naturally occurring Brazil nut trees (*Bertholletia excelsa*) for income (Haugaasen & Peres, 2006). Alongside this, villagers also rely on small-scale commercial fishing, highly selective hunting of large rodents and ungulates and logging for both income and subsistence

(Haugaasen & Peres, 2006). Land cultivation is limited to a small area of slash and burn concentrated around the village.

The nearest town, Codajás, is approximately 52 km from the lake and at least a two day journey from Manaus depending upon the season. During low water the fluvial route to Codajás along the Rio Solimões is impassable, limiting access to the lake from the Rio Purús (Haugaasen & Peres, 2006). The main pressure from outsiders comes during the fruiting season of the açaí palm (*Euterpe precatoria*); the fruits are collected and processed into a drink and ice cream (Haugaasen & Peres, 2006). This sees an increase of outsiders to the region especially from Codajás, an area well known for its production of açaí (Haugaasen & Peres, 2006). While there is no hunting for sport that takes place in the region, commercial hunting from outsiders is increasingly becoming a problem (Haugaasen & Peres, 2006). This little effect from human disturbance, along with the mosaic of juxtaposed terra firme, whitewater and blackwater flooded forest, present an opportunity to investigate the effects of habitat on avifaunal species composition and richness.

## Study Design

This study will use the same sampling method as Laranjeiras, Naka & Cohn-Haft (2019), allowing for maximum detectability of species and removing any issues associated with the use of mist nets. Further to this, to reduce any geographical effects, the study area used here contains terra firme, whitewater flooded forest and blackwater flooded forest in closer proximity to each other than other studies of this type. Additionally, by repeating transects for each season, the sample size is doubled and direct comparisons between seasons can be drawn.

Avifauna was sampled at a total of nine transects, once during high water and once during low water, totalling 18 samples: three in whitewater flooded forest, three in blackwater flooded forest and three in terra firme per season. Each transect was sampled once per season. All ten points at each transect (see below) were fixed for resampling and were resampled in the same order to allow for direct comparisons between seasons.

There is a confluence of white and black waters at the entrance to the lake; flooded forest sites were situated a minimum of 2km from the entrance to ensure there was no mixing of habitats in the ecotonal area. Sites were reached with a small motorised boat and surveyed by land during low water, and by boat during high water, with the exception of terra firme.

At each site, ten 15-minute point counts were carried out along the transect, with unlimited radius distance detection. All points within a single site were of the same habitat type. Point counts were conducted every 200m along the transect, in line with most frequently used published studies, and to avoid overlapping of sampling (Lynch, 1995; Ralph, Droege, & Sauer, 1995; Sutherland, Newton, & Green, 2005; Bispo, et al., 2016). Distances between points were measured linearly, regardless of any relief variations (Bispo, et al., 2016). A minimum distance of 2km between sites is recommended to assure the distance between sites is greater than the maximum distance between sampling points to avoid overlapping samples (Bispo, et al., 2016). However, due to the study using predetermined transects, two sites were 1.8km and two 1.7km apart. This is unlikely to affect results as this distance is not too dissimilar to the recommendation (Bispo, et al., 2016).

All ten points at each site were surveyed on the same non-precipitous day, beginning at dawn (approximately 6:00 a.m.) and ending by late morning (approximately 11:00 a.m.) as this timeframe is when bird activity is greatest. If weather conditions were unsuitable, sampling was conducted on the next available day. Surveys were completed with at least one individual with more than ten years' experience in Amazonian bird records, among other participants. All bird species observed or heard were noted, but individuals were not counted.

Rather than counting individuals, the total number of points with detections acts as a substitute for abundance (Laranjeiras, Naka, & Cohn-Haft, 2019). As the sampling unit was the site as a whole and not the individual points, it is assumed ten points with detections along a single transect would identify the normal variation within a site, helping to firstly avoid the double counting of individuals, especially due to the 15 minute point counts used here and the fact that the majority of detections were auditory, and secondly to minimise local trends, for instance large groups of flocking birds or the presence of a fruiting tree at certain points and variations in microhabitat between points (Laranjeiras, Naka, & Cohn-Haft, 2019).

In a previous study, 12 points were sampled for 10 minutes, with an additional 2 minute wait time prior to recording observations to reduce the effects of disturbance (Bispo, et al., 2016). Within this study, ten points were sampled for 15 minutes with no wait period; the extra time at each point removed the need for an additional wait period and allowed more time for detections. As the sampling unit is the collective ten points in each site, any avifauna identified between points was noted. Detections identified to genus level were excluded from analyses.

## Data Analysis

Species richness and composition were analysed using all detected species. For all analyses, data from all ten point counts at a site were merged to provide a single list of species for each site, using the site as a whole as the sampling unit. All data analysis was conducted using R software version 3.6 (R Core Team, 2019).

The effectiveness of sampling was evaluated for each habitat using sample based accumulation curves using the *vegan* package (*specaccum* function) (Oksanen, et al., 2019). Rarefaction curves were used to extrapolate the number of species and detections for each habitat using the *iNext* package (Hsieh, Ma, & Chao, 2020) and visualised with the *ggplot2* package (Wickham, et al., 2020).

Comparisons of species richness between all three habitats and seasons were made using a generalised linear mixed effects model (GLMM), using Poisson distribution and log-link link function. This test incorporates random effects, while allowing for nonnormal data using family distribution and link functions, through combining both a linear mixed model and generalised linear model (Bolker, et al., 2009). This means statistical assumptions associated with transforming nonnormal data (e.g. homogeneity of variance) are therefore removed (Bolker, et al., 2009). The *glmmADMB* package (Skaug, et al., 2019) was used as there were a high number of zeroes (absences) in the data and this package is able to test zero inflated and truncated distributions.

Likelihood ratio tests, using the *lmer* function in the *lme4* package (Bates, et al., 2020), were then used to establish whether the interaction effect and main effects were significant in affecting species richness. This was done by modelling each effect: the interaction effect of habitat and season (habitat*season), additive effect of habitat and season (habitat+season), habitat, and season. These models were then compared by comparing a more complex model with a simpler one with an ANOVA using the *anova* function in the *lme4* package (Bates, et al., 2020). Finally any significant effects were further analysed using a general linear hypotheses test with single-step adjustments to identify how species richness was affected by means of the *glht* function in *multcomp* package (Hothorn, et al., 2020).

Non-metric multi-dimensional scaling (NMDS), utilizing the Bray-Curtis index for abundance data, was applied to visualise the variation in species composition between sites, using the *metaMDS* function in the *vegan* package (Oksanen, et al., 2019) and visualised using the *ggplot2* package (Wickham, et al., 2020). For each species, abundance data was characterised as the number of points within a site where that species was detected (0-10). The statistical significance of any observed variation in species composition was assessed using a permutational analysis of variance (PERMANOVA) using the *adonis* function in the *vegan* package (Oksanen, et al., 2019). This test uses permutations (999) with pseudo-F ratios to compare within and between group variances in order to assess statistical significance (Anderson, 2001).

To test if any species of bird were significantly associated with either terra firme, whitewater or blackwater flooded forest, or a combination of two habitats, an indicator species analysis (ISA) was conducted. This was done using the *multipatt* function in the *indicspecies* package (De Cáceres, Jansen, & Dell, 2020). Only species with a minimum of five detections in total were included in this analysis. For each species, an indicator value of between 0 and 1 is produced, with 0 signifying no association to that habitat and 1 signifying not only complete association with that habitat, but also all sites throughout that habitat (Dufrêne & Legendre, 1997). The indicator value was then assessed through 9999 permutations to identify any statistical significance.

# Chapter 3 - Results

## Descriptive Results

There were a total of 2656 detections of 284 species recorded, of which there were 1431 detections of 223 species during low water and 1225 detections of 236 species during high water. Survey effort did not approach asymptote for all sites as indicated by species accumulation curves (Figure 2). A total of 99 species (35%) were detected only once or twice, while 149 species (52%) were detected five or more times. Extrapolated results with rarefaction show terra firme to closely follow the curve of whitewater for species richness as the number of detections increases, albeit with a much wider confidence interval, with blackwater retaining higher levels of species richness (Figure 3).

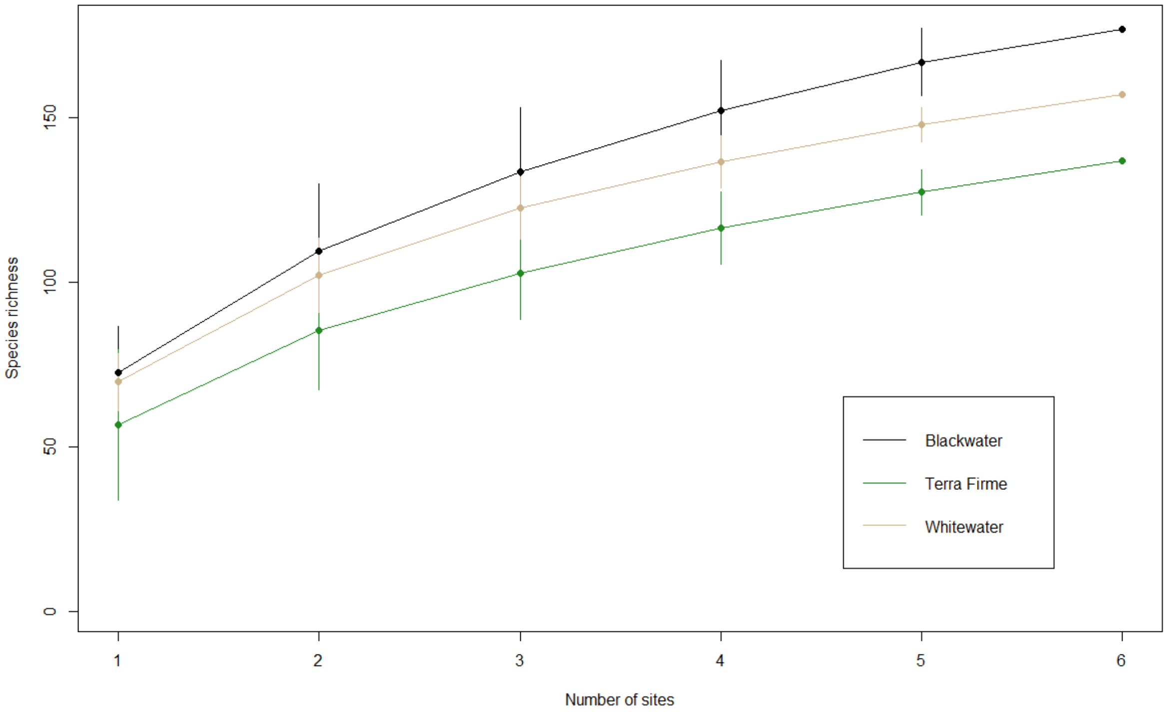

Figure 2. Number of species accumulated with increased sampling for all detected species of bird in blackwater, whitewater and terra firme sites. Error bars indicate standard deviation.

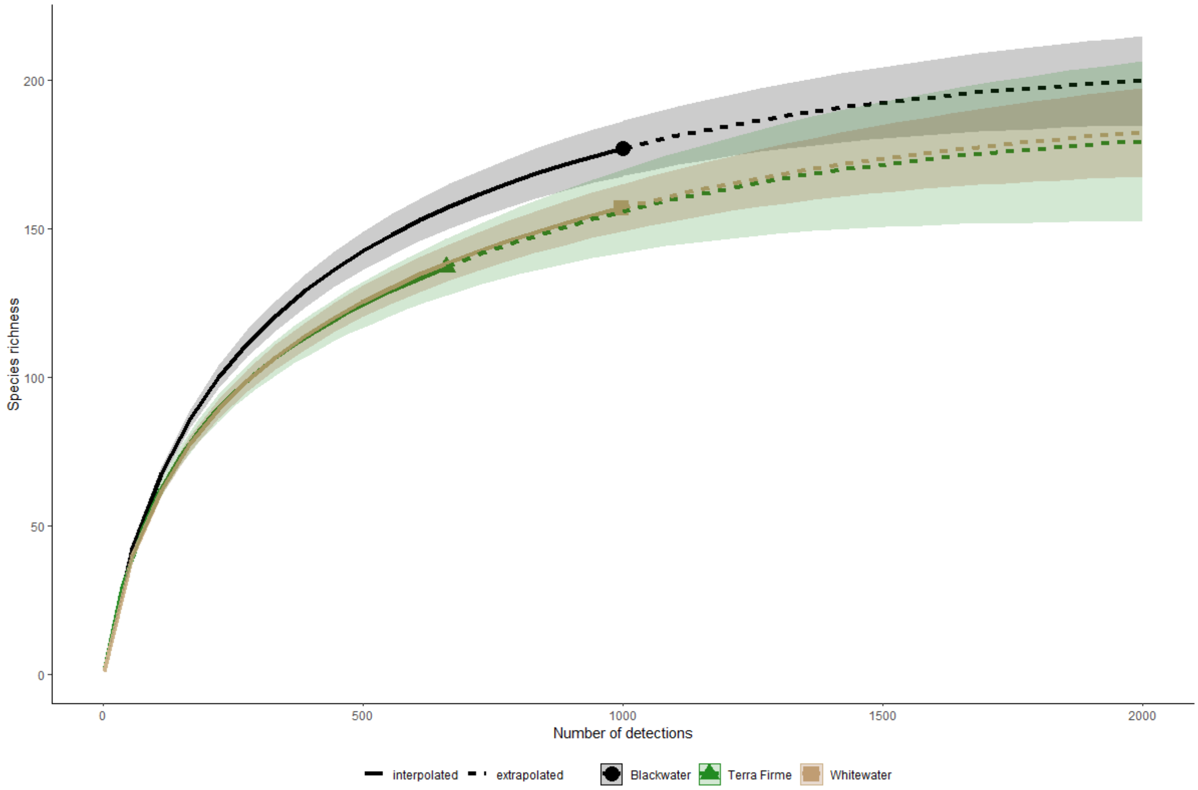

Figure 3. Detection based extrapolated rarefaction curves of species richness for each habitat with a 95% confidence interval

## Species Richness

Overall species richness was significantly different between habitats; it did not differ by season (Table 1). The only significant effect found by likelihood ratio test was habitat, with no effect by season or the interaction of the two on species richness (Table 2). Terra firme had significantly lower species richness than both blackwater and whitewater sites, with no difference between flooded forest sites (Table 3).

Table 1. Results of generalised linear mixed model for comparisons of species richness between habitats and seasons

| | Estimate | S.E | z | P |
|---|---|---|---|---|
| (Intercept) | -1.354 | 0.067 | -20.08 | <0.001 |
| Terra Firme | -0.357 | 0.105 | -3.39 | <0.001 |
| Whitewater | -0.023 | 0.096 | -0.24 | 0.810 |
| Low water | -0.009 | 0.096 | -0.1 | 0.924 |
| Terra Firme: Low water | 0.154 | 0.146 | 1.06 | 0.291 |
| Whitewater: Low water | -0.043 | 0.137 | -0.32 | 0.751 |

Table 2. Results of model comparisons based on likelihood ratio tests

| Comparison | d.f | AIC | BIC | log lik | deviance | Chisq | d.f | P |
|---|---|---|---|---|---|---|---|---|
| habitat+season v habitat*season | | | | | | | | |
| habitat+season | 6 | 5688.2 | 5727.5 | -2838.1 | 5676.2 | | | |
| habitat*season | 8 | 5690.5 | 5742.8 | -2837.2 | 5674.5 | 1.739 | 2 | 0.419 |
| habitat v habitat+season | | | | | | | | |
| habitat | 4 | 5695.7 | 5721.9 | -2843.8 | 5687.7 | | | |
| habitat+season | 6 | 5688.2 | 5727.5 | -2838.1 | 5676.2 | 11.465 | 2 | 0.003 |
| season v habitat+season | | | | | | | | |
| season | 5 | 5686.3 | 5719 | -2838.2 | 5676.3 | | | |
| habitat+season | 6 | 5688.2 | 5727.5 | -2838.1 | 5676.2 | 0.101 | 1 | 0.751 |

Table 3. Results of general linear hypothesis test when comparing species richness between each habitat

| Habitat Comparisons | Estimate | S.E | t | P |
|---|---|---|---|---|
| Terra Firme - Blackwater | -0.062 | 0.014 | -4.305 | <0.001 |
| Whitewater - Blackwater | -0.011 | 0.014 | -0.772 | 0.720 |
| Whitewater - Terra Firme | 0.051 | 0.014 | 3.534 | 0.001 |

## Species Composition

There was a clear divergence between avifaunal communities in each of the habitats as shown in the NMDS ordination (Figure 4). This divergence was shown to be significant by PERMANOVA (pseudo-F = 6.62, $r^2 = 0.47$, $p = < 0.001$). It is evident that whitewater and terra firme sites noticeably differ in their avian community composition, clearly separated at opposing sides of the ordination, with no overlap on the NMDS1 axis. While the blackwater sites show distinction from other sites, clustering between whitewater and terra firme, there is some overlap on the NMDS1 axis with whitewater. Seasonality was found not to be a significant determinant of avian community composition by PERMANOVA (pseudo-F = 1.64, $r2 = 0.09$, $p = < 0.102$).

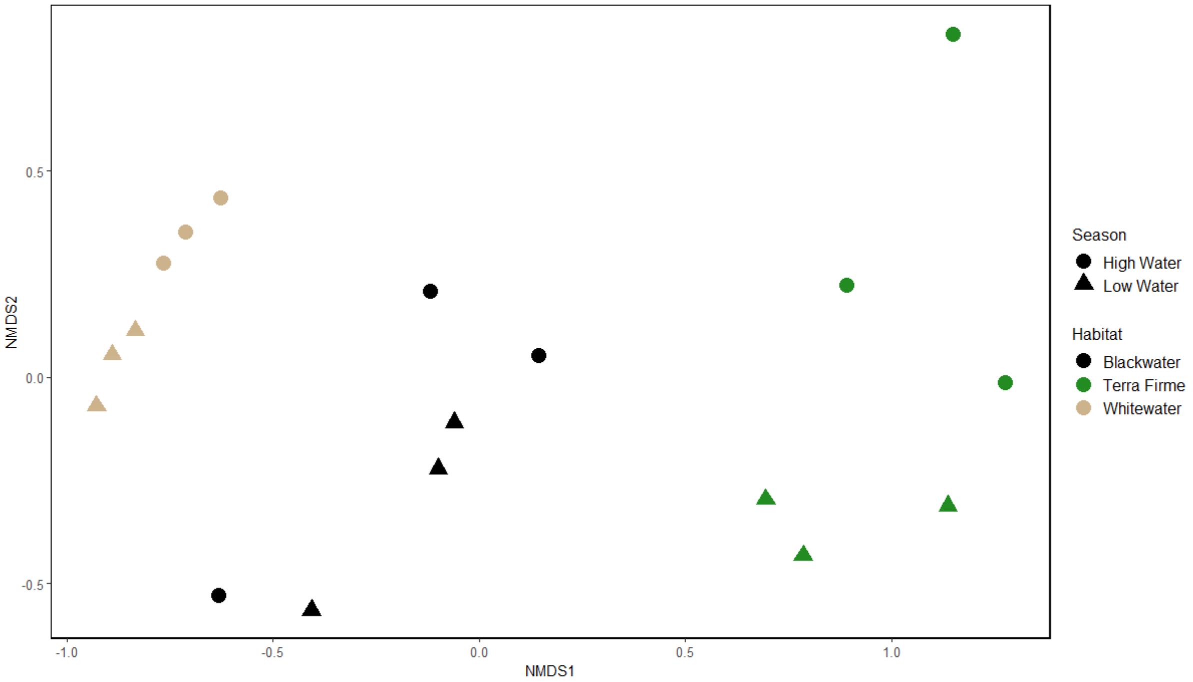

Figure 4. Non-metric multi-dimensional scaling (NMDS) ordination of species composition variation among habitat types and seasons, based on abundance data for all species

## Indicator Species Analysis

Overall, 47 species were identified as being significantly associated with one of the three habitats by the ISA (Table 4). A total of 9 species were associated with blackwater flooded forest, 22 with whitewater flooded forest and 16 with terra firme. A further 12 species were significantly associated with two of the three habitats. Blackwater flooded forest and terra firme had 5 associated species and there were 7 species associated with blackwater and whitewater flooded forest. Conversely there were a total of 90 species with no significant association to any habitat; of these, 32 species were detected at least once in all three habitats.

Table 4. Bird indicator species of blackwater, terra firme or whitewater habitats, including the overall number of detections (and overall number of sites with detections) in each habitat in addition to the indicator value with level of significance, with species divided by habitat and arranged by indicator value (descending)

| Species | Indicator Value | Records (Sites) | | |
|---|---|---|---|---|
| | | Blackwater | Terra Firme | Whitewater |
| Indicators of blackwater flooded forest | | | | |
| *Hylophilus thoracicus* | 0.78** | 11 (5) | | |
| *Myiopagis gaimardii* | 0.74** | 17 (6) | 5 (2) | 3 (3) |
| *Trogon collaris* | 0.71* | 9 (5) | 1(1) | 1 (1) |
| *Patagioenas cayennensis* | 0.68** | 30 (6) | | 8 (1) |
| *Thamnophilus amazonicus* | 0.66* | 12 (5) | | 4 (3) |
| *Herpsilochmus praedictus* | 0.64* | 6 (4) | | 1 (1) |
| *Trogon curucui* | 0.63* | 19 (5) | 2 (2) | 6 (4) |
| *Rupornis magnirostris* | 0.62* | 8 (4) | 1 (1) | 2 (2) |
| *Hylophilus semicinereus* | 0.62* | 12 (4) | | |
| Indicators of terra firme | | | | |
| *Campephilus rubricollis* | 0.93*** | | 7 (6) | |
| *Lepidothrix coronata* | 0.83** | | 19 (5) | |
| *Hemitriccus griseipectus* | 0.82** | | 6 (5) | |
| *Monasa morphoeus* | 0.81** | | 11 (5) | |
| *Xiphorhynchus elegans* | 0.78** | 3 (1) | 25 (5) | |
| *Tinamus guttatus* | 0.75* | | 18 (4) | |
| *Trogon rufus* | 0.74** | | 16 (5) | |
| *Sciaphylax hemimelaena* | 0.74* | | 10 (4) | |
| *Myrmoborus myotherinus* | 0.70* | | 5 (4) | |
| *Attila citriniventris* | 0.70* | | 8 (4) | |
| *Deconychura longicauda* | 0.70* | | 8 (4) | |
| *Crypturellus variegatus* | 0.67* | | 7 (4) | |
| *Vireolanius leucotis* | 0.67* | | 7 (4) | |
| *Selenidera reinwardtii* | 0.66* | 1 (1) | 8 (4) | |

| | | | | |
|---|---|---|---|---|
| *Thamnophilus murinus* | 0.60** | 1 (1) | 13 (5) | |
| *Ceratopipra rubrocapilla* | 0.59* | 3 (1) | 11 (5) | |
| Indicators of whitewater flooded forest | | | | |
| *Capito aurovirens* | 0.86*** | | 1 (1) | 29 (6) |
| *Galbula tombacea* | 0.84** | | | 27 (5) |
| *Patagioenas subvinacea* | 0.82*** | 5 (2) | 1 (1) | 25 (6) |
| *Campylorhynchus turdinus* | 0.81** | | | 21 (4) |
| *Bucco tamatia* | 0.81** | 1 (1) | | 15 (5) |
| *Trogon melanurus* | 0.80** | 8 (5) | 1 (1) | 31 (6) |
| *Thamnophilus schistaceus* | 0.78** | | | 11 (5) |
| *Brotogeris sanctithomae* | 0.77** | 18 (3) | 6 (2) | 50 (6) |
| *Myrmotherula assimilis* | 0.74** | 2 (2) | | 24 (5) |
| *Dendroplex kienerii* | 0.73** | 8 (5) | | 16 (6) |
| *Amazona festiva* | 0.73* | | | 7 (4) |
| *Tolmomyias sulphurescens* | 0.73** | 9 (4) | | 19 (6) |
| *Xiphorhynchus obsoletus* | 0.71*** | 8 (5) | 1 (1) | 17 (6) |
| *Lathrotriccus euleri* | 0.70* | | | 9 (4) |
| *Schiffornis major* | 0.70* | | | 9 (4) |
| *Campephilus melanoleucos* | 0.68* | 3 (2) | 1 (1) | 12 (6) |
| *Anhima cornuta* | 0.67* | | | 10 (4) |
| *Myiopagis flavivertex* | 0.67* | | | 7 (4) |
| *Sakesphorus luctuosus* | 0.67* | | | 14 (4) |
| *Attila cinnamomeus* | 0.66* | 6 (2) | | 20 (6) |
| *Pachyramphus polychopterus* | 0.65** | | | 10 (5) |
| *Pheugopedius genibarbis* | 0.57* | 14 (3) | 2 (2) | 28 (6) |
| Indicators of both blackwater flooded forest and terra firme | | | | |
| *Trogon viridis* | 0.75** | 21 (6) | 20 (6) | 1 (1) |
| *Celeus grammicus* | 0.66* | 9 (5) | 18 (6) | |
| *Ramphastos tucanus* | 0.65* | 14 (5) | 19 (6) | 3 (3) |
| *Capito auratus* | 0.64* | 15 (5) | 25 (6) | |
| *Lipaugus vociferans* | 0.62* | 12 (5) | 12 (5) | |

| | | | | |
|---|---|---|---|---|
| Indicators of both blackwater and whitewater flooded forest | | | | |
| *Monasa nigrifrons* | 0.82*** | 27 (6) | | 24 (6) |
| *Hypocnemoides melanopogon* | 0.79*** | 40 (6) | | 27 (6) |
| *Cercomacra cinerascens* | 0.71** | 26 (6) | | 16 (6) |
| *Hemitriccus minor pallens* | 0.67* | 28 (6) | | 15 (5) |
| *Dendroplex picus* | 0.66* | 17 (6) | | 11 (5) |
| *Tyrannulus elatus* | 0.63* | 20 (6) | 9 (6) | 22 (6) |
| *Nasica longirostris* | 0.60* | 10 (4) | 3 (2) | 17 (6) |

Notes: ***p<0.001; **p<0.01; *p<0.05

# Chapter 4 - Discussion

## Species Richness

Previous studies have found terra firme to have the highest species richness for birds followed by whitewater flooded forest and blackwater flooded forest having the lowest (Borges & Carvalhaes, 2000; Borges, 2013; Laranjeiras, Naka, & Cohn-Haft, 2019). However the opposite was found in this study. Species richness in terra firme was significantly lower than both flooded forests. Due to the high species richness usually found in terra firme, many species are rare and many more highly inconspicuous, decreasing their detectability (Cohn-Haft, Whittaker, & Stouffer, 1997). The considerably lower number of total detections in terra firme compared with both flooded forests given the same sampling effort (Figure 3), also suggests that birds are rarer and so more sampling is required in terra firme. This supports arguments by Cohn-Haft et al. (1997) that productivity is related to abundance and not necessarily to species richness in Amazonian birds. The species accumulation curves (Figure 2) also suggest that further sampling may be required in order to fully identify the species that inhabit each habitat. Further sampling, especially within terra firme, would help to identify those species that are rare and highly inconspicuous (Cohn-Haft, Whittaker, & Stouffer, 1997).

Blackwater flooded forest had the highest species richness compared with terra firme and whitewater habitats, which was unexpected as other studies have found blackwater flooded forests to have low species richness in comparison to other habitats (Borges & Carvalhaes, 2000; Beja, et al., 2010). Blackwater flooded forest throughout the study area is often found in small strips close to terra firme sites. This could mean that during surveys of blackwater flooded forest sites, species usually associated with terra firme were recorded due to their close proximity to terra firme. This is unlikely to be the case in whitewater flooded forest sites as they were situated much further from other habitats.

Interestingly, no species in the ISA (Table 4) were identified as being significantly associated with both terra firme and whitewater flooded forest, whereas five species were associated with both terra firme and blackwater flooded forest. The reason for this could be due to their proximity; many terra firme species will often use blackwater flooded forests opportunistically, moving in when there are resources available, such as a fruiting tree, before returning to their preferred habitat. For instance, species such as white-throated toucan (*Ramphastos tucanus*) were an indicator species for both terra firme and blackwater flooded forest in the ISA; previous research suggests they show a preference for terra firme but are known to occur in flooded forest (Haugaasen & Peres, 2008), likely living on the edge between the two habitats and exploiting available resources. It is also possible that terra firme specialists with loud vocalisations were falsely detected at blackwater flooded forest sites. For instance, the screaming piha (*Lipaugus vociferans*), a terra firme specialist with a loud call, was found to be an indicator species for both blackwater flooded forest and terra firme in the ISA. Furthermore, both possibilities of movement of species between terra firme and blackwater flooded forest as well as incorrect habitat attributions are facilitated by the fact all blackwater sites are found in a narrow extent adjacent to terra firme, whereas large expanses of whitewater flooded forest without direct contact to terra firme can be found, and were sampled, in the study area. The intermediate position of blackwater flooded forest sites on the NMDS (Figure 4) is further evidence of this as it can be interpreted as containing a mix of both flooded forest and terra firme species, as well as some species unique to blackwater flooded forest.

## Species Composition

The clear differences in species composition between habitats are similar to those reported both elsewhere in the Amazon (Remsen & Parker III, 1983; Borges & Carvalhaes, 2000; Beja, et al., 2010) and within the same study region (Haugaasen & Peres, 2008). This is partly due to species abundant in one habitat being relatively rare or missing from other habitats. This is further evidenced by the indicator species. Almost one third of species (47 of 149 with 5 or more detections) are significantly associated with one habitat. The ISA also identified closely related pairs of species that replace one another between habitats (Table 5).

Table 5 - List of closely related species and their habitat preference

| Blackwater flooded forest | Terra Firme | Whitewater flooded forest | Flooded forest |
|---|---|---|---|
| *Patagioenas cayennensis* | | *Patagioenas subvinacea* | |
| *Myiopagis gaimardii* | | *Myiopagis flavivertex* | |
| *Trogon collaris* & *Trogon curucui* | *Trogon rufus* | *Trogon melanurus* | |
| *Thamnophilus amazonicus* | *Thamnophilus murinus* | *Thamnophilus schistaceus* | |
| | *Campephilus rubricollis* | *Campephilus melanoleucos* | |
| | *Hemitriccus griseipectus* | | *Hemitriccus minor pallens* |
| | *Monasa morphoeus* | | *Monasa nigrifrons* |
| | *Xiphorhynchus elegans* | *Xiphorhynchus obsoletus* | |
| | *Attila citriniventris* | *Attila cinnamomeus* | |

As in the Remsen and Parker III (1983) study, black-fronted nunbird (*Monasa nigrifrons*) in flooded forest was replaced by white-fronted nunbird (*Monasa morphoeus*) in terra firme. Further to this, species varied between flooded forests as well as terra firme; Trogonidae varied between habitats with black-throated trogon (*Trogon rufus*) in terra firme, black-tailed trogon (*Trogon melanurus*) in whitewater flooded forest and collared trogon (*Trogon collaris*) and blue-crowned trogon (*Trogon curucui*) in blackwater flooded forest.

The overlap of points in whitewater and blackwater sites on the NMDS1 axis (Figure 4) suggest that these habitats are closer in species composition, sharing some species, than they are with terra firme. This is in line with previous studies that have found less divergence between the two flooded forests than between either of the flooded forests and terra firme (Haugaasen & Peres, 2008; Beja, et al., 2010). However, the results of this study show the species community of each of the two flooded forests as being far more distinct than previous studies; as blackwater sites were in close proximity to terra firme, this may have falsely increased the number of terra firme species recorded in blackwater sites, meaning the species composition of the two flooded forests types may be more closely related.

The results concerning species composition and habitat are expected due to the often observed relationship between habitat structure, floristic diversity and birds (Cody, 1985; Rosenzweig, 1995), but this study shows clear distinctions between each habitat. The distinction between species composition of flooded forest and terra firme was expected as flooding, independent of water type, should influence the structure of a forest, resulting in flooded forests containing a simpler understory structure. Shared species between black and whitewater forests, such as the seven species identified in the ISA (Table 4), could be classed as flooded forest specialists. This suggests the flooding process creates structurally similar habitats for many species of bird, despite differences in nutrient input and floristics.

Whilst there were similarities in the species compositions of the two flooded forests, the identification of different species in each was expected given the high dissimilarity in terms of floristic composition between blackwater and whitewater flooded forests (Haugaasen & Peres, 2006). This is caused by the differences in flood water nutrients, sediment load and pH of black and whitewater, affecting floristic diversity (Haugaasen & Peres, 2006; Junk, et al., 2011; Junk, Piedade, Schöngart, & Wittmann, 2012; Junk, Wittmann, Schöngart, & Piedade, 2015).

## Seasonal Foraging Sites

Overall, seasonal changes in water level bore no effect on species richness or composition. However, for some species of aquatic and ground-feeding birds, seasonal flooding was linked with changes in species composition and richness. This may be evidence of resources within flooded forest that become temporarily available being tracked by birds. For instance, sunbittern (*Eurypyga helias*) were only detected during high water, and predominantly in flooded forest, and twice as many kingfisher (*Cerylinae*) were detected during high water (18) than low water (9). During high water, fish migrate into flooded forest for food and shelter (Saint-Paul, et al., 2000; Castello, 2008), thus increasing food availability for these aquatic-feeding species. During low water, *Crypturellus* were detected 19 times in forests subject to flooding during high water, whereas throughout high water, all detections were within terra firme. As water levels recede, invertebrate numbers increase in flooded forests as they recolonise the forest floor, and decrease in terra firme (Adis & Junk, 2002), thus attracting ground-feeding species from terra firme to flooded forest.

The influx of ground dwelling species from terra firme was mainly observed within blackwater flooded forest, with less evidence of movement into whitewater flooded forest.

For example, of the 19 detections of *Crypturellus* in flooded forest during low water, 13 were within blackwater flooded forest. It is thought that this lack of movement from terra firme into whitewater flooded forest is due to the habitats division by river channels (Beja, et al., 2010), but birds with poor flight capability, such as the undulated tinamou (*Crypturellus undulates*), have been observed crossing open water of up to 500m (Remsen & Parker III, 1983), so the 50m wide paranã channel separating whitewater flooded forest sites from terra firme is unlikely to be a sufficient barrier to the movements of birds. It is more likely that the spatial configuration, with blackwater flooded forest sites adjacent to large areas of terra firme and whitewater forest sites a much greater distance from terra firme, is a factor influencing the species composition of birds.

## Conservation Implications

Results from this study show that each habitat contains a unique community of birds, each playing a significant role in maintaining bird diversity in the Amazon. While terra firme forests are widely considered to contain the highest species richness (Cohn-Haft, Whittaker, & Stouffer, 1997), flooded forests contribute to overall species diversity in the Amazon by providing habitats for several unique species that are absent or rare elsewhere. These flooded forests contain some species of bird with the most restricted ranges throughout the Amazon (Vale, Cohn-Haft, Bergen, & Pimm, 2008), making them highly susceptible to any loss or change of habitat. This study also adds to the evidence that flooded forests provide seasonal foraging sites for species from surrounding terra firme and riverine habitats, further safeguarding the long term viability of highly mobile species that depend on different habitats at different time of the year (Haugaasen & Peres, 2008; Beja, et al., 2010). There are an increasing range of threats to both terra firme and flooded forests such as deforestation, agricultural conversion and the building of hydroelectric dams. However, flooded forest is underrepresented in Amazonian reserves, approximately only 3% of flooded forest is currently protected, with terra firme receiving the greatest amount of protection (Fearnside & Ferraz, 1995).

Brazil has one of the highest rates of deforestation in the Amazon (Armenteras, Espelta, Rodríguez, & Retana, 2017) due to industrial mining, logging and improved infrastructure which not only directly affects forests through removal, but also indirectly by increasing access to forests for agriculture and ranchers (Laurance, et al., 2001; Vilela, et al., 2020). Deforestation models predict planned infrastructure projects, should they go ahead, will not only reduce the size of the forest, but also greatly increase fragmentation of remaining forests (Laurance, et al., 2001; Vilela, et al., 2020). Further models have identified that whitewater flooded forest bird species are at highest risk due to deforestation (Vale, Cohn-Haft, Bergen, & Pimm, 2008). This is of particular concern especially considering the majority of species identified as indicators of whitewater in this study already show decreasing population trends, mainly due to loss of habitat. Most logging has taken place in whitewater flooded forests due to the large quantity of timber and ease of access from rivers reducing transport costs (Barros & Uhl, 1995). Owing to the fertile nature of whitewater flooded forests, agricultural conversion for soybeans and clearcutting for cattle ranching have become an increasing problem, especially as demand for export of both has increased (Boucher, 2011a; Boucher, 2011b). Brazilian federal legislation states that landowners must retain some of the forest on their land if clearcutting; however, this often leaves small patches of unconnected forest that only retain a small proportion of its original species richness (Lees & Peres, 2008).

The most significant threat to flooded forests are hydroelectric dams which have the potential to adversely affect huge areas throughout the Amazon. There are already over 100 dams either functioning or currently under construction in the Amazon basin with planning in place to potentially more than double this (Latrubesse, et al., 2017). These dams, if constructed, will increase the stress on the Amazon river and tributaries as well as surrounding habitats by reducing the flow and connectivity of rivers (Grill, et al., 2015). These changes to the hydrological regime have the potential to change the floristic composition of flooded forests, as flora in these habitats are adapted to a particular pattern of flooding (Ferreira, 1997). Areas upstream of dams will become permanently inundated, increasing the mortality of trees and reducing available habitat and resources for all terrestrial bird species (Borges & Carvalhaes, 2000). Further to this, understory species will move upland, increasing competition and heightening the risk of local extinctions (Borges & Carvalhaes, 2000). Finally, a reduction in productivity of aquatic systems will negatively impact aquatic birds (Borges & Carvalhaes, 2000).

In conclusion, it is clear the habitat mosaic of flooded forest and terra firme within our study area increased the diversity of birds in the region. Thus, there is a need for large heterogenous habitats consisting of a mosaic of terra firme, whitewater and blackwater flooded forest to be incorporated into future conservation planning in order to protect the future of Amazonian birds (Peres, 2005). In a fragmented landscape, it is also important to consider connecting patches of terra firme and flooded forest in order to provide habitats for specialist species

(Lees & Peres, 2008), generalists (Peres, 2005), and species that track resources seasonally (Haugaasen & Peres, 2008; Beja, et al., 2010).

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